THE SENSE-ORGANS ON THE LEGS OF OUR WHITE ANTS, TERMES FLAVIPES, KOLL.

BY DR. ALFRED C. STOKES, TRENTON, N. J.

In an eyeless creature that habitually shuns some influence in the light, and lives in subterranean passages, or in tunnels or dark fissures within decaying wood, we should hope and rather expect, if we considered the matter solely from the human standpoint, to find either an extra number of sense-organs or a supply of an unusual variety, as a compensation for the absence of sight and for the limitations of a restricted environment. Such human expectations would be realized in the case of the white ants, *Termes flavipes*, so common within the rotting stumps and the fallen branches of our damp woods, for these Platyptera possess what may be considered to be an ample exchange for sight, for they have on all of the six legs a wonderful number and variety of sense-organs, which should certainly meet the needs of a peculiar life, as they doubtless do.

It is generally agreed among naturalists that certain insects, perhaps the greater number, possess some senses different from any owned by man and of which we therefore can have no idea. Sir John Lubbock says, "It is, I think, generally assumed, not only that the world really exists as we see it, but that it appears to other animals pretty much as it does to us. A little consideration, however, is sufficient to show that this is very far from being certain, or even probable."

On each of the legs of *Termes flavipes* there are seven organs which are plainly sense-organs, with three forms of appendages which may be sensory, but are probably ornamental only. The blind, subterranean *Termes*, then, with six legs and with seven sense-organs on each, is right well prepared for whatever may happen, even for the forceps of the predatory microscopist. The forceps conquers in the end, but the insects seem to feel its presence before it touches them, retreating and sometimes backing away from it as from some obnoxious object. Yet upon this apparent fact I should put no great reliance, as the observation was made with a single nest and late in the season, although the lateness of the season would probably have no effect, except to render impossible, as it did, a repetition of the experiment. It may, therefore, have been an event "viewed unequally."

The appendages referred to as being doubtfully sensory are mere elevations of the chitinous walls, ornamental in their arrangement, minute in size, and if possessing any special nervous connections, these have escaped my notice. The appendages, or ornaments, vary much in appearance on the coxa, the trochanter and the tarsus, the femoral and the tibial ones being similar to those on the coxa. On the latter the elevations are simply aculeate, the aculei being exceedingly minute; on the trochanter and on the femur they take the form of minute prickles, which, at first glance, appear to mark out the impressions of the chitinogenous cells, as in Fig. 1, from the femur; on the tibia the elevations become still more aculeate (Fig. 2); they are more widely separated, and the delicately elevated ridge which bears them gives the markings much the aspect of irregular, thick-edged scales, especially at the distal extremity, as in Fig. 3; on the tarsus the change from these clusters of aculei is abrupt, more or less semicircular scales, with thickened and elevated margins taking their place, as in Fig. 4, the edges of these being sometimes minutely denticulate. Viallanes, speaking of the situation of the sensory hairs of insects in reference to the chitinogenous cells, says that there are "two kinds of hairs, distinguished by their size and structure. The smaller spring from the boundary between contiguous polygonal areas, and have no sensory character. The larger ones occupy unusually large areas, surmount chitinogenous cells of corresponding size, and receive a special nervous supply." It is more than probable, therefore, that these minute appendages have in no place a significance different from that possessed by the minute elevations so common on the exo-skeleton of so many insects. But to notice the different form and arrangement on the different portions of the leg is at least interesting and suggestive.

The chitinous bristles, or "hairs" (Fig. 6), have here the usual form, and the structure described by Viallanes, being slightly constricted at base and inserted in a hemispherical depression as a socket-joint, and furnished with a nerve-fibre, of which Viallanes says: "The nerve expands at the base of the hair into a spindle-shaped, nucleated mass (bipolar ganglion-cell), from which issues a filament which traverses the axis of the hair, piercing the chitinogenous cell, whose protoplasm surrounds it with a sheath which is continued to the tip of the hair. Such sensory hairs are abundant in parts which are endowed with special sensibility."* On the legs of *Termes flavipes* these are, as elsewhere, sense-organs of great delicacy, with a sense of touch probably as sensitive as that of man himself.

In the same list with these sensory hairs may be mentioned organs of a similar character and of apparently great importance to the insect, which are found at the distal extremity of each tibia, each leg of the second and of the third pair bearing two, while those of the first pair have three. They are stout thorns, or spurs, projecting, in the first or anterior pair, two from the lower lateral margin of the tibia, with one from the upper lateral border, as shown in Fig. 9, where the other sensory hairs have been omitted.

They are conical organs, measuring about 1-450 inch in length, and are, during life, well supplied with nerve-substance. But that which gives them their unique character is the presence of a more or less circular aperture near the basal or tibial portion of the thick wall, as shown in Fig. 9, and more in detail by Fig. 15, each insect thus possessing no less than fourteen of these peculiar perforations. The circular aperture is externally surrounded by a thick-walled, elevated, marginal ring, and across it, apparently at the level of the general surface of the tibial wall, extends a delicate membrane, supplied with a rather conspicuous, centrally disposed nerve-fibre, as shown in Fig. 15, where a nerve is also delineated as passing from the tissues within the hollow of the spur to the mass of nerve-tissue which is here retracted from the walls, probably by the processes of preparation. Within the mass thus withdrawn ganglion-cells are plainly visible.

What may be the function of these fourteen organs, which are doubtless sense-organs of importance, must be left to the reader to explain. I do not know that they have been previously observed; yet it is more than possible that I may have overlooked some parts of the scattered literature of the general subject. If any plausible conjectures have been published in regard to the function of these or of similar organs, I should be pleased to know what they are, although all such statements must necessarily be conjectural. It is easy to state that certain depressions on the antenna of a bee are auditory or olfactory, but it is quite another matter to do more than to make the assertion. When it comes to the making of experiments to learn the actual function of these minute structures, the obstacles met with are practically insurmountable. But if these tibial spurs of the white ants, with their prominent basal apertures, have been previously studied, and if any probable guessing has been done as to

*Cf. "The Cockroach," by Miall and Denny, p. 30.

their character, I should like to know at what result the philosophical observers have arrived.

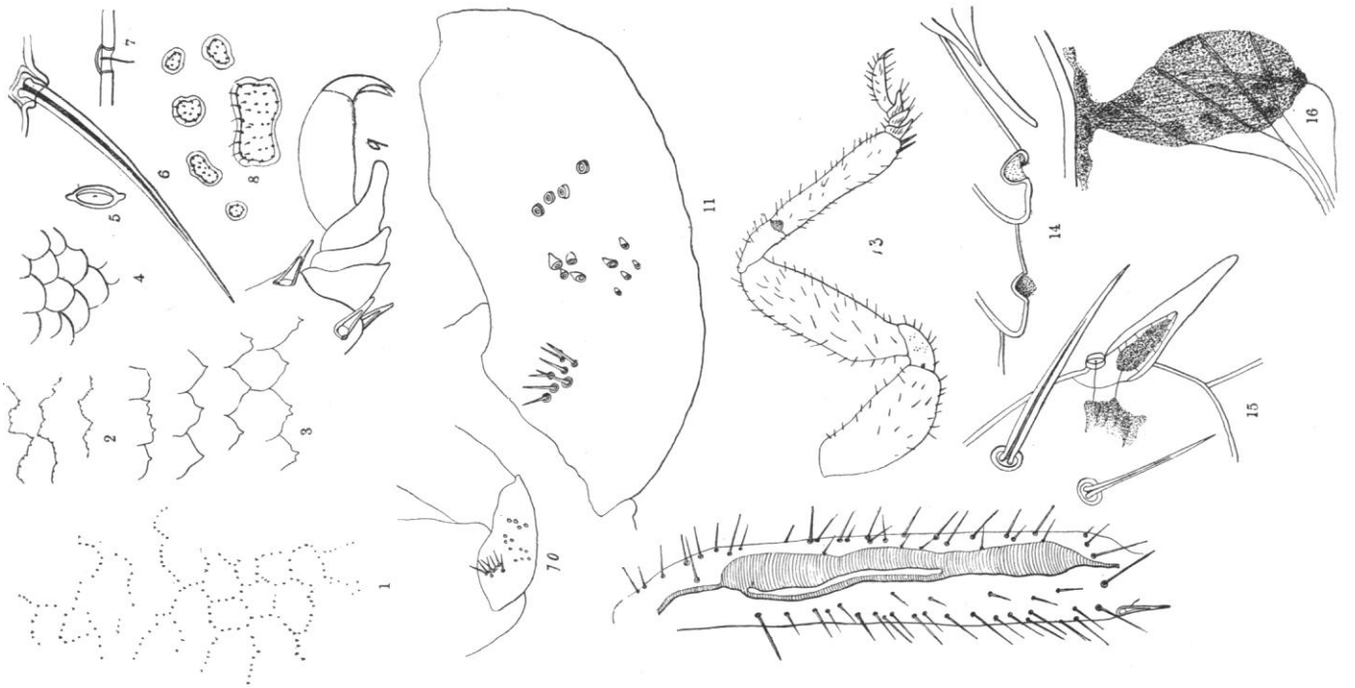
At first glance the organs might be supposed to be auditory, on account of the membrane, which closes them, and the only reason for rejecting such a supposition is that I have not seen any trace of the staff-like rods or the pyriform bodies which Graber found so well developed in what could not be imagined to be anything but organs of hearing in the tibia of the locust, *Locusta viridissima*, and of some other members of the same, or of an allied, order. The auditory organs of our white ants seem to be in an entirely different position and of an entirely different structure.

On the outer wall of the upper, or coxal, end of the trochanter is a group of just seven conical, setose and colorless hairs, surrounded by a circumvallate base, and on the upper outer wall of the coxa is another group of similar hairs, always ten in nnmber, and, presumably, having the same function. These groups are entirely absent from the inner walls. To show its locality, the cluster is exhibited on the trochanter by Fig. 10, and greatly enlarged in Fig. 11.

sides, and are sparingly scattered over the surface of the tibiæ. In Figs. 10 and 11 their general form and usual position and arrangement are shown, although in these particulars they are not constant. The number is also uncertain within known limits, varying on the outer side of each trochanter from thirteen to fifteen, thirteen being the common number; on the femur two and on the upper lateral wall of the tibia, from two to five, with sometimes an unusually large subcentral one, similar to a large one on the inner wall of each tibia; the inner walls of each trochanter also bear from four to five; on the upper part of the femur are from three to four; the central tibial surface has one, and one is near the lateral border of the distal extremity of the tibia.

In structure they closely resemble the circular apertures at the bases of the tibial spurs, each consisting of an elevated ring, having, at the level of the general surface, a delicate membrane furnished with a nerve-fibre, which elevates the centre into a minute but conspicuous papilla. These points are shown in Figs. 5 and 7, the latter being an optical section of a pit.

On the trochanters these organs are arranged somewhat



EXPLANATION OF THE FIGURES.

Fig. 1, surface markings from the femur; Figs. 2 and 3, from the tibia; Fig. 4, from the tarsus; Fig. 5, sensory pit from the tibia; Fig. 6, sensory hair from the general leg-surface; Fig. 7, optical section of a sensory pit; Fig. 8, pilose depressions on the lower end of the tibiæ; Figs. 10 and 11, sensory hairs, pits and hooded pits on the trochanters; Fig. 12, tibial trachea, with recurrent branch; Fig. 13, position of supposed tibial auditory organ; Fig. 14, pits on the lower surface of the first and second segments of the tarsus, one filled with crystalline excretion; Fig. 15, sensory pit at the base of a tibial spur; Fig. 16, tibial auditory organ, partly diagrammatic. All the figures are much enlarged.

These hairs differ widely in size, form, and general aspect from the sensory bristles of the general leg-surface. Underlying them is a specialized group of nerve-cells, which supplies each with a fine nerve-filament.

It is a fact worthy of note that these and other sense-organs are on the outer wall of the various parts of the legs which bear them, and that they either have no representatives on the surface toward the insect's body, or are there smaller and in much less abundance. Even the large sensory hairs of the general leg-surface are much fewer on the inner aspect of the legs.

In addition to these setose appendages, each trochanter bears other sensory organs, which take the form of elevated, circular, or oval rings, surrounding apertures of the same form in the thickness of the walls, some being capped by a conical, often oblique, hood-like membrane. They, as usual, are found chiefly on the external walls of the trochanters, but exist in fewer numbers on the inner in three groups, according to size, and the three or four largest, resembling flat-topped papillæ pierced with a central depression above the membrane, frequently become confluent, those of the other two groups being capped by a conical, often oblique, hood-like membrane, as shown in Fig. 11. These hooded apertures bear some resemblance to the "canoe-cells" of certain authors, and which are said by Huxley to be only ordinarv pits overarched by a fine hair. In the present case, however, there is no arching hair, but a distinct hood-like elevation, which is especially conspicuous on the trochanters of the soldier.

It is reasonable to suppose that the capped depressions have a function differing from that of the flat-topped papillæ on the same surface. Those without the hooded covering seem analogous to the sensory pits discovered on the antennæ of certain plant-lice by Dr. John B. Smith, of Rutger's College (*Science*, Jan. 20, 1893). A rather hasty

examination of the antennæ of the white ants does not reveal pits of any kind on the surface, although I am not prepared to say that they are not there. Dr. Smith also found on the posterior tibiæ of the plant-lice a series of the pits, exactly similar in structure, he says, to those of the antennæ in the male. Their function in *Termes flavipes* is as problematical, as Dr. Smith remarks in reference to the sensory pits of the plant-lice. They are present in both the workers and in the soldiers of the white ants, varying in the latter as they vary in the workers.

Perhaps the most interesting of these sense-organs, by reason of their position and of their probable character, are certain depressed spaces, several of which are on the tibiæ, and one on each of the first two segments of the tarsus, where the parts come in contact with the surface over which the insect may walk. With every step taken, these sense-organs perform their work, and probably leave on the surface walked over traces of the presence of their owners, as may readily be imagined, to impress the senses of those that follow. In all this remarkable collection of sense-organs there is none that seems to explain so clearly its reason for being as do these. Yet my supposition that they leave some special evidence of their owners' former presence which shall be manifest to the other members of the insect community, is based upon the observation of appearances in the tarsal organs of some individual *Termes* which are not apparent in those of others. This is that the deep depressions always present on the first and second segments of the tarsus are sometimes filled with a crystalline mass, which projects beyond the general surface as a hemispherical protuberance, especially, as it now seems, late in the season, and with presumably old subjects, thus suggesting the idea that the tarsal organs, at least, are glandular in function, and that the crystalline substance is the hardened secretion collected through abnormal, or sluggish, action of the parts.

On the tibiæ the organs referred to are shallow depressions in the wall, bordered by thickened margins, and with the plane surface of the shallow studded with delicate, exceedingly minute hairs, whose tips project slightly beyond the general level, and necessarily come in contact with any surface over which the insect may walk. The tibial depressions, while they are always present, are not always of the same outlines or of the same number. In some instances there may be one large depression with several small ones scattered about, as in Fig. 8, or the single large depression may be divided into several smaller portions, which shall be scattered over the region without any regularity of arrangement.

On the first and second segments of the tarsus the organs are always present, and always in the same position on the surface which must come in contact with the ground. Each of the two segments bears one in the form of a thick-walled, deep, hemispherical pit, the smooth inner surfaces of which are also studded with fine hairs similar in appearance to those of the tibial depressions, and with presumably the same functions. It is these hollows that are in many specimens choked with the crystalline excretion already referred to, and shown in Fig. 14, where one pit is filled and the other apparently in its normal condition. Each is plentifully supplied with fine nerve-fibres. Not rarely there are two pits, instead of one, on one or the other of the two segments; in a single instance, I have seen three on the second joint. But these hairy hollows deserve more extended investigation by some microscopist that may be more conveniently situated for that work than I am, and that may have the resources of a laboratory at his disposal.

To such an investigator, thus fortunately situated, the internal structure of these remarkable legs will also offer important subjects for examination. This is especially true of what I suppose, for reasons to be mentioned hereafter, to be the insects' auditory organs, one being present in each tibia, a supply of internal ears that would seem to be more burdensome than necessary or agreeable. (Fig. 13.)

It is possible that these organs may have some connection with the tracheæ, although that connection cannot be close; yet here, as in some other insects, the tibial tracheæ are specially notable on account of the sac-like enlargement of the upper and of the lower ends of the main tube, and of the presence of a smaller, recurrent branch, which leaves the upper inflated portion to enter near the lower at a varying distance from the extremity. This structure has been observed in the locust (*Locusta viridissima*), the cricket (*Gryllus campestris*), and in various Orthoptera by Graber; while Sir John Lubbock describes a similar arrangement in the tibiæ of the ants, especially in *Lasius flavus*. This tracheal structure is well developed in all the tibiæ of *Termes flavipes*, varying in the length of the recurrent branch and in the more direct or more undulating course of the main trunk of the trachea. In Fig. 12 is shown the appearance in one of the tibiæ of the white ants.

In the locust (*Ephippigera vitium* Serv.), according to Graber, and in certain other Orthoptera, the main tracheal trunk bears a collection of ganglion-cells and globules supposed to be auditory in function, at least in part, and which, if present in *Termes flavipes*, have escaped my notice. Yet in each tibia of this insect, situated near the outer wall of each, between it, the nerve and the trachea, is the more or less ovate organ referred to, the structure of which bears considerable resemblance to that of what has been accepted as a tibial auditory organ in certain of the Orthoptera. Its position near the upper third of the tibia of *Termes flaviges* is shown in Fig. 13.

It is connected with the nerve, and is itself formed of a collection of ganglionic cells and globules, with plainly developed, staff-like bodies, the apical extremities of which are conical, and through the middle of their apparently hollow length passes what seems to be a fibre, presumably a nerve. The external extremity is continuous with a nerve-fibre, five of which, with as many elongated, staff-like bodies, being easily made out, the nerves passing singly and separately up toward the femero-tibial joint, near which they are lost to view, especially after my imperfect methods of preparation.

Similar organs have been discovered by Graber in the tibiæ of the Locustidiæ, and by Lubbock in those of certain ants. In reference to the latter, Lubbock says: "At the place where the upper tracheal sac contracts there is, moreover, a conical striated organ, which is situated at the back of the leg, just at the apical end of the upper tracheal sac. The broad base lies against the external wall of the leg, and the fibres converge inwards. In some cases I thought I could perceive indications of bright rods, but I was never able to make them out very clearly. This also reminds us of a curious structure which is in the tibiæ of the Locustidiæ, between the trachea, the nerve, and the outer wall. * * * On the whole, then, I am disposed to think that ants perceive sounds which we cannot hear."

In *Termes flavipes* its position is somewhat different, although its situation and its structure are essentially similar to those referred to by Lubbock and by Graber. It is an organ of fibres, of ganglionic cells and globules, the latter being large and nucleated, and of the long, staff-like bodies already referred to. A partly diagrammatic sketch of the organ is shown in Fig. 16, its outer, narrow extremity being attached to the wide nerve just within the external wall of the tibia and the broad base directed toward the external wall of the trachea.

The rod-like bodies bear a rather remote resemblance to some observed by Graber, in what he considers to be

the auditory organ of the locust, although in the *Locusta viridissima* there are also others broadly clavate and surrounded by a plainly delimited, granular substance.

In *Termes flavipes* there are no external appendages to suggest an auditory function, as there are in the locust and in some other insects, there being here only a slight concavity of the wall over the internal organ, and two or three of the sensory pits scattered about the surface. If the similar organs among members of the Orthoptera have such a function, it seems not unreasonable to suppose that such may be the use of these appendages within the tibiæ of our common white ants.

But, however this may be, the legs of these insects merit careful investigation by some competent observer, so situated that he may have access to all the luxuries of modern microscopical research, most of which are at present beyond my reach, my paper being, therefore, necessarily superficial and imperfect.

LETTERS TO THE EDITOR.

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THE OSAGE RIVER AND THE OZARK UPLIFT.

MR. ARTHUR WINSLOW'S account of the Osage river and its meanders in *Science* for July 21, 1893, commenting on my previous suggestion concerning the development of that river in *Science* for April 28 of this year, has only lately come to my attention in looking over papers accumulated at home during vacation absence. It raises several questions on which discussion may prove of interest.

In explaining the existing meanders of the Osage and other deep-valleyed rivers of Missouri and Arkansas, Mr. Winslow maintains that the rivers had originally curved courses consequent on the form of the land on which they were initially formed; that these irregularities of flow are still perceptible, although they have been increased during the down cutting of the valleys; and that the down-cutting of the valleys and the general sculpturing of the region now going on is in consequence of an uplift that was essentially completed in Paleozoic time. I am not sure as to my correct understanding of the third point, although such appears to be Mr. Winslow's meaning.

The explanation that was suggested in my article included a long lost beginning of river development in Missouri; the attainment of an oldish topographic condition in the cycle of denudation preceding the present cycle; and an inheritance by the rivers of a meandering course, normally characteristic of the wide-open valleys of the preceding cycle, in the deep-sunk valleys of the present cycle.

Mr. Winslow's first point—that the existing meanders are simply exaggerations of initial consequent river courses—seems to me inadmissable for several reasons. In the first place, this involves the persistence through all of Mesozoic and Tertiary time of relatively trivial peculiarities of river courses, begun on the surface of the carboniferous strata about the close of Paleozoic time. It is certainly true that rivers are long lived, but it is very unlikely that the land history of Missouri has been so simple as to allow so extraordinary a perpetuation of relatively small river features. My reason for this opinion is not simply an *a priori* objection to the opposite view; but a careful examination of the developmental changes of other rivers. In Pennsylvania, for example, the changes in the course of rivers during a period corresponding to that of the land history of Missouri has been so great that I cannot think that the rivers of Missouri still maintain any close trace of their ancient initial courses down to these modern days. It is true that there has been much greater opportunity for variation of river courses among the tilted rocks of Pennsylvania than upon the nearly horizontal strata of Missouri; but to conclude that even in the latter region there have been no essential changes of river courses since the end of Paleozoic time implies to my mind altogether too passive a conception of post-Paleozoic time. It is impossible to say exactly what has happened, for the records are rubbed out; but to conclude that practically nothing has happened in the way of oscillation and warping and river change seems to me the most unlikely of all plausible conclusions.

In the second place, the postulate that the present meanders are directly descended from originally irregular consequent courses does not well accord with the distribution of deep meandering valleys in other parts of the world. They are not found in regions of one cycle of development; that is, in regions that are now in process of degradation following their first uplift. They characterize regions which for other reasons—of which more below—must be interpreted as having a composite topography; that is, having topographic features produced in two or more cycles of degradation. Moreover, the fact that the radius of the valley meanders is greater where the rivers have great volume is not consistent with the origin of the meanders from a control so irrelevant to river volume as the constructional inequality of the original land surface must have been.

Mr. Winslow's second point—that the existing meanders are increased in sinuosity over some former condition of meanders—seems to be an important correction to my brief explanation. It is a point that I had not in mind at the former writing; but in now recalling the form of the meandering valley of the North Branch of the Susquehanna in northeastern Pennsylvania, I see that the correction applies there as well as in Missouri. One might at first suppose that if a meandering river were uplifted, it would tend to straighten out its course, on account of gaining a stronger current; but it also seems possible that an even uplift with no change of grade (except by the action of the river itself in cutting down its channel towards the new base level) may even provoke an increased meandering, instead of straightening out former meanders. Professor J. C. Branner has in a letter called my attention to essentially this interpretation of certain deep meandering valleys in northern Arkansas.

As to Mr. Winslow's third point—that the present valley-making Missouri is the incompleted work of the denudation begun at the end of Paleozoic time—I cannot agree to this at all. Indeed, such a conclusion appears to me so improbable, and so contrary to both local and general evidence, that I fear it is not a correct statement of Mr. Winslow's meaning. He says: "The sculpturing of the topography [of Missouri] must have been uninterruptedly in progress from the end of the Paleozoic to the present time." He implies that the present altitude of the Osarks above the margin of the Tertiary strata in southeastern Missouri is the same as the altitude that the Osarks had above the waters in which the Tertiary strata were deposited; thus excluding all chance of tilting and local warping since that time. Differential movements have been determined even as late as in Tertiary and post-Tertiary time in the west; and there is good evidence of similar late geological movements in the Appalachians along the Atlantic slope. It therefore seems entirely improbable that Missouri should have taken an attitude at the close of Paleozoic time from which it has not since significantly changed and entirely impossible, if