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Publisher: Taylor & Francis
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Annals and Magazine of Natural History: Series 6

Publication details, including instructions for authors and subscription information:
<http://www.tandfonline.com/loi/tnah12>

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Published online: 06 Oct 2009.

To cite this article: H.McE. Knower (1896) XLIII.—The development of a termite—*Eutermes (Rippertii?)*: a preliminary abstract , *Annals and Magazine of Natural History: Series 6*, 18:106, 277-282, DOI: [10.1080/00222939608680456](https://doi.org/10.1080/00222939608680456)

To link to this article: <http://dx.doi.org/10.1080/00222939608680456>

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THE ANNALS

AND

MAGAZINE OF NATURAL HISTORY.

[SIXTH SERIES.]

No. 106. OCTOBER 1896.

XLIII.—*The Development of a Termite*—*Eutermes* (Rippertii?) : a Preliminary Abstract. By H. MCE. KNOWER*.

DURING my tenure of the Adam T. Bruce Fellowship this past winter I have studied the development of a species of termite closely related to *Eutermes Rippertii*, Rambur. The material was collected in Jamaica, and the work was undertaken as part of a more extended investigation of the biology of the Termites and because of the primitive character of the group, the embryology of which has not been hitherto studied.

In its general features the embryology is quite similar to that described by Brandt for the Libellulid *Calopteryx* (1); but, on the whole, I should say it resembles rather more the development of certain of the Orthoptera. Like *Stenobothrus*, *Ecanthus*, &c., the first rudiment of the embryo is a small disk near one pole of the egg. In the termite this disk is on the ventral surface, just beneath the micropyles, near the posterior pole of the egg. I have studied the segmentation and early stages of the formation of the disk to find out how this rudiment arises. As a result, it is clear to me that the germ-disk is not formed immediately during the segmentation, by cells wandering from the interior of the egg directly to their places in the embryonic area. On the contrary, the cells

* From the 'Johns Hopkins University Circulars' for June 1896, pp. 86, 87.

resulting from segmentation become about equally distributed to all parts of the egg. At an early stage most of the cells have reached the surface of the yolk, only very few remaining behind as vitellophags. After attaining the surface the cells of the blastoderm (it may, perhaps, be spoken of by this term, though protoplasmic continuity between its cells cannot be shown) continue to divide at all points, though the nuclei in the posterior end divide more rapidly. For a number of stages this becomes more noticeable, but it is also evident that the actively dividing nuclei are not confined to the restricted area on the ventral surface to be occupied by the disk. The nuclei of the dorsal surface near the posterior pole are as numerous and as near together at this time as those on the ventral surface. From this stage to one exhibiting a sharply outlined germ-disk about to be covered by an amnion there is apparently a concentration of the cells on the surface toward the ventral side of the egg to a point just beneath the micropyles. This, as has been said, is the place where the primary rudiment of the embryo is finally situated. Hence the embryonic disk is seen to be due not simply to an active multiplication of the cells of a restricted area of the blastoderm, but likewise to a concentration of the blastoderm-cells. This, it will be remembered, is what McMurrich has recently shown to be true in the development of Isopods (5). A similar concentration has been observed in the establishment of the first rudiment of other insect embryos; but in the termite it is especially marked, owing to the comparatively small size of the germ-disk (see Patten for the Phryganids (6) and Wheeler for *Doryphora* (8)). Sections of the disk during this concentration show that cells are crowded beneath the surface from a very early stage in its formation. This takes place at all points in the area of the disk, and the surface nuclei also divide tangentially here and there to separate cells which adhere to the lower surface. This is the beginning of the formation of the "under-layer."

Surface views of older embryos show two changes in the disk. Near the centre a dark spot appears, and in the same stage the posterior margin becomes marked out as a semicircle of especially closely crowded nuclei. Sections of such disks show that the "under-layer" cells have become more numerous, and have collected into a plug projecting into the yolk and making the dark spot seen on the surface. The posterior semicircle of crowded nuclei represents the first rudiment of the amnio-serosal fold. It is, at this period, merely a more thickened margin of the disk. The area between the central plug and the amnion thickening (if it

may be so spoken of) is quite thin, being a single layer of cells. These stages, as well as later ones, agree in showing no gastrula invagination, the "under-layer" being formed, as described, rather by a process of delamination or in wandering due to crowding, and the plug being a later secondary formation.

The facts of the origin of the "under-layer" support Heymons's (10) recent views as to the formation of this layer in the Orthoptera, in as far as they indicate that invaginate gastrulas may be secondary phenomena among insects.

As to the origin of the amnion. In the termite it is apparently, as has been said, a thickening of the posterior edge of the disk before any trace of a fold can be distinguished in section. When this thickening folds over the disk the amnion is seen to differ in no essential from the rest of the embryonic disk (of course leaving the "under-layer" plug out of consideration).

The enclosure of the germ-disk takes place by the single posterior semicircular fold growing forward to its anterior extremity. Just after the amniotic cavity is closed in this way the amnion is still found to be quite thick and like the upper layers of the disk (see Bruce's figure xliii. of *Mantis* at this stage (2)). A like similarity has been observed in many insects between the ectoderm of the embryo and the amnion.

The further growth of the embryo is much like that figured by Graber for *Stenobothrus* (3). While the anterior end of the disk remains fixed the tail-end grows back over the posterior pole. In this way an embryonic band is formed which makes a cap over this pole. Both ends of the band are at first of the same shape. Soon, however, the anterior extremity spreads out into a broad cephalic area, which has reached its greatest extent by the time the posterior end of the band has pushed up about one third of the dorsal surface of the egg. Segmentation now sets in—the antennary (postoral), mandibular, first and second maxillary, and first thoracic segments appearing almost simultaneously.

There are no macrosomites, as in *Stenobothrus* (Graber). The remaining thoracic and abdominal segments are added successively from before backward, as the band grows still further toward the anterior end of the egg. The labrum appears as a median unpaired fold over the mouth.

Sections of these early stages of the elongating embryonic band show that the "under-layer" does not extend anteriorly beneath the ectoderm, which has spread out anteriorly over the yolk to form the cephalic lobes. Posteriorly, however,

the "under-layer" follows the growth of the ectoderm, which is somewhat more rapid. A sagittal section of a band before segmentation shows the "under-layer" as a single row of cells beneath the anterior portions of the ectoderm, where its cells are sharply marked off from the ectoderm. Beneath the tail-end of such an embryo the "under-layer" cells are collected into a large mass, which is not sharply separated from the ectoderm. Most of the extension of the "lower-layer" is apparently due to the multiplication of its own cells. I have not yet studied the differentiation of this layer, but can state that the endoderm appears after the establishment of segments, and is not formed from vitellophages.

The sections just referred to show well the changes of the amnion until it has become a thin lamella. This is brought about as a result of the anterior and posterior extension of the embryo. The cells of the amnion are pulled out into a single row anteriorly, while posteriorly for some time the membrane retains something of its early appearance. When the tail-end of the germ-band has reached the anterior pole of the egg in its elongation, the abdominal region sinks gradually into the yolk and the posterior extremity coils over ventrally toward the head, giving the embryo an S shape. The appendages have meanwhile grown to nearly their definitive length. The first and second maxillæ are trilobed, and ten rather prominent rudimentary abdominal appendages have appeared. The cephalic region has changed considerably. Just after the appearance of the appendages the lateral margins of the cephalic lobes began to roll up toward the mid-dorsal line. As this process continued a little pocket was formed on either side of the head, which grew gradually larger as the folds of the cephalic lobes approached the median dorsal line. Finally the two lateral pouches fused to form the head-cavity. The antennæ were included in this folding, and hence now enclose a portion of the head-cavity.

When the embryo has reached the stage just described it resembles Brandt's figure 11 of *Calopteryx* (1), but it is not "immersed" in the yolk. It is impossible to say just how long this "inverted" position is maintained. There is, perhaps, a rather short interval before "revolution," which is accomplished as described by Brandt for the Libellulid (that is, judging from preserved specimens). When "revolution" is over the embryo lies with its head at the anterior pole of the egg, while the tail-end lies beneath the micropyles at the posterior pole. The ventral surface of the embryo, as in early stages, lies on the micropylar side of the egg.

I have not studied the development beyond the appear-

ance of appendages, in detail, as yet, but may state that the central nervous system arises from neuroblast cells, as described by Viallanes (7) and Wheeler (9) for certain of the Orthoptera.

I had hoped to make out the history of the reproductive system; but, as far as can be determined, no trace of these organs is developed until sometime after hatching. In the workers and soldiers (*nasuti*), both larvæ and adult, of this species the reproductive organs are entirely aborted.

In reference to the general bearings of my study of this form I shall have something to say in the paper of which this is a preliminary abstract. It may be said here that I do not regard the *Libellulids* as the best examples of the ancestral type of development among insects, as has been so prominently claimed of late (4) (*Korschelt and Heider*). On the contrary, I think that the termite and those Orthoptera having a superficial embryo beginning in a disk which must elongate considerably to attain the definitive number of segments have most nearly adhered to the typical method of development for arthropods, and probably best represent the development of the ancestral insects. My reasons for this cannot be given in this note, but will appear in the full paper.

There is not sufficient space here to discuss the question of the origin of the amnion, but I will say that Wheeler's (9) adaptation to insects of Ryder's theory of a mechanical origin of the membranes of vertebrates seems a most inadequate explanation. (Of course the word "mechanical," as used here, is used in the narrow sense of the term, referring the subject to simply stated conditions of pressure and mechanical strain.) This theory is opposed by what we know of the development of the Crustacea, the Myriopods, and the Apterygota. As far as can be shown, the same conditions of pressure are brought to bear on the developing embryos of these forms as on those of the amniote insects; yet no amnion is formed. In those higher forms of insects, which are characterized by the non-appearance of membranes, their failure to appear is even more marked. Here, in the very face of the conditions stated to be efficient to produce them, no membranes are developed.

The origin of the amnion is in all probability referable to physico-chemical forces; but at present I do not believe the problem can be stated in more definite terms than as follows:—There was a suitable basis among the anamniotic ancestors of winged insects for the formation of membranes, but a further condition was necessary before the amnion should arise. This was a change in the environmental influences, making

it a necessity (perhaps for protection against injury, as Korschelt and Heider suggest (4)) for the embryo to be covered over at an early stage in its development. The physico-chemical forces which led to the origin of this adaptive covering cannot be defined at present, but the result was that as soon as the first rudiment of the embryo, the germ-disk, became established a portion of it folded over the rest and became the amnion. This would occur most readily in forms which, like some Orthoptera and the termite, begin in a small germ-disk. When forms arose among the higher insects as adaptations to special conditions of life the early completion of this process became less important, and in a few extreme cases this led to the degeneration and disappearance of the membranes.

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- (2) BRUCK, A. T.—'Embryology of Insects and Arachnids.' 1887.
- (3) GRABER, V.—'Vergleichende Studien am Keimstreif der Insecten.' 1890.
- (4) KORSCHULT und HEIDER.—'Lehrbuch der vergleichenden Entwicklungsgeschichte.' 1890.
- (5) McMURRICH, J. P.—'Embryology of Isopod Crustacea.' 1895.
- (6) PATTEN, WM.—'The Development of Phryganids.' 1884.
- (7) VIALLANES, H.—'Sur quelques points de l'histoire du développement Embryonnaire de la Mante religieuse.' 1889-90.
- (8) WHEELER, W. M.—'The Embryology of *Blatta germanica* and *Doryphora decemlineata*.' 1890.
- (9) WHEELER, W. M.—'Contributions to Insect Embryology.' 1893.
- (10) HEYMONS.—'Development of Orthoptera and Dermaptera.' 1895. (Abstracted in Journ Roy. Micr. Soc. 1894.)

XLIV.—Contributions from the New Mexico Biological Station.
 —I. *Descriptions of new Bees collected by Prof. C. H. T. Townsend in the State of Vera Cruz.* By T. D. A. COCKERELL.

WHEN Prof. Townsend lately went for a collecting trip in Mexico I pointed out to him that, although many bees had been described from that country, we were totally ignorant of their habits, the flowers they visited, and so forth. Accordingly he collected a large series of specimens, noting in every case the exact locality and date, and preserving specimens of the flowers on which the bees were caught. The collection thus brought together is of great interest, not only for the