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STUDIES OF THE COLLEMBOLAN EYE.

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Plate XVIII.

In any primitive group of animals, there is an unusual interest attached to any organ which shows a simple structure, as having a possible bearing upon the history of the organ in a more highly specialized condition, as found in higher, closely related groups. Sometimes organs of seemingly simple structure are very puzzling from the fact that we are at a loss to determine whether their condition is primitive, or is due to degradation or partial atrophy. Embryological studies are often of value in determining the case, but not always. In entomology we have surprisingly few embryological studies which are specific enough to guide us in such determinations. When a group of insects varies widely however, in relation to any specified structure, a comparative study of its adult condition in the different members of the group may be of value.

In the minute, wingless insects of the order (or sub-order) Collembola, often included, along with the true Thysanura, under the ordinal name of Thysanura as constituting a lowly branch upon the insectan phylogenic tree, we find no compound eyes, nor do we generally find any isolated ocelli. The ocelli are bunched or gathered together in the post-antennal regions on the right and left eye-spots.

It is not impossible, I think, that each eye-spot may represent all that remains of an ancient compound eye, the few ocelli being modified survivors of some of the component ommatidia. Embryological research must be looked to for the determination of this question if it ever is determined. If this should prove to be true, we must regard the compound eye as having undergone a certain very definite amount of decadence at a period remote enough to antedate the general branching off of species. A modern Thysanuran, *Machilis*, shows many characters that must have been likewise possessed by the ancestor of the Collembola. *Machilis*, moreover, has well-developed compound eyes; so that it seems not unlikely that the Collembolan eye has descended from that type.

The present paper, however, has to do rather with the modifications of the eye from the Collembolan type, than with its possible pre-Collembolan history.

The eyespots are situated dorso-laterally, caudad to the bases of the antennae, as may be seen in Figures 1 to 4. The first two show a typical horizontal-headed species; the following two a species with the head vertical. Each eyespot may contain eight or fewer ocelli, but never more than that number. There are abundant indications that when fewer than eight ocelli are present, the condition denotes atrophy of one or more of the oceller units, for eight seems to be the typical number of ocelli for the Collembolan eye. Some whole genera, it is true, show a

smaller number, but there is reason for believing that their condition is not a primitive one, but one derived from that mentioned above. Thus, in the genus Tomocerus, each eyespot contains but six ocelli. In Sir John Lubbock's great "Monograph of the Thysanura", there appear some errors concerning the ocelli of certain genera of the Collembola; he state that *Isotoma* and *Tomocerus* have each seven ocelli on a side. His figures, however, are at variance with the statement, and show eight for *Isotoma*, which is the usual number in that genus, and but six for *Tomocerus*, which is likewise correct, Figs. 1 and 7. He states that *Orchesella* has six, and with this his figure of the eye in that species agrees. I have examined specimens of four species of *Orchesella*, and all appear to have eight ocelli, though one of these is usually quite small. Fig. 6.

A study of their positions indicates that the individual ocelli are probably homologous in all the different species; and that there is not only a typical number of ocelli, but a typical pattern for the placing of them upon the eyespot. This may vary somewhat, but usually seems to have the ocelli placed along the course of a more or less elongated letter S. Certain of the ocelli in this figure seem to be less tenacious of existence than others, and in certain genera we may find these growing smaller and less important as we pass from species to species until they entirely atrophy and actual numerical diminution results.

The Collembola show a strong tendency to the cave habit, and thus we find more or less profoundly modified species in many of the genera. In many cases, the modifications induced by the cave habit have so differentiated species along common lines, as to have led to the formation of new genera for their reception. It is to be expected that the visual organs would be most quickly and deeply modified by a habit which led to a life in situations where light was obscure or absent.

I have recently re-examined all the species in my collection, as well as all accessible figures of the eyes of species I have not, and find some very interesting gradations. The eyespot containing the ocelli is usually very dark, often deep black. It often gives bronzy reflections when viewed by reflected light, excepting the ocelli themselves which appear dense black. In shape the eyespot varies considerably, according to species. While it is commonly of a more or less elongated rectangular shape, with the longer axis corresponding to that of the animal, it may be oval, ovoid, reniform, triangular or crescentic, and is often irregular upon the edges. The shape corresponds rather closely to the placing of the ocelli; sometimes persisting, however, over areas from which the ocelli have atrophied. When the ocelli disappear from the middle of an eyespot, as they do in some instances, the pigment may also disappear from the middle part of the eyespot and still be retained at its two ends where the ocelli still persist. This gives rise, of course, to the appearance of two eyespots on each side of the head. One of these may even disappear, leaving but one small one on each side. Fig. 5 shows an eyespot which may be considered fairly typical. In this species (*Isotoma muskegis* Guthrie) the ocelli are approximately of the same size, while the densely pigmented eyespot is elongate, and pretty

regularly shaped. For convenience of comparison I have lettered the ocelli in a definite order, like the stars in a constellation. This constellation, as has been stated, shows somewhat of the form of the letter S. The ocelli are lettered in order, beginning with the one most cephalolaterad in position. In looking through a collection of drawings of the ocellar constellations of species scattered throughout the different genera, we find ocellus D to be somewhat variable in position. This might be termed the central ocellus if we had only to deal with species having the eyespots broad. In forms with the narrower eyespot, where ocelli A and E are strung out farther apart, opportunity seems to be offered for D to take position on the lateral edge where I judge that it is the most useful, for reasons to be stated later. Ocellus H is another which is quite variable in position. It oftener shows positional affinity with C than with G, though in some instances it seems to have moved caudad nearer the latter. Now it may be merely a coincidence, but it certainly is true that when there is atrophy among the ocelli, these two are usually the first to decrease in size, and the first to be eventually lost. When D is central in position, as in the members of that group of *Sminthuri* including *Sminthurus minutus* MacG., *S. 4-maculatus* Ryder, *S. aureus* Lubb. and *S. niger* Lubb,, this is notably true, it being always small though not necessarily the only small ocellus of the constellar S. See figure 8. Ocellus H appears to have usually the slightest hold on existence of any, though some exceptions will be noted. In *Sminthurus aureus* Lubb., fig. 8, all the ocelli excepting D and H are of approximately equal size. Ocellus D, which is central in position, is very small; while H is yet smaller and is somewhat triangular in shape, and is situated close to G. In the genus *Papirius*, Fig. 10, is found a condition which shows the fate of the ocellus which becomes crowded toward the center, losing its position upon the margin. *Papirius maculosus* Schött, Fig. 9, shows H of normal size and on the edge of the very convex eyespot. The shortening of the eyespot has apparently crumpled the line, forcing C out of the marginal row. It is small, though not so small as D, which is also nearly central. Some of the species of *Sminthurus* show a condition similar to the *Papirius*, though not usually so well marked. Probably the shortening of the eyespot is to be co-ordained with the shortening of the dorsal surface of the head, due to the vertical instead of horizontal position of the head among the Sminthuridae. The prominent position of the eyespots is heightened by their own great convexity, while the positions of the most useful ocelli being around the edge of the raised area, an outlook is secured in all directions by each eyespot. The insect's demand for a view straight dorsad seems to be so little as to allow central ocelli to atrophy through disuse.

In the genus *Lepidocyrtus*, we find in a typical species, *L. purpureus* Lubb. Fig. 10, a somewhat elongate eyespot. Ocelli D and H are decadent, but still present. In this genus there was once an eyeless species, but it had the honor of being later considered as the type of a new genus *Cyphodeirus*. Two species of *Lepidocyrtus* which I have described from

Minnesota, *L.* 10-*oculatus* and *L.* 6-*oculatus*, are interesting in their stages of ocellar atrophy. See figures 11 and 12. In the former the eyespot is shortened and C forced in from the margin as in *Papirius*, fig. 9. This ocellus is small, while the two preceding it are large. D has apparently disappeared, and from the position of the next ocellus, it seems probable that E has also atrophied. Two are found in the caudal end of the eyespot which are probably F and G, if we assume, as we safely may, the atrophy of H. In the closely allied *L.* 6-*oculatus* the small ocellus C has been lost, also one corresponding to the smaller of the two caudally placed ones in Fig. 11. This leaves for *L.* 6-*oculatus* only A, B and F, a considerable portion of the eyespot between the first two and the last being destitute of ocelli. This intermediate space, having lost the ocelli, has also lost its pigment; and there remain a cephalic and a caudal spot, containing, respectively, two and one ocelli. In the genus *Isotoma* there is a species, *Isotoma* 4-*oculata* Tullberg, Fig. 13, with similarly divided eyespots, but in this the cephalic portion contains but one ocellus. Probably, from its positional relation to the postantennal organ, it is ocellus B, and the caudal spot contains F. In Wahlgren's species *Isotoma binoculata*, the small cephalic spot alone is present, and contains the single ocellus. In the blind species *Isotoma fimetaria* (L), there is no evidence of ocelli or even of pigmented areas. In the genus *Sminthurus* we have a blind species in which some specimens possess very little pigment upon the general surface, while others show a considerable amount of fine reddish pigment dots. This species does not possess ocelli, and seldom shows evidence of a pigmented eyespot, but some specimens have been taken in which unmistakable pigmented areas representing eyespots were present. A species very closely related, structually, but with a well-pigmented body, shows a single small ocellus on each side of the head situated on a very small black eyespot. This ocellus is probably either A or B.

There are but a few examples of the peculiar conditions of ocellar atrophy obtaining among this interesting group, but they may be sufficient to call attention to the following conclusions: The number and arrangement of ocelli, subject to various modifications may be recognized throughout the Collembola. Members of this group occupying marginal positions have greater tenacity of existence than others. Central ocelli are usually the first to go. A more advanced stage of atrophy deprives the whole middle part of the eyespot of ocelli and at the same time or a little later of its pigment. The last part of the eyespot to persist with its ocelli is the most cephalic end. Vestigial pigment may determine the position of an eyespot after all the ocelli have been lost.

EXPLANATION OF PLATE.

Figure 1. Dorsal view of head of *Isotoma leonina* Packard.
2. Lateral " " " " " *sensibilis* Tullberg.
3. Dorsal " " " " *Sminthurus aureus* Lubbock.
4. Lateral " " " " " " "
5. Dorsal view of right eyespot of *Isotoma muskegis* Guthrie.
6. " " " " " " *Orchesella albosa* Guthrie.
7. " " " " " " *Tomocerus niger* Bourlet.
8. " " " " " *Sminthurus aureus* Lubbock.
9. " " " " " " *Papirius maculosus* Schött.
10. " " " " " " *Lepidocyrtus purpureus* Lubbock.
11. Dorsal " " " " " " 10-*oculatus* Guth.
12. " " " " " " " 6-*oculatus* Guth.
13. Lateral view of head of *Isotoma* 4-*oculata* Tullberg.

The ocellar S referred to in the text is indicated by the dark stripe connecting the ocelli.

In figures 7, 11 and 12 the X situated on the course of the ocellar S denotes the position from which the ocellus indicated in each case is supposed to have disappeared by atrophy.