II. *On the Structure and Biology of* Archotermopsis, *together with Descriptions of New Species of Intestinal Protozoa, and General Observations on the Isoptera.*

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[Plates 3–10.]

Contents.

PAGE

I. Introductory remarks 76
II. The Structure and Biology of *Archotermopsis wroughtoni*, Desn. 79
A. Historical 79
B. Systematic Position 79
C. External Features of Anatomy 81
1. The First Stage Larva 81
2. The Later Larval Forms 82
3. The Late Larval Soldier 84
4. The Soldier 85
5. The Nymphal Stages 94
6. The Female 95
7. The Male 100
8. The Queen 101
9. The King 101
10. Worker-like Forms 101
D. Internal Anatomy 103
1. The Body Wall 103
2. The Tentorium 104
3. The Digestive System 106
4. The Fat Body 115
5. The Nervous System and Corpora Allata 115
6. The Circulatory System 118
7. The Reproductive System 119
(i) The Male Organs 119
(ii) The Female Organs 120
(iii) The Ova 125
(iv) General Remarks on the Reproductive System 125
E. Observations on the Biology of the Species 125
F. Intestinal Protozoa, with Descriptions of New Species 130
G. Affinities 135

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CONTENTS—*continued.*

PAGE

III. General Observations on the Isoptera 137
A. External Sexual Differentiation in the Soldiers 137
B. On the Occurrence of a Resting Period in the Ontogeny of Termites and its possible bearing on the Origin of the Pupal Stage among Insects 138
C. Remarks on Polymorphism among Termites 140
D. On HOLMGREN'S "Exudation Theory" and the supposed Existence of "Exudation Tissue" 151
E. The Presence of Intestinal Protozoa and their Significance 153
F. On Termites in Captivity 163
G. Affinities of the Isoptera 164
IV. Summary of General Conclusions 166
Bibliography 168
Description of the Plates 175

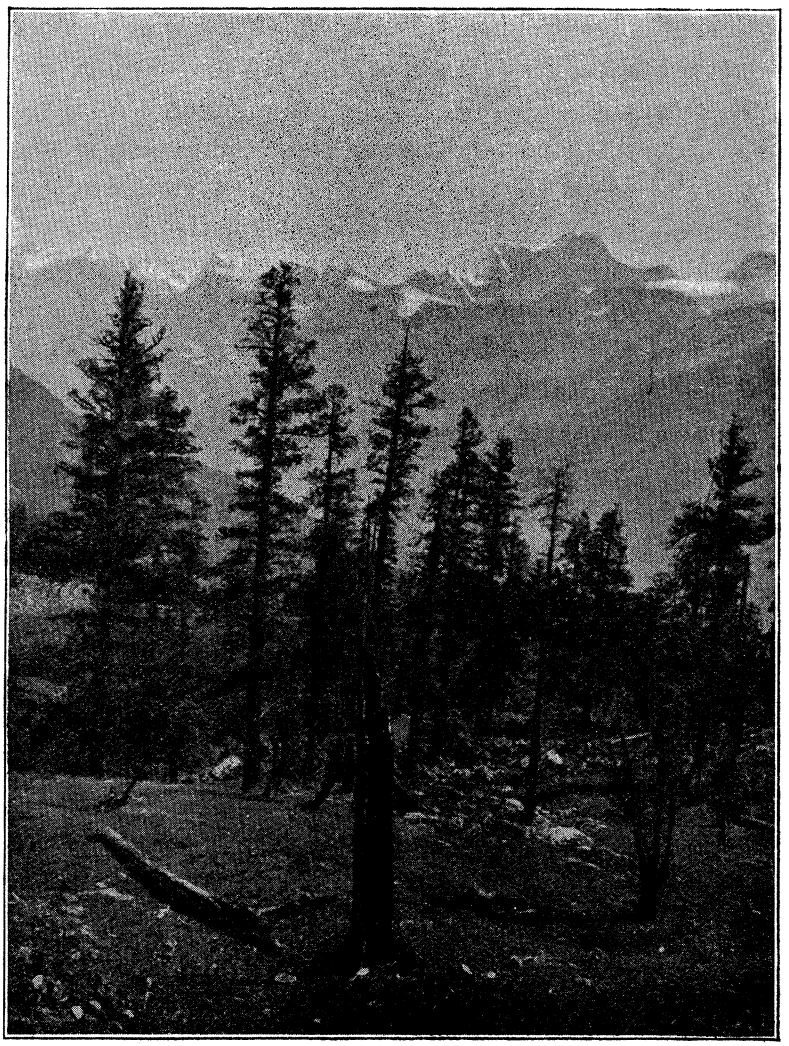
I. INTRODUCTORY REMARKS.

The following paper is intended as a contribution towards a knowledge of the structure and biology of *Archotermopsis wroughtoni*, Desn., one of the most primitive of living Termites. Included herewith are also observations and deductions bearing upon some of the more important general biological problems which are associated with the Isoptera.

Archotermopsis wroughtoni was described 12 years ago by DESNEUX from examples taken by WROUGHTON in June, 1903. They were discovered in old stumps of trees, chiefly *Pinus excelsa*, in the Kashmir Valley. Since its discovery, this species has remained a great rarity, and practically nothing had been ascertained concerning its biology. In June, 1910, I first came across this insect in a decaying fallen trunk of *Pinus excelsa*, in a forest area situated between the Kuari Pass and Ramni, at an altitude of about 8,500 feet, in the Himalayas of British Garwhal. In the same month during 1912 I had the good fortune to meet with it in great abundance in a dead fallen trunk of *Pinus longifolia* near Dharmoti, in the Ranikhet District. This locality is situated at an altitude of about 4,000 feet in the Kumaon Himalaya. Being aware of the biological and phylogenetic interest likely to be afforded by a study of this species, I made a prolonged search in many other likely localities in the North Western Himalayas during the years 1912–13. It was subsequently found plentifully at Bhowali, near Naini Tal, at an elevation of 5,800 feet, near Nadh in the Chakrata District of Jaunsar, and I have also been able to procure examples from near Gulmerg in Kashmir. It seems probable, therefore, that it will eventually be found to be generally distributed in the lower-level coniferous forests of the North Western Himalayas, up to an elevation of about 9,000 feet.

My observations on this species have been conducted partly in India and partly on specimens living in captivity in Cambridge. I am indebted to Prof. J. STANLEY GARDINER, F.R.S., for allowing me the advantage of working in his laboratory. The

work has suffered frequent interruptions over a period of four years, and has been completed in the Entomological Department of the University of Manchester. Prof. S. J. HICKSON, F.R.S., has also granted me the use of several facilities afforded by his Department. Mr. C. BEESON, B.A.,* of the Forest Research Institute, Dehra



TEXT-FIG. 1.—View in a coniferous forest near Ramni (Garhwal, Himalaya). The fallen log in the fore-ground contained extensive colonies of *Archotermopsis wroughtoni*. A. D. IMMS photo.

Dun, India, has rendered most valuable assistance in keeping me supplied with living specimens of *Archotermopsis*, and in conducting further observations with regard to its distribution and food plants. I am also indebted to Dr. L. DONCASTER, F.R.S., for

* Since writing the above Mr. C. BEESON has kindly made a search for this insect, and has found the species in the following localities, situated in the Jaunsar forests: Bodyar (8000–8500 feet), Mundali (8500–8800 feet), Deoban (9000 feet), and Kanesar (8000 feet), and Mr. N. C. CHATTERJEE, B.Sc., has also supplied me with further material from these same forests.

valuable criticism with regard to the subject of polymorphism, and to Mr. C. C. DOBELL, F.R.S, for examining certain of my preparations of the intestinal Protozoa.

The first portion of this paper is concerned with the morphology, biology and affinities of *Archotermopsis*. I have investigated the soldier more fully than the winged forms, primarily for the reason that it appeared more likely to shed light upon the complex problem of polymorphism. In the case of the winged individuals, worker-like forms, and larvæ I have confined myself mainly to pointing out those features wherein they differ from the soldiers and from one another. As these differences are in many cases inconsiderable, an equally detailed account of their morphology would add very greatly to the size of the present contribution, and involve a large amount of repetition. An examination has also been made of the intestinal Protozoa; five species of these, or allied organisms, have been met with, and two, pertaining to the genera *Trychonympha* and *Trichomonas*, are described as new.

The second portion of the paper is devoted to a discussion of the more important general biological problems associated with the Isoptera and their relationships with other insects. Particular mention may be made of the subject of polymorphism and the various theories which have been advanced to account for the facts observed. A provisional hypothesis, based upon the Mendelian inheritance of mutations, is suggested as a possible explanation of the phenomena associated therewith. The presence of intestinal Protozoa among the wood-feeding Termites is also fully discussed, and I have endeavoured to show that most of these organisms are more probably symbiotic, rather than parasitic, in their relations with their hosts.

The morphological work has been carried out both by means of dissection and serial sections. The dissections were made in salt solution on freshly killed specimens, alcohol-preserved material only being resorted to in a few cases. For histological purposes, individuals which had freshly undergone ecdysis were utilised in most instances, and no great difficulty was experienced in obtaining an adequate supply of serial sections. Various methods of fixation were used including Gilson's sublimate acetic alcohol, and Carnoy's fluid with chloroform; less satisfactory results were obtained with picric acid. For purposes of staining, brazilin and also Heidenhain's iron-alum hæmatoxylin were chiefly adopted, and in a few cases Mann's methyl-blue and eosin stain was also used with good results. For investigating certain of the more delicate chitinous parts in the young larvæ, dissected preparations were stained with acid fuchsin, which gave good differentiation; any excess of the reagent was afterwards removed by a few minutes' treatment in a saturated solution of picric acid, after the method suggested by GREEN (1914, p. 98) for Coccidæ. Canada balsam was chiefly used as a mounting medium for serial sections, but in cases where sharpness of outline rather than minute detail was required, excellent results were achieved by using colourless euparal, which has a lower refractive index. In some instances the material was transferred directly from absolute alcohol, while in others it was first cleared with "essence d'euparal," but there was no noticeable difference in the two cases.

II. THE STRUCTURE AND BIOLOGY OF *ARCHOTERMOPSIS WROUGHTONI.*

A. Historical.

This Termite was first described by Desneux under the name of *Termopsis wroughtoni*, and only the male imago and the soldier were known to him (Desneux, 1904 A, p. 45). In another publication Desneux has pointed out certain primitive features in its organisation (1904 B, pp. 280–285), and in his monograph of the family Termitidæ in 'Genera Insectorum' (1904 C, p. 13) he created the new sub-genus *Archotermopsis* for its reception. In this memoir he figures the male imago after the wings have been cast (Plate 1, fig. 3) and the soldier (fig. 3A). The latter figure, however, is somewhat inaccurate in certain details. In a later paper Desneux has added some further details of external structure (1906, p. 293). *Archotermopsis* has since been elevated by Holmgren to generic rank. In his 'Termitenstudien' (1911, p. 36) this author gives a brief diagnosis of the winged form, the soldier, and the "worker," together with a sketch (text-fig. 3) of the basal portions of the nervures of the fore-wing. He also gives two very indistinct photographs of the soldier (Plate 1, fig. 6) and the fore and hind wings of the imago (Plate 2, fig. 1).

Holmgren in his later memoir on the 'Oriental Termites" (1913, p. 31) adds a few additional structural details. No further contributions to our knowledge of this Termite have been made and, moreover, no adequate figures have so far been published.

B. Systematic Position.

Desneux (1904 C) regards the Termites as belonging to the order Isoptera comprising the single family of the Termitidæ. He places *Archotermopsis* as a sub-genus of *Termopsis*, in the sub-family of the Calotermitinæ, and its position in his scheme of classification is as follows :—

Sub-family I : Mastotermitinæ, Desn.
Genus : *Mastotermes*, Frogg.

Sub-family II : Calotermitinæ (Frogg), Desn.
Tribe I : Termopsis, Desn.
Genus : *Termopsis*, Heer.
Sub-genus 1 : *Archotermopsis*, Desn.
Sub-genus 2 : *Termopsis*, Desn.
Tribe II : Hodotermitini, Desn.
Genus 1 : *Hodotermes*, Hag.
Genus 2 : *Stolotermes*, Hag.
Genus 3 : *Porotermes*, Hag.

Sub-family II : Calotermitinæ (Frogg), Desn.—*continued.*
Tribe III : Calotermitini, Desn.
Genus : *Calotermes*, Hag.
Appendix :
Genus : *Psammotermes*, Desn.

Sub-family III : Termitinæ, Desn.
(Including the remainder of the Termites.)

Holmgren has evolved the latest classification in his extensive 'Termitenstudien' (1911, pp. 13 *et seq.*), and regards the Isoptera as being divisible into four separate families, which he classifies in the following manner :—

Family I : Mastotermitidæ, Silv.
(Sub-family : Mastotermitinæ, Desn.)
Genus : *Mastotermes*, Frogg.

Family II : Protermitidæ, Holmgr.
(Sub-family : Calotermitinæ, Desn.)
Sub-family I : Termopsinæ, Holmgr.
Genus 1 : *Archotermopsis*, Desn.
Genus 2 : *Termopsis*, Heer.
Genus 3 : *Hodotermopsis*, Holmgr.
Sub-family II : Hodotermitinæ, Holmgr.
Genus 1 : *Hodotermes*, Hag. (and sub-genera).
Genus 2 : *Pterotermes*, Holmgr.
Sub-family III : Stolotermitinæ, Holmgr.
Genus : *Stolotermes*, Hag.
Sub-family IV : Calotermitinæ, Holmgr.
Genus 1 : *Porotermes*, Hag.
Genus 2 : *Calotermes*, Hag. (and sub-genera).
Family III : Mesotermitidæ, Holmgr.
Sub-family I : Psammotermitinæ, Holmgr.
Genus : *Psammotermes*, Desn.
Sub-family II : Leucotermitinæ, Holmgr.
Genus : *Leucotermes*, Silv.
Sub-family III : Coptotermitinæ, Holmgr.
Genus 1 : *Arrhinotermes*, Wasm.
Genus 2 : *Coptotermes*, Wasm.
Sub-family IV : Termitogetoninæ, Holmgr.
Genus : *Termitogeton*, Desn.

Family III : MESOTERMITIDÆ, Holmgr.—*continued.*
Sub-family V : RHINOTERMITINÆ, Frogg.
Genus 1 : *Parrhinotermes*, Holmgr.
Genus 2 : *Rhinotermes*, Hag. (and sub-genera).
Sub-family VI : SERRITERMITINÆ, Holmgr.
Genus : *Serritermes*, Wasm.
Family IV : METATERMITIDÆ, Holmgr.
Sub-family : TERMITINÆ, Holmgr.
(Including the remainder of the Termites.)

A synopsis of the various schemes of classification of Termites is given by HOLMGREN (1911, pp. 4–12), and I regard the one proposed by him as the nearest approximation to a natural system. In both the classifications of DESNEUX and HOLMGREN, it will be noted that *Archotermopsis* is regarded as being closest related to the Australian genus *Mastotermes* on the one hand, and to the New World *Termopsis* on the other. A discussion of its relationships and affinities is given later on in the present paper (p. 61).

C. EXTERNAL FEATURES OF ANATOMY.

1. *The First Stage Larva.*

It has not been my good fortune to observe the actual emergence of the larva from the ovum, as none of the eggs which were kept under observation hatched out. The following description consequently applies to the youngest larvæ which I have been able to discover. It is perfectly clear, however, that larval dimorphism is present from a very early stage in development, and is probably evident at the time of emergence from the egg. The youngest larvæ measured 2 mm. long, and individuals in the first stage of development were met with up to 3·5 mm. in length. They exhibit well-defined morphological characters, indicating the caste of the adult they are ultimately to produce. The dimorphism is mainly evident with reference to the size of the head, and, after examining a large number of examples, I find that it is possible to separate them into large-headed and small-headed forms, as was observed by GRASSI and SANDIAS among the young larvæ of *Calotermes*. In the case of the small-headed larvæ, the abdomen is usually rather more elongate and slender than in the large-headed forms.

The Head.—The head is only very slightly broader than long, and is invested, dorsally, with rather long scattered hairs. The *antennæ* measure 1·2 to 1·4 mm. in length, and consist of 11 or 12 well-defined joints, together with a zone of growth comprising four partially differentiated joints (Plate 6, fig. 29), making 15 or 16 joints in all. The *eyes* are undeveloped, though in one larva, measuring 3·5 mm. long, slight pigmentary indications were noticeable. The *mouth-parts* do not differ

in any important detail from those of the adult-winged forms, except in size and their slight degree of chitinisation. The same elements are clearly recognisable, and detailed descriptions or figures are consequently unnecessary.

The Thorax.—The thorax is somewhat more contracted than in the adult insect, its length being slightly less than the breadth. The general form of the segments is similar to that of the adult winged individuals; the meso- and metathoracic *epimera* are relatively large and conspicuous. The *legs* have proportionately short *tibiæ*, which are slightly less than twice the length of the tarsi (excluding the claws). With the exception of a pair of short blunt apical spines, no other tibial spines are present. The *tarsi* are four-jointed (fig. 26), with only a very faint indication of the developing rudiment of the reduced second joint. No *onychium* is present between the claws.

The Abdomen.—The abdomen measures on an average 0·5 mm. longer than the combined length of the head and thorax. Dorsally, each segment carries a transverse band of rather long hairs, which dwindles away laterally, and is absent from the ventral surface. Ten *terga* and nine *sterna* (2–10) are present, the first sternum being only represented by a membranous area immediately behind the posterior border of the metathorax. The two terminal segments closely resemble the condition found in the adult male. The *cerci* are very short and single-jointed, measuring only 0·17 mm. in length (fig. 5); *sub-anal styles* are present, and are only very slightly shorter than the *cerci*, being 0·15 mm. in length.

Size.—Larvæ at this stage measure from 2 to 3·5 mm. in length. Measurements made on individuals 2·5 mm. long were as follows :—

	Large-headed forms with 11 or 12 complete antennal joints.	Small-headed forms with 12 complete antennal joints.
	mm.	mm.
Length of head to base of labrum	0·64	0·48
Breadth of head	0·8	0·6
Breadth of prothorax	0·56	0·48
Length of mandible from apex to condyle—		
1. Right mandible	0·46	0·36
2. Left mandible	0·51	0·46
Breadth of mandible from condyle to pars molaris—		
1. Right mandible	0·51	0·46
2. Left mandible	0·48	0·35

2. *The Later Larval Forms.*

After the first moult, growth is manifested externally in an increase in the size of the individual, in the addition of further joints to the antennæ and cerci, in the more prominent chitinisation of the mouth-parts and the increasing development of the eyes.

The exact number of moults which occur during the larval period I am unable to definitely ascertain. Selected individuals were kept in captivity for the purpose of noting the ecdyses. In order to make the necessary observations, it became imperative to frequently split up the wood, into which the larvæ gnaw their tunnels. Information gathered by this means proved unreliable, owing to the discovery that the larvæ often devour their exuviæ, in fact, it was only on rare occasions that exuviæ were noted at all. There are, however, excluding the final change to the adult, at least four moults during the whole period of growth.

An important feature to be observed is the gradual addition of joints to the antennæ, and the consequent increase in the length of the latter. This takes place by means of successive divisions of the third joint, which, along with the newest formed joints, constitutes a zone of imperfectly differentiated elements, where growth is actively going on (Plate 5, fig. 26). It is further noteworthy that the number of joints in the antennæ increases without any apparent relationship to the number of moults that take place.

When the larvæ have attained a length of 4 mm., those which are destined to become soldiers (fig. 5) have 16 well-defined antennal joints, together with three imperfectly differentiated elements in process of development, making 19 joints in all. The cerci are two-jointed, and faintly pigmented rudiments of the eyes can be distinguished. The head measures, from the frontal margin of the labrum to the hind border of the cranium, 1·6 mm., and 1·5 mm. in greatest breadth. The mandibles are similar in form to those of the first stage larva, the right jaw bearing three and the left six teeth. The left mandible measures 0·6 mm. long and 0·4 mm. in breadth. The abdomen is broad and very slightly flattened.

Larvæ of the same length, which develop into the winged sexual forms, have smaller heads, measuring 1·4 mm. in length and 1·1 mm. in breadth; the mandibles are also smaller, but otherwise quite similar, and measure 0·5 mm. long and 0·3 mm. in width. The antennæ are 18-jointed, and the abdomen is narrow and more cylindrical.

When the larvæ have attained a length of at least 7 mm., and have 21 or more joints to the antennæ, dimorphism becomes still more marked. Those larvæ which eventually give rise to winged adults can be recognised by the presence of minute wing rudiments, which are visible with the aid of a lens. It is owing to these vestiges that the meso- and meta-thorax in such larvæ have their posterior angles markedly square in appearance (fig. 21). Also, the hind margins of these segments are longer than those of larvæ which develop into soldiers. In larvæ of the latter caste the posterior angles of the meso- and meta-thorax slopes obliquely inwards, and the hind margins of these segments are much shorter in consequence (fig. 20). Wing rudiments are totally wanting. Such larvæ can be further distinguished by their larger heads, and by the presence of 22–24 joints to the antennæ. Larvæ of the winged forms, on the other hand, have, as a rule, 21–23 antennal joints.

Soldier larvæ, 7 mm. long, possess heads which measure 2·2 mm. from the anterior margin of the labrum to the hind border of the cranium, and 2 mm. in maximum breadth; the left mandible measures 1·2 mm. long and 0·6 mm. wide. Larvæ of the winged forms of the same length have heads measuring $2 \times 1{\cdot}8$ mm., and the left mandible measures $0{\cdot}7 \times 0{\cdot}5$ mm. The older the larvæ become the more evident is their dimorphism. Soldier larvæ, 9 mm. long, have heads measuring $2{\cdot}6 \times 2{\cdot}4$ mm., whereas larvæ of winged forms, 10 mm. in length, possess heads which measure only $2{\cdot}4 \times 2{\cdot}1$ mm. There is, however, still no essential difference in the mandibles in the two forms other than that of size. The eyes also exhibit at this stage no differences in their degree of development, irrespective of whether the larvæ are destined to produce soldiers or winged adults. In larvæ 7·5 mm. in length, with minute wing rudiments and 21 joints to the antennæ, the eyes take the form of black elongate-oval areas, 0·4 mm. long and 0·2 mm. in width. In the case of soldier larvæ, they do not undergo any further development beyond this condition, or assume the kidney-shaped form characteristic of the later nymph and winged adults. Sub-anal styles are present in all larvæ irrespective of sex, and the cerci have six or seven imperfectly differentiated joints—the lower number occurring more frequently among soldier larvæ. The tibiæ have only their apical spines developed, but the tarsi exhibit little or no difference from those of the adults.

Length is by no means a trustworthy criterion of the age of the larvæ, as it is dependent to a considerable extent upon nutrition. When, however, they attain a length averaging from 8·5 to 10 mm., they undergo an important moult. Those bearing wing rudiments pass into the nymphal stage, while the soldier larvæ exhibit after this moult a further development in the size and shape of the head and jaws.

3. *The Late Larval Soldier.*

The late larval stage in the soldier (prior to the last moult which gives rise to the adult) exhibits certain of the characters of the fully developed form, though it still maintains important differences (Plate 4, fig. 6). Particularly noticeable is the very slight chitinisation of all parts, the small size of the head and jaws, and the whitish or "larval" coloration.

Coloration.—Uniformly whitish, with the head, legs, cerci and sub-anal styles somewhat grey (especially in alcohol specimens).

The Head.—The head is intermediate in its characters between that of the young larvæ and the adult soldier. It measures in length 3·3 mm. from the frontal margin of the labrum to its hind border; in greatest breadth it attains 2·75 mm. The *eyes* exhibit the characters of those of the adult soldier. The *antennæ* (fig. 19) are 25–26-jointed, but the third to seventh joints (inclusive) are less clearly demarcated from one another than is the case in the remaining joints. The *mandibles* are much broader in proportion to their length than in the adult form. They measure 2·5 mm. long, and attain 1 mm. in greatest transverse measurement. The left mandible is armed

with four teeth and the right with three; the *pars molaris* is much more limited in extent than is the case in the fully-grown soldier.

The Thorax.—This region has all the morphological characteristics of the fully developed form, except that it is not any more strongly chitinised than the abdomen. The *legs* exhibit the characteristic meso- and meta-thoracic *epimera*, and the *tarsi* are 5-jointed on their inner aspects. The *spines* of the legs, however, exhibit marked differences—they are much smaller than in the adult, and the lateral spines are fewer in number or entirely absent.

The Abdomen.—The abdomen agrees in all essential measures with that of the completely developed soldier. The cerci are 6–7-jointed, and the *sub-anal styles* are fully formed.

Size.—The length varies from 13·45 to 14·5 mm., and the following measurements have been made on an average specimen :—

	mm.
Length of mandible	2·5
Length of head	3·3
Breadth of head	2·75
Length of thorax	3
Breadth of thorax	2·25
Length of abdomen	6
Breadth of abdomen	3
Total length	14·25

4. *The Soldier.*

i. *Coloration*—

(a) *Dorsal Aspect.*—The head is rich yellow-brown, darkening over its anterior half to mahogany colour, and inclining to black, or almost black, along the frontal margin; it becomes paler as the hind margin is approached, but darkens along each side. The mandibles are deep shining black; the maxillary palpi dark brown, each joint becoming paler near the articulations. The labrum is yellowish-brown, and the clypeus pale yellowish-white. The antennæ are russet-brown, each joint with a pale distal band close to where it articulates with the joint in front. The prothorax is bright yellow-brown, similar in colour to the head; its anterior border is edged with darker brown, which is less prominent along the other borders. The abdomen is straw coloured, or dirty white, inclining to yellowish at its apex. The tibiæ are yellow-brown, but the remaining joints of the legs are dark straw coloured, the tarsi being the palest; the claws of the feet are piceous at their apices. The cerci and sub-anal styles straw coloured.

(b) *Ventral Aspect.*—The head is rich yellow-brown, or almost orange, becoming paler posteriorly; the middle area, occupied by the mental plate, is mahogany coloured. The mandibles are quite black, and the remaining mouth-parts are rich

brown, becoming paler at the articulations of the joints. The thorax, legs, cerci, and styli are dark straw coloured, and the abdomen cream coloured with the two apical segments inclining to light yellow.

ii. *The Head* (Plate 3, fig. 1)—

The *head* is hirsute, longer than broad, and (excluding the jaws) measures 3·75–5·5 mm. in length and 3·5–4 mm. in breadth. Its sides are nearly parallel, and its diameter slightly increases towards the posterior margin.

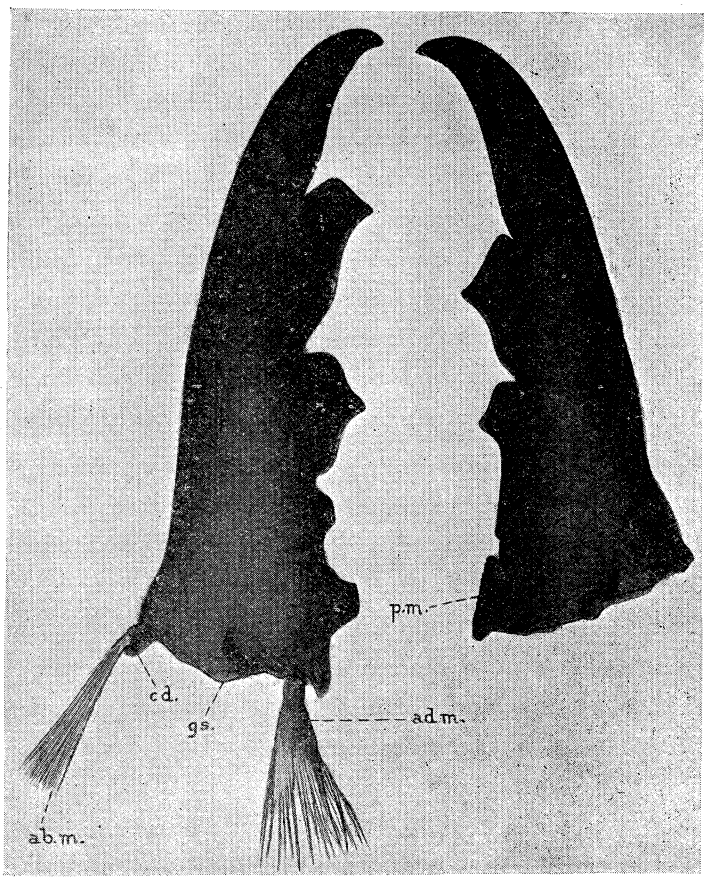
The *head capsule* is formed dorsally by the *epicranial plates*, and, except for a faint indication in some specimens, the median suture between the two is absent. Anteriorly, the epicranial plates are separated from the frons by a V-shaped suture, the two arms of the V being inclined at a very obtuse angle with one another. The *frons* is easily recognised by its much darker colour; along its anterior margin is carried the *clypeus*. The floor of the head is formed by the *mental plate* and, on either side of the latter, by the *genæ*. The genæ become confluent laterally with the epicranial plates, there being no sutures between them.

The *eyes* (*e.*, in fig. 1) are only partially visible from the dorsal aspect, and take the form of an oval area on either side. They are placed a short distance behind the bases of the antennæ, and measure 0·5 mm. × 0·2 mm., with their long axes situated at right angles to the plane of the surface of the head. They are much less developed than in the other castes, and their corneal surfaces exhibit no differentiation into separate facets. *Ocelli* are absent.

The *antennæ* (fig. 28) measure, on an average, 6 mm. in length, and are composed of 22–27 joints, a very frequent number being 26. The antennal socket is large, and the dorsal margin thereof is produced outwards into a prominent projecting ridge, which conceals the point of insertion of the antenna when viewed from above. This ridge is provided with a backwardly directed extension, which terminates just anterior to the eye of its side. The basal joint of the antenna is the largest, being of much greater diameter than any of the succeeding joints. The third and fourth joints are the shortest, and the first four joints are mutually related in length in the proportion of 9 : 5 : 2 : 3. The remaining joints are subequal: they are somewhat hairy, the longest hairs being arranged in a whorl near the apex of each joint.

The *labrum* (fig. 12) is nearly as broad as it is long, averaging 1 mm. × 0·9 mm. Its anterior border is prominently rounded and provided with a row of setæ; there are also a few scattered bristles over its dorsal surface. It projects prominently forwards, overlapping the bases of the mandibles (fig. 1), and is movable in the vertical plane, articulating with the anterior portion of the clypeus. The cuticle investing its oral surface is covered with very minute closely set "papillæ." A group of hairs arises on either side near the hinder border of the labrum. Each group is prolonged backwards in the form of a longitudinal area, passing over the oral surface of the clypeus to the pharynx. The hairs are possibly gustatory in function.

The *clypeus* (fig. 12) is a transverse membranous sclerite situated just behind the labrum. It appears to correspond with the ante-clypeus of the Embiidæ (IMMS, 1913, p. 169, Plate 38, fig. 8) and other insects. No definite post-clypeus is noticeable, and, if one is present, it is fused up with the anterior region of the head capsule. The *mandibles* (text-fig. 2, and Plate 3, fig. 1) measure 4 mm. in length and 1·5 mm.



TEXT-FIG. 2.—Right and left mandibles of the adult soldier. × 26; *cd.*, condyle; *gs.*, ginglymus; *ab.m.*, abductor muscle; *ad.m.*, adductor muscle; *p.m.*, pars molaris.

in diameter at the base. They are slightly curved downwards, and when closed the left mandible overlies the right in all of the 25 examples that were examined. Each jaw is incurved, pointed at its apex, and armed with two powerful teeth. The two jaws are not symmetrical, the left chiefly differing from the right in possessing a small additional tooth in front of the pars molaris (text-fig. 2). The *pars molaris* (*p.m.*) is present on both jaws, and the two combined form a pair of striated basal masticatory surfaces. The right is more prominently ridged and grooved than the left, and its surface is flat or very slightly convex; the left pars molaris is concave, and the combined effect of the two is to crush the food by means of a kind of pestle and mortar action, the right pars molaris acting like a pestle and the left functioning

as the mortar. Each mandible is hinged to the head capsule by means of—(1) A dorsal articular surface or *ginglymus* in the form of a cup-shaped cavity. This articulates with a strongly chitinised facet situated at the outer angle of the clypeus, at the point where the anterior arm of the tentorium unites with the head capsule, immediately anterior to the eye of its side. (2) A ventral articulation or *condyle* which fits into a cup-like cavity on the anterior border of the floor of the head, a little to the outside of the maxillary palp. The *adductor muscle* (text-fig. 2) is inserted ventrally by means of a large fan-like tendon into a sinus situated on the inner aspect of the mandible near the base of the pars molaris. The *abductor muscle* is inserted by a stout tendon into a small process situated at the external angle of the mandible.

The *first maxillæ* (fig. 11) each consist of a five-jointed palp, a membranous galea, and a more chitinised lacinia, together with the cardo and stipes. The *maxillary palp* (*mx.p.*) measures 3·4 mm. long and is elbowed between the third and fourth joints, with the result that the fourth and fifth joints are inclined inwards. The joints are mutually related in length in the proportion of 5 : 2 : 24 : 26 : 26. The *lacinia* (*la.*) terminates in two long strongly chitinised teeth, and along its inner edge is a row of small setæ. It lies beneath the *galea* (*ga.*) which is excavated for its partial reception when in repose. The *stipes* (*s.*) is a larger and broader sclerite than the *cardo* (*c.*), and is movably hinged on the latter. Each cardo articulates with the ventral surface of the head, in the angle where the mental plate becomes free from the genæ. The point of articulation is immediately in front of, and in close association with, the ventral arm of the tentorium. The first maxillæ lie in close association with the labium, and form with it the floor of the oral cavity. A *palpifer*, such as is present in *Termopsis angusticollis* (PACKARD, 1898, fig. 54) and other Termites, is not separately developed.

The *second maxillæ* or labium (fig. 14) consists of the following elements:—An elongate *mental plate* (*g.p.*) averaging 4 mm. in length and 1·3 mm. in breadth. This sclerite forms the whole of the mid-ventral region of the head, and terminates posteriorly at the occipital foramen. Laterally it unites with the genæ, and appears to represent the mentum and gula of other insects, which, in the case of *Archotermopsis*, are not separately demarcated from one another. A flexible membranous *palpiger* (*pgr.*) carries the labial palpi, and is clearly separated from the mental plate on the pharyngeal aspect, but not so on the ventral or external surface. The *labial palpi* (*l.p.*) measure 1·7 mm. long; they are three-jointed, and their joints are related to one another in length in the proportion of 1 : 8 : 6. Distally the palpiger carries the galea and lacinia. Each *galea* (*ga.*) is broader and very slightly shorter than the *lacinia* (*la.*), and both elements are marked off from the palpiger by definite sutures. The *hypopharynx* (fig. 15) is partially united with the pharyngeal surface of the labium. Its free distal portion is an oblong process measuring 1 mm. long and 0·35 mm. in width; and is closely covered dorsally with

fine hairs. It is strengthened laterally by a chitinised area (*sl.*) on either side, which is prolonged downwards on the ventral aspect towards its fellow of the opposide side. These two areas of chitin appear to be homologous with a pair of plates situated in a similar position and described by MANGAN (1908, p. 3, Plate 1, fig. 1, reference letter *z*) in *Periplaneta australasiæ*. He suggests that they may represent vestiges of *maxillulæ* (HANSEN) which have become fused with the tongue. Maxillulæ are present in many Apterygota, but so far have only been identified with any certainty in very few Pterygota. That the rudiments present in *Archotermopsis* and *Periplaneta* represent true maxillulæ, and not merely local chitinisations in the membrane covering the hypopharynx, is very probable. It is necessary, however, to examine a large number of the lower insects before the true significance of these plates can be definitely determined. Situated behind these areas on either side is a more strongly chitinised plate (*c.p.*), which gives off a stout dorsal arm extending transversely across the hypopharynx to nearly meet that of its counterpart in the mid-dorsal line; the body of the plate is provided with a number of stout setæ. Basally the hypopharynx is strengthened on either side by an ⌐-shaped rod (*b.r.*), whose proximal end serves for muscular attachment. The smaller arm of the rod is anterior and directed downwards, while the longer arm extends backwards, parallel with the long axis of the hypopharynx. A second rod ($b.r._2$) runs alongside and below the rod *b.r.*, and is loosely attached to the ventral extremity of the shorter arm of the latter. In the mid-ventral line the hypopharynx receives the opening of the common salivary duct.

iii. *The Cervical Region.*

The neck is enclosed in a flexible transparent membrane, strengthened by several chitinous plates or *cervical sclerites* (Plate 4, fig. 10). In the Orthoptera and certain Neuroptera these sclerites are seen in what appears to be their least modified condition, and consist of dorsal, ventral and lateral plates. In *Archotermopsis* the *dorsal cervical sclerites* are doubtfully represented by two minute chitinised spots, one on either side of the median line, and separated from each other by a broad interval. They lie beneath the projecting anterior margin of the prothorax and are not easily seen. The *lateral cervical sclerites* ($c.s._1$ and $c.s._2$) are two pairs of relatively large plates. They are convex on their ventral aspects, and hollowed internally, to give attachment to certain of the neck muscles, concerned with the movement of the head. The anterior pair ($c.s._1$) articulates by means of a forwardly directed process with the posterior margin of the mental plate. The posterior pair ($c.s._2$) articulates with the preceding pair in close association with one another in the mid-ventral line of the neck; along its hinder border each sclerite articulates with the *episternum* (*ep.*) of its side. Situated just behind the mental plate is a small *ventral cervical sclerite* (*v.c.s.*). The lateral sclerites appear to be clearly homologous

with those described by HUXLEY (1877, p. 403), and later by MIALL and DENNY (1886, p. 57) in *Periplaneta*. The ventral cervical sclerite corresponds with the anterior ventral sclerite of *Periplaneta*, there being no counterpart in *Archotermopsis* of the posterior ventral sclerite of the former insect.

iv. *The Thorax.*

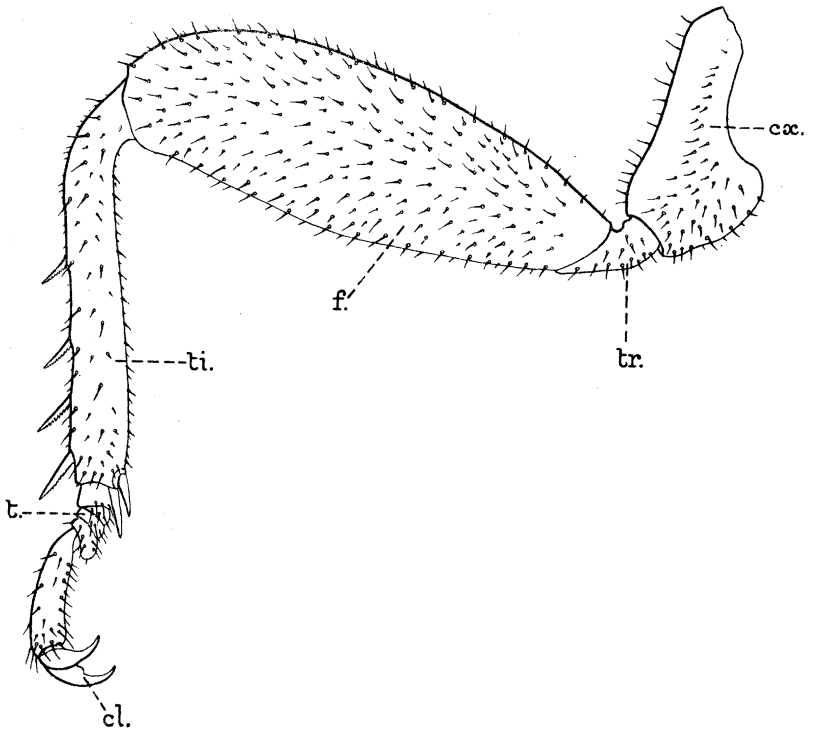
The thorax (fig. 1) averages 3·5–4 mm. in length, and its three segments are sub-equal in size. The tergal shield of the prothorax is more strongly chitinised than those of the succeeding segments, and it overlies that of the mesothorax to the extent of about one-fifth of the length of the latter. In a similar fashion the posterior borders of the meso- and metathorax overlie the segment immediately behind them.

The sternal region (*st.* in Plate 4, figs. 8 and 9) is membranous and but little chitinised; the limits of each sternum are consequently ill-defined and difficult to trace with accuracy. The anterior and middle pairs of legs are sub-equal, but the posterior pair is somewhat longer owing to the more elongate tibiæ. Associated with the legs are the undermentioned basal sclerites. (i) The *episternum* (*es.*), usually separated from the outer margin of the sternum by means of a lateral plate or sclerite. (ii) The *laterosternite* (*lpl.*) which is the side plate just referred to, and probably to be regarded as a dismembered portion of the sternum. (iii) The *epimeron* (*ep.*), which is associated as a rule with the dorsal border of the meron. (iv) The *trochantin* (*tn.*) which is subdivided into two elements by means of an oblique suture; its principal articulation is with the inner border of the episternum. (v) The *coxa*, separable into a true coxa or *coxa genuina* (*cx.*), which is marked off by means of a deep sulcus from a posterior element or *meron* (*m.*); the latter is wanting in many of the higher insecta.

In the first pair of legs (fig. 9), the episternum is modified to form a strongly chitinised band associated with the sternum at its inner or ventral extremity, and with the under surface of the pronotum at its dorsal or apical extremity. The epimeron is small and inconspicuous, while the meron cannot be distinguished as a separate element of the coxa. I have been unable to recognise any traces of laterosternites in the prothorax. In the two succeeding pairs of legs (fig. 8), the episterna are much less chitinised and more intimately related with their corresponding limbs. The epimera are very large, sub-triangular in form, and, curving upwards and outwards, project dorsally on either side of the tergal shields of their respective segments (figs. 1 and 8). That these elements have no relation to wing vestiges, notwithstanding their appearance, is obvious from the fact that they are present on the prothoracic segment and are, moreover, recognisable in the winged forms also. The meron is a large and conspicuous component of the coxa, and has the appearance of being a flattened wing-like outgrowth of the latter. Placed between the sternum and episternum is a separate sclerite or laterosternite. The interpretation of the basal elements of the limbs is far from easy, especially owing to the lack of agreement

in the terminology utilised by morphologists. In this paper I have largely followed the nomenclature adopted by CRAMPTON in his recent articles on the thoracic sclerites of insects (1914, p. 56; 1915, p. 1).

Articulating with the coxa genuina is the *trochanter* (*tr.*). This, in its turn, carries the *femur* (*f.*), which is the stoutest element of the leg. The *tibiæ* (*ti.* in text-fig. 3)

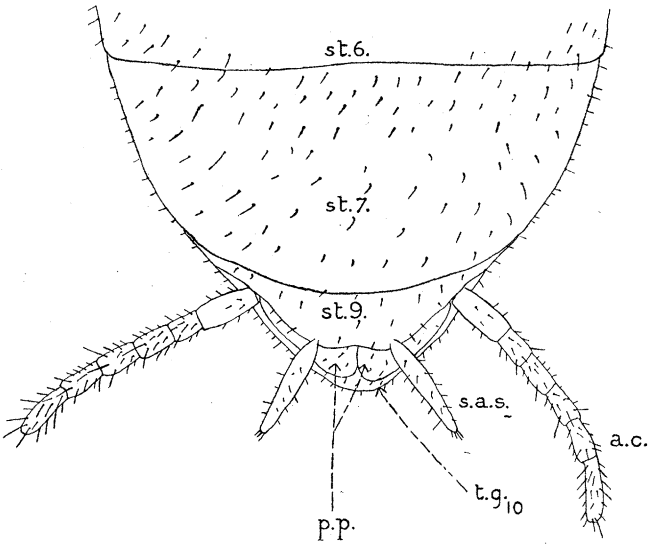


TEXT-FIG. 3.—Left fore leg of an adult soldier. × 30; *cx.*, coxa; *tr.*, trochanter; *f.*, femur; *ti.*, tibia; *t.*, tarsus; *cl.*, claws.

are slender but are the most strongly chitinised portions of the limbs. Those of the fore legs are armed with from three to five prominent spines, disposed in a longitudinal row along its external border. There are, furthermore, three or four spines situated around the distal extremity of the tibia. In the middle pair of legs the tibiæ carry a variable number of 1–4 spines along the external border, and 4–6 spines along the inner border; there are also two or three spines at their distal extremity. The hind legs, as a rule, bear no spines along the outer border, but there are usually 4–6 present along their inner margin, and two apical spines. A feature of these spines is their extreme variability, even the legs of the same pair often differ in respect to the number of spines they carry. The *tarsi* are remarkable in that they are five-jointed, a feature only occurring elsewhere among living Termites in the genera *Mastotermes*, *Termopsis* and *Hodotermopsis*. In the adult soldier of *Archotermopsis* the second tarsal joint is retained in a reduced condition, and is visible on the inner aspect of the tarsus (text-fig. 3).

v. *The Abdomen.*

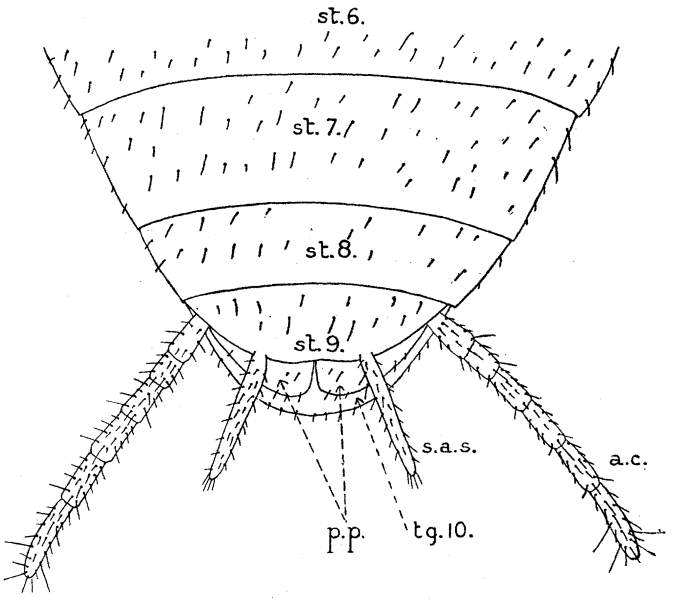
The abdomen is rather more elongate than is usual among Termites, it consists of 10 segments, and attains its greatest diameter in the region of the fourth and fifth segments (Plate 3, fig. 1). Viewed from the dorsal aspect, 10 terga are clearly visible; each tergum overlaps the one following it to about half the length of the latter. The tenth and apical tergum differs from those of the preceding segments in being triangular in shape, and rather more strongly chitinised. Beneath the tenth tergum, and not visible from the dorsal aspect, are a pair of *podical plates* (*p.p.* in text-figs. 4 and 5), which probably represent the divided sternum of the tenth segment.



TEXT-FIG. 4.—Ventral view of the apex of the abdomen of a female soldier, showing external sexual characters. × 20; *a.c.* anal cercus; *p.p.*, podical plates; *s.a.s.*, sub-anal styles; $st._6$–$st._9$, sixth to ninth abdominal sterna; $tg._{10}$, tenth tergum.

The first sternum is atrophied, and for this reason the first apparent sternum is morphologically the second. Each sternal plate overlaps its fellow behind in very much the same manner as happens in the case of tergal plates. In male soldiers the eighth sternum (or seventh apparent sternum) is small and transparent, and overlies the base of the ninth sternum. The latter carries the *sub-anal styles* on its posterior margin. These organs are unjointed structures measuring 0·8 mm. in length; they taper somewhat distally and are terminated by a tuft of short setæ (*vide* text-figs. 4 and 5). Arising from beneath the tenth tergum are the *anal cerci* (*a.c.*), which are movable appendages measuring 1·7–2 mm. in length and composed of six or, in some instances, seven joints. These are related to one another in length in the proportion of 13 : 6 : 7 : 9 : 8 : 12, the first and terminal joints thus being the longest. In some specimens the first joint exhibits a division into two separate elements, the cerci then being seven-jointed. Female soldiers (text-fig. 4) differ in possessing only eight

apparent sterna. This is due to the fact that the seventh sternum is very large and entirely overlies the eighth sternum, which is small and membranous. Sub-anal styles are present as in the male soldiers, and are carried similarly by the ninth sternum; the cerci do not exhibit any sexual differences. Adopting, with some modification, the method of BERLESE (1909, p. 275), the abdominal segments in the



TEXT-FIG. 5.—Ventral view of the apex of the abdomen of a male soldier, showing external sexual characters. × 20. Lettering as in preceding figure.

soldier may be expressed as follows; the upper numerals representing the terga and the lower the sterna :—

$$\text{♂}\quad \frac{\text{I–II–III–IV–V–VI–VII–VIII–IX –X}}{\text{(I)–II–III–IV–V–VI–VII–VIII–IX}_{\text{S}}\text{–X}_{\text{C}}},$$

$$\text{♀}\quad \frac{\text{I –II–III–IV–V–VI–VII– VIII – IX –X}}{\text{(I)–II–III–IV–V–VI–VII–(VIII)–(IX)}_{\text{S}}\text{–X}_{\text{C}}}.$$

The brackets indicate the atrophy or reduction of a shield and the letters S and C signify the segments bearing the sub-anal styles and cerci respectively.

vi. *Size.*

The soldiers exhibit considerable variation in size among themselves, and measure from the tips of the jaws to the apex of the tenth abdominal segment, 16–21 mm. They rank, therefore, among the largest of Termite soldiers.

The following measurements were made from three typical specimens, the maximum length and breadth in each instance being given.

	Specimen 1.	Specimen 2.	Specimen 3.
	mm.	mm.	mm.
Length of mandible	3·25	3·5	4·5
Length of head	3·75	4·5	5
Breadth of head	3·5	4	4
Length of thorax	3·5	3·5	4
Breadth of prothorax	2	2·5	3
Length of abdomen	5·5	6	6
Breadth of abdomen	2·75	3	3
Total length	16	17	19·5

5. *The Nymphal Stages.*

The term nymph is an expression which is incapable of precise definition. This is due to the fact that the only feature, in insects undergoing incomplete metamorphosis, which serves to distinguish the larva from the nymph is the wings, which are already present in larvæ of a definite age. It will thus be evident that no hard and fast criterion can be adopted to distinguish between larvæ and nymphs. I have, therefore, followed Lespès, Hagen and Grassi in applying the term nymph to that stage in which wing rudiments are sufficiently in evidence to be readily distinguishable by the unaided eye.

i. *The First Nymph Stage.*—At this period the insect as a general rule attains a length of about 9·5 mm. or more, the antennæ are 23-jointed, and there is no external manifestation of the sex of the individual. The wing-rudiments take the form of flattened leaf-like outgrowths from the sides of the terga of their segments. The hind pair are in close contact with the upper surface of the abdomen, and the anterior pair lie immediately over them. They are entirely dorsal in position, and at no stage in their development do they assume the lateral and vertical arrangement described by Grassi and Sandias (1897, p. 265) in the nymphs of *Calotermes*. The anterior rudiments measure on an average 1·75 mm. in length and extend backwards to near the hind margin of the first abdominal tergum. The posterior wing rudiments reach to the corresponding border of the third tergum. The eyes are deeply pigmented and very conspicuous. They measure 0·4 mm. × 0·3 mm. and are to be distinguished from those of the larvæ by their greater breadth, and the presence of a shallow anterior concavity or sinus.

ii. *The Second Nymph Stage.*—In this stage (fig. 2) the insect has increased in its general size, there are 23 or more joints to the antennæ, and it has larger wing-rudiments. These latter structures are no longer thin and leaf-like and adpressed to the

abdomen, but have become greatly thickened owing to the contracted, though fully formed wings, exerting pressure from within. The anterior rudiments measure 2·5 mm. in length but, owing to an increasing growth of the thorax, they extend backwards only a little beyond the hind border of the metathorax. Similarly the posterior rudiments reach only to the hind border of the second abdominal tergum. The eyes have now become markedly reniform and measure 1 mm. in length and 0·5 mm. in greatest breadth. They are only very slightly smaller than those of the perfect insect. The cerci are fully formed, and the sub-anal styles are still present in both sexes. It is only after the final moult, to assume the perfect winged condition, that the sub-anal styles are no longer present in the female.

6. *The Female.*

Coloration.

Viewed from the dorsal aspect, the head, behind the transverse epicranial suture, and the prothorax, are orange-brown. In front of the epicranial suture, the head, and also the mandibles, are deep brown or almost black. The antennæ and remaining mouth-parts are light brown, the labrum and clypeus yellowish-white, and the eyes black and very conspicuous. The meso- and meta-thorax and the abdomen are pale yellow-brown or dark straw-coloured. In the mid-dorsal region a longitudinal line, not clearly visible to the naked eye, passes down the prothorax. In the meso- and meta-thorax this line is much thicker, dark brown and clearly visible to the unaided eye. The cerci are light brown and the legs straw-coloured, with the exception of the tibiæ, which are reddish-brown.

Beneath, the head is uniformly orange-brown, the thorax and abdomen dark straw-coloured.

The wings are hyaline; the veins, in relation to the anterior margin of both wings, are straw-coloured, the remaining veins being hyaline. In de-alated specimens the wing scales are brown.

The Head.

The *head* (Plate 3, fig. 3) differs from that of the soldier in its much smaller size, its rounded form, and the small size of the mandibles. It measures 2·75 mm. in length and 2·5 mm. in breadth; in front of the eyes it narrows considerably, and behind the eyes it is hemispherical in shape. Distributed over the surface of the head are a number of very minute scattered hairs. The *eyes* are very large, markedly reniform, and to a large extent visible from the dorsal side; the cornea is divided into hexagonal facets. *Ocelli* are absent. A faint *epicranial suture* is recognisable between the eyes, and in some specimens there is also an indistinct backwardly directed median suture. The *supra-antennal ridge* is less developed, and not so strongly chitinised as in the soldier. The *labrum* and *clypeus* do not differ in any essential details from those of the latter caste. The *antennæ* (fig. 18) average

5·5–6 mm. in length, and their most usual number of joints is 25. The first five joints are mutually related in length in the proportions of 10 : 5 : 2 : 3 : 3, while the remaining joints differ but little among themselves. Each joint is invested with a few fine scattered hairs, and most joints carry a whorl of longer hairs towards their apices. The *mandibles* (figs. 24 and 25) are scarcely visible dorsally, being hidden beneath the projecting labrum. They both measure 1·2 mm. in length, and, across the base, the right mandible measures 1 mm. and the left 1·3 mm. As in the soldier, the left mandible lies above the right one when in repose; its biting edge is armed with three large sub-equal teeth, followed by a smaller basal tooth between them and the *pars molaris*. The latter is a prominent basal projection, somewhat concave on its surface and faintly striated. The right mandible differs from the left in possessing only three teeth, of which the distal one is the longest; moreover, the *pars molaris* is more extensive, prominently convex, and more deeply striated. In each mandible the *ginglymus* (*gs.*) is the large dorsal articular cavity situated on the proximal margin of the jaw. In the left mandible it is placed at the inner angle, whereas in the right mandible it is situated about the middle of the posterior border. Lying nearly beneath the ginglymus, on the ventral aspect of each jaw, is a prominent sinus, into which is attached the strongly chitinised tendon of the *adductor muscle*.

The *first maxillæ* closely resemble those of the soldier, and do not call for any special comment; the only marked difference is their smaller size. The *hypopharynx* also agrees with that of the soldier.

The *labium* (*second maxillæ*) has a much shorter *mental plate* than in the soldier, a feature which is in conformity with the shortening of the head (Plate 6, fig. 27). From the tips of the laciniæ to the posterior margin of the mental plate, the labium measures about 2·2 mm., the length of the mental plate itself being 1·6 mm., and its breadth 0·8 mm. It will be remembered that in the soldier it attains a length of 4 mm. The *labial palpi* differ from those of the soldier in that the third joint is longer than the second, the three joints being related in length in the proportion of 5 : 9 : 13. In other respects the labium in the two cases is very similar.

The Cervical Region.

The *cervical sclerites* consist of the same elements as in the soldier, the only obvious difference being that the ventral sclerite in the female is slightly broader.

The Thorax.

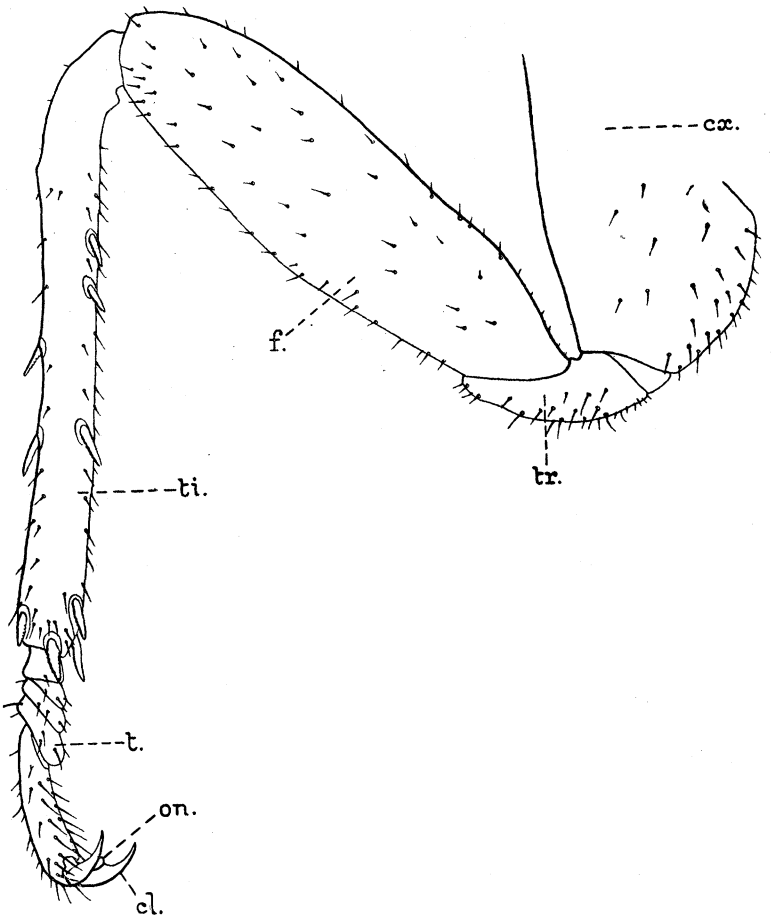
The *thorax* (Plate 3, fig. 3) measures 3–3·5 mm. in length; the *prothorax* is more strongly chitinised, and a little broader and rather shorter than the two succeeding segments. Unlike the condition in the soldier, the thoracic segments do not overlap one another to any marked degree. The sterna are more strongly chitinised than in the soldiers; the *prosternum* consists of two small triangular plates, which are

separated from one another in the median line, and in contact with the ventral extremities of the episterna. The *mesosternum* is the largest of the three sterna, and is an irregularly ◇-shaped shield. The conformity of the mesosternum results in the anterior and middle pairs of legs being more widely separated from one another than in the soldier. Articulating with its posterior angle is a minute rod-like *mesosternellum*. The *metasternum* is elongated in the transverse direction, and partially hidden from view by the bases of the middle pair of legs. A *metasternellum* is present, and similar to its counterpart in the preceding segment. The basal sclerites of the legs (fig. 13) consist of the same elements as in the soldier, though they differ in certain details. In the fore-legs, the *episternum* is similarly a strongly chitinised band articulating with the sternum at its ventral extremity, and with the under surface of the pronotum at its dorsal end. The *epimeron* exhibits no essential differences and, furthermore, no indications of a *meron* as a separate element of the *coxa* are to be observed. In the second pair of legs the *episternum* (*es.*) is very large, and reaches to the base of the wing; the *epimeron* (*em.*) exhibits a small rounded tubercle, the sole representation of the triangular upwardly directed process present in the soldier. The *trochantin* (*tr.*) is well developed and somewhat larger than in the soldier, and a *meron* (*m.*) is present, being marked off from the rest of the coxa by a deep suture. *Latero-sternites* (*lpl.*) are also present. In the third pair of legs the various joints differ but little from the preceding pair, the only marked difference being the total absence of any rudiment representing the upwardly directed process of the epimeron found in the soldier.

The *legs* (text-fig. 6) closely resemble those of the soldier, both in form and in the number and distribution of the tibial spines. In the fore-legs there are three or four spines along the external border of the tibia, and four distal spines around the apex of that joint. The middle pair of legs usually bear two tibial spines on the outer border, but in some specimens there is only one present, while in a few examples three were present. Four or five spines occur on the inner border, together with three terminal spines. The hind legs usually have no spines upon the outer margin, 4–6 along the inner margin, and two terminal spines. The legs of each pair seldom agree exactly in the number of their spines, thus demonstrating the variable nature of the latter. As in the soldier, the tarsi are 5-jointed, and the second joint is much reduced, and present only on the inner aspect of the tarsus. Between the claws a small *onychium* is present, a feature only found outside the Termopsinæ in *Mastotermes* among Termites.

The *wings* (Plate 5, figs. 16 and 17) attain 43–48 mm. in expanse from tip to tip. The fore wing (including the basal scale) measures 19·5–22 mm. in length and 6 mm. in greatest breadth; the hind wing is a little smaller, averaging 19–21 mm. in length and 6 mm. in breadth. The veins in association with the anterior margin of each wing (*e.g.*, the costal, sub-costal, and radial veins) are clearly visible to the unaided eye, but the remaining veins are hyaline and indistinct. Immediately after

the last ecdysis, when the adult state is just assumed, all the wing veins stand out with tolerable clearness the chitinisation of the anterior veins and the transparency of the remaining veins being assumed afterwards. It is in correlation with the weakness of flight, and the comparatively brief and slight use to which the wings are subjected, that the veins over the posterior two-thirds of each wing show indications of degeneration among Termites. As WOODWORTH remarks (1906, p. 106): "The peculiarity of the venation of the Termitidæ is in part dependent on



TEXT-FIG. 6.—Left middle leg of the female; *on.*, onychium. Other lettering as in fig. 3. × *circa* 32.

the extremely short period the wings are used—a structure that will wear well not being required—and in part on the manner of specialisation, whereby the posterior two-thirds practically become veinless; all the formative material is apparently appropriated by the primary and the veins adjacent to it." The veins of the two pairs of wings differ in certain features, and there is, furthermore, a large amount of variation in the venation among different specimens.

The terminology of the wing veins used in this paper is that advocated by COMSTOCK and NEEDHAM* (1898, p. 423), which is based on a study of their phylogenetic development.

* The primary vein of WOODWORTH is the equivalent of the radial vein of COMSTOCK and NEEDHAM.

In the fore wing, the roots of the principal veins lie within the area of the *basal scale* (fig. 17), and the latter is marked off from the remainder of the wing by the *basal suture* (*b.l.*) which, however, is frequently incomplete in that it does not always extend to the costal margin. The *costal vein** (*c.v.* in fig. 16) is coincident with the whole of the anterior margin of the wing to the apex. The *subcostal vein* (*s.c.*) runs for a short distance sub-parallel to the costal vein before uniting with it. The *radial vein* (r_1—r_3) consists of three main stems which arise closely together within the basal scale. The first stem (r_1) passes directly to the costa, joining the latter at about two-fifths the length of the wing from the base. With regard to this stem HOLMGREN remarks (1911, p. 36): "Radius, von der Basis aus einfach, teilt sich bald ausserhalb der Schuppe in zwei Äste, von denen der längere sich über das erste Drittel des Flügels erstreckt." From an examination of nine examples taken at random, I find that the first stem of the radial vein remained unbranched in five specimens, in one example it bifurcated at about half its length, and in the remaining three specimens it gave off a small branch towards the apex; it is, therefore, extremely variable.

The second and third stems of the radial vein (r_2 and r_3) arise from a common root, which is frequently known as the "radial sector." The second stem (r_2) usually passes directly to the costal margin without branching, joining it at about half the length of the wing from the base. As an occasional variation, however, it was found to bifurcate near the apex. The third stem (r_3) gives off about five branches along its anterior border, which passes outwards to the costa. The *median vein* (*m.v.*) is hyaline and slender, and arises near to the root of the cubital vein. It usually gives off three branches before reaching the outer margin of the wing. It is, however, extremely variable, examples with but a single branch being not uncommon. The *cubital vein* (*cub.*) divides at its apex into two branches; it further gives off ten or more simple branches which pass towards the posterior margin of the wing. A vestigial *anal area* (*a.a.* in fig. 17) is present and marked off from the rest of the wing by a faint *anal furrow* (*a.f.*). No trace of an *anal vein* is to be detected.

The hind wing differs from the fore wing in the following features of its venation: (1) The *sub-costal vein* runs for a longer course before uniting with the costal vein. (2) The *radial vein* consists of two stems only, the stem corresponding to r_1 in the fore wing being absent. (3) The *median vein* arises from the third stem of the radial vein, and usually has fewer branches. (4) A well defined vestige of an *anal vein* is present. (5) There is no basal suture.

The Abdomen.

The abdomen measures on an average 7 mm. in length, and is composed of ten segments (Plate 3, fig. 3) which are represented dorsally by ten overlapping tergal

* According to COMSTOCK (1918) no costal trachea is present in *Termopsis*, and it is, therefore, probable that a similar condition is present in case of *Archotermopsis*.

shields. Ventrally only seven sternal shields are evident, together with two podical plates. The first sternum is atrophied, and the seventh sternum is a greatly enlarged shield. The posterior margin of this plate is strongly arched, and almost completely overlies the membranous eighth and ninth sterna, the latter alone projecting very slightly from beneath it on either side (Plate 5, fig. 22, and text-fig. 4). The eighth sternum is much reduced but entire, not being divided as in almost all other Termites. The tenth sternum is probably represented by the pair of *podical plates* which lie one on either side of the anus. *Cerci* are present as in the soldier, and measure 1·3–1·4 mm. in length. They are composed of either seven or eight joints, there being some variation in this respect. The joints are mutually related in the proportion of 11 : 6 : 8 : 11 : 13 : 15 : 23, or as 5 : 5 : 6 : 9 : 10 : 13 : 14 : 21 in those instances where eight joints are present.

Sub-anal styles are wanting.

The abdominal segments may be schematically represented as follows :—

$$\frac{\text{I–II–III–IV–V–VI–VII– VIII – IX –X}}{\text{(I)–II–III–IV–V–VI–VII–(VIII)–(IX)–X}_{\text{C}}}.$$

Size.

Measurements were made of seven examples, and from the tip of the mandible to the apex of the abdomen, the length varied from between 12 and 13·75 mm.

	Specimen 1.	Specimen 2.
	mm.	mm.
Length of head and mandibles . . .	2·5	2·75
Breadth of head	2·4	2·5
Length of thorax	3	3·5
Breadth of prothorax	1·75	2
Length of abdomen	6·75	7·5
Breadth of abdomen	3	3
Total length	12·25	13·75

7. *The Winged Male.*

The foregoing description of the female applies equally well to the male, with the exception of the last three abdominal sterna (fig. 23), which alone exhibit external sexual differences. The three terminal segments of the abdomen are similar to the condition found in the male soldier, the eighth sternum (seventh apparent sternum) being small, and overlying partially the base of the ninth sternum. The latter narrows along its posterior margin, and arising therefrom are the *sub-anal styles*. The tenth sternum is probably represented by the podical plates, and in close association with them are the *anal cerci*. These latter organs agree closely with those of the female, and similarly may be either seven or eight-jointed.

The abdominal segments may be represented as follows :—

$$\frac{\text{I–II–III–IV–V–VI–VII–VIII–IX –X}}{\text{(I)–II–III–IV–V–VI–VII–VIII–IX}_S\text{–X}_C}.$$

8. *The Queen.*

The queen differs very little from the ordinary unfertilised winged female. Owing to her greater age, she is usually somewhat darker in colour, her wings have been lost, and only the scales or wing stumps remain, in the form of two pairs of small, dark brown, triangular appendages (fig. 7). The *anterior wing scales* in some examples are very small, measuring only half of the length of the mesothorax. In another specimen, however, they almost reached the hind margin of their segment. The *posterior wing scales* usually attain a length of half that of the segment bearing them. In length the queen generally exceeds that of the winged female, and measures on an average 15 mm. The abdomen is slightly more bulky, and attains a width of 4·5 mm. across its broadest region. The antennæ were imperfect in the queens which were examined, one or more of the terminal joints being missing. Heath (1903, p. 51) has recorded the same fact in *Termopsis*, and mentions that he has observed the mutilation actually taking place. In some instances the insect bites off joints of its own antennæ, and on other occasions its companions performed the operation on one another. The significance of this process is unknown.

In *Archotermopsis* the queen has hitherto remained undiscovered, and it is remarkable in exhibiting none of the specialisation or great size seen in the queens of the majority of Termites.

9. *The King.*

The king can be distinguished from the winged male by the absence of wings, only the wing scales remaining, and by being usually darker in colour, but no other external differences are evident.

10. *Worker-like Forms.*

The presence of workers in colonies of *Archotermopsis* has not so far been established. Desneux (1906, p. 294) mentions that they appear to be larval in shape, and later in the same paper he remarks (p. 297) that " A number of specimens similar in shape to the nymphs, 10–11 mm. long, with distinct scars at the posterior borders of the meso- and meta-notum, as if the wing buds had been broken there. These individuals are, perhaps, used as workers ; their head is a little larger than that of the nymphs."

Holmgren (1911, p. 37) mentions the existence of workers, but, in his later memoir (1913, p. 33), he refers to them as " Arbeiterähnliche Formen." During a tolerably intimate acquaintance with this species in India for nearly two years, I never came across any true workers, and no evidence is forthcoming proving that such a

caste exists. The only individuals which could be interpreted as belonging to that caste are worker-like forms (Plate 3, fig. 4), which agree in their characters with those referred to by HOLMGREN under the same name. During the month of May I found, on one occasion near Bhowali (Kumaon), about forty worker-like forms in one colony, but, on the other hand, I have found them absent in other colonies. To all appearances they resemble the nymphs, but differ therefrom in the absence of the characteristic wing-pads. Their heads are also very slightly larger, and usually rather more strongly chitinised. The mandibles, on the other hand, do not differ from those of the nymphs, and sub-anal styles are present in both sexes.

These worker-like forms are straw coloured, with the head and thorax darker than the abdomen, the depth of the coloration depending upon the age of the individual. The *antennæ* are, as a rule, 23-jointed. The *eyes* are pigmented, with a very slight indication of the reniform shape, and are in a stage of development similar to that found in the younger nymphs. The V-shaped *epicranial suture* is clearly marked, and a faint median line passes down the dorsal aspect of the three thoracic segments. Traces of curious irregular scars in the positions occupied by the wing rudiments are often present, but they are seldom developed on both sides of the thorax in the same individual (fig. 4). An examination was made of 20 individuals with special reference to these scars. Their occurrence was found to be extremely irregular, and in 12 examples they were totally wanting; in the remaining eight specimens they were distributed as follows. Their presence is indicated by × :—

		1.	2.	3.	4.	5.	6.	7.	8.
Mesothoracic scars	Right	×	×	×	×	—	×	—	×
	Left	×	—	×	—	×	×	×	—
Metathoracic scars	Right	—	—	×	—	×	—	—	—
	Left	×	—	×	—	—	—	—	—

Very possibly these scars are to be regarded as vestigial remains of the wing-pads of the nymph. They are also occasionally present in the soldier.

The *cerci* are 6–7-jointed; the tarsi and the tibial spines resemble those of the older larvæ or young nymphs. *Sub-anal styles* are present in both sexes, and the males and females can be clearly recognised by the condition of the seventh, eighth, and ninth abdominal sterna, as in the winged forms and soldiers.

When fully grown the worker-like forms vary in size from 12 to 14·5 mm.; the following measurements were made on a male and female, each with 23 joints to the antennæ :—

	Female	Male.
	mm.	mm.
Length of head to apex of labrum . . .	3·25	3
Maximum breadth of head	2·75	2·5
Length of thorax	3	3
Maximum breadth of thorax	2·6	2·3
Length of abdomen	7·5	7
Maximum breadth of abdomen . . .	2·8	2·5
Total length	13·75	13

Smaller individuals, 10–11·5 mm. in length, are also not infrequent, and are difficult to distinguish from ordinary larvæ.

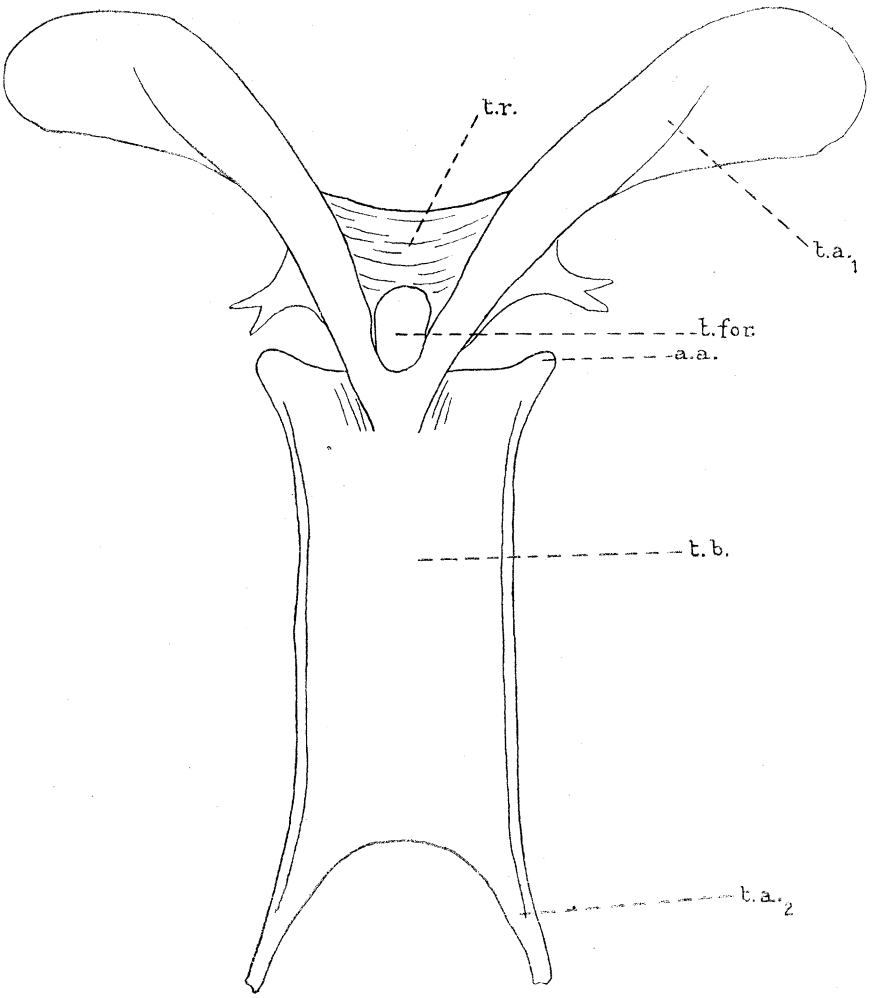
D. Internal Anatomy.

1. *The Body-Wall.*

The histology of the body-wall does not differ appreciably in the two castes, and the winged forms have been selected as exhibiting the typical condition. The *cuticle* (Plate 9, fig. 55) is divisible into two layers, the outermost being much thinner and more highly refractive than the remainder. On the general surface of the abdomen the cuticle has an average thickness of 0·003 mm., on the head capsule 0·007 mm., and on the dorsal aspect of the prothorax 0·011 mm. Its surface is for the most part smooth, except in the regions of the basal articulations of the legs and between the head and prothorax (c_1 in fig. 55). In these situations it is sculptured with small chitinous elevations or papillæ, many of which carry minute spines. Beneath the cuticle is the *hypodermis* (*h.*), which varies in thickness in different regions of the body. Its degree of development is in direct proportion to the thickness of the cuticle, and in the abdominal body-wall it is represented by a very thin layer of flattened cells. Typically the hypodermis is a protoplasmic layer containing frequent rounded or ovoid nuclei, cell boundaries not usually being evident. At those points where the muscles become inserted into the body-wall, especially in the head, the hypodermis totally alters in its character (fig. 55). The cells become extremely elongate, frequently resembling fibres, they are more openly spaced apart, and each cell is bounded by a definite and distinct membrane. The muscle fibres are attached to the *basement membrane* (*b.m.*), which everywhere bounds the inner or hæmocœlic surface of the hypodermis. At the point of muscular attachment, the basement membrane becomes slightly thickened and more deeply staining than elsewhere. The modification of the body-wall at the points of muscular insertion has been observed in various insects, notably by Berlese, in the case of the parasitic Hymenopteron *Monodontomerus* (1909, p. 471, fig. 520), and also by other histologists.

2. *The Tentorium.*

(a) *The Soldier.*—The tentorium or endoskeleton of the head (text-fig. 7) is a stout, well-developed framework of chitin. Its function is four-fold: (1) To give rigidity to the head; (2) to lend support to the brain; (3) to strengthen the points of articulation of the head with the ginglymus of the mandibles and the cardines of the first maxillæ; (4) to afford a basis of attachment for certain of the cephalic muscles.

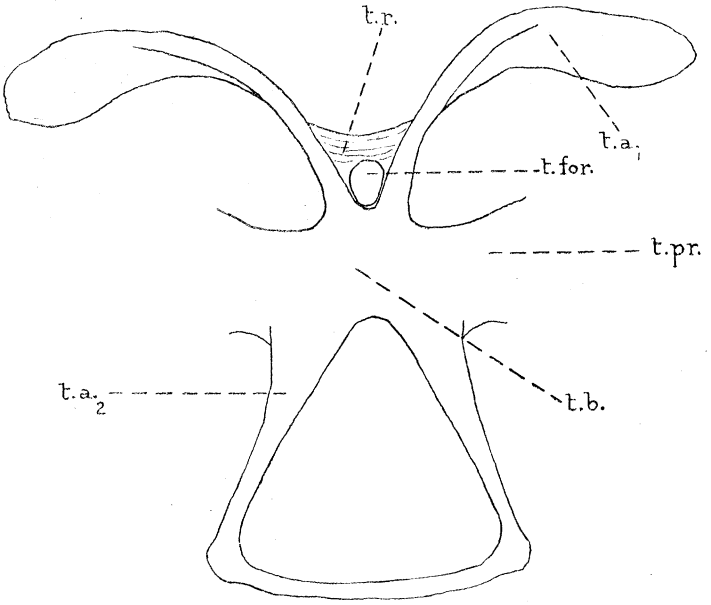


TEXT-FIG. 7.—Tentorium of the soldier seen from the dorsal aspect. × 31; *a.a.*, anterior angle (right); *t.a.*$_1$, right anterior arm; *t.a.*$_2$, right posterior arm; *t.r.*, transverse rod or bridge of tentorium; *t.b.*, body of tentorium; *t.for.*, foramen of tentorium.

The body of the tentorium (*t.b.*) is oblong in shape, measuring approximately 3 × 1 mm.; its sides are nearly parallel, and their edges are fused with the lateral margin of the mental plate. It is slightly arched upwards, forming, together with the floor of the head, a chitinous tunnel through which pass the nerve connectives uniting the sub-œsophageal ganglion with the pro-thoracic ganglion. Posteriorly,

the tentorium gives off a pair of backwardly-directed arms ($t.a._2$), which become confluent with the margin of the occipital foramen. The anterior arms of the tentorium ($t.a._1$) form the strongest and most powerfully chitinised portion of the structure. They are inclined towards one another at an obtuse angle forming a wide V ; at the apex of the latter they are firmly fused together, and also with the body of the tentorium. Each arm passes obliquely upwards and outwards, expanding at its apex until it becomes fused with the frontal margin of the head. The fusion commences close to the point where the head capsule presents an articular surface for the ginglymus of the mandible. The two arms are also bound together by means of a transverse bar (*t.b.*), which at the same time forms the anterior border of a prominent foramen (*t.for.*) through which pass the para-œsophageal connectives. The two anterior angles (*a.a.*) of the body of the tentorium are slightly produced as short thickened processes, which serve to strengthen the points of articulation of the cardines of the first maxillæ.

(b) *The Winged Forms.*—In the winged males and females the principal difference from that of the soldier is seen in the much shorter body of the tentorium (*t.b.*) in text-fig. 8. The anterior arms ($t.a._1$) are shorter and more slender than in the



TEXT-FIG. 8.—Tentorium of the winged form (female) seen from the dorsal aspect. × 31 ; *t.pr.*, transverse process of tentorium (right). Other lettering as in text-fig. 7.

soldier, and moreover, the posterior arms ($t.a._2$) are prolonged to become continuous with a complete thickened margin surrounding the whole of the occipital foramen. The anterior angles are not specially differentiated, but the sides of the body of the tentorium are laterally extended in the form of two thin plates (*t.pr.*), which become confluent with the head capsule on either side of the mental plate.

3. *The Digestive System.*

(i) *The Soldier* (Plate 6, figs. 30 and 31).

(a) *The Fore-Gut.*—The fore-gut is derived from the stomatodæum of the embryo, and is lined throughout by a chitinous membrane. It is divisible successively into an œsophagus or gullet, the crop, the gizzard, and the œsophageal valve. The *œsophagus* (*œs.*) is a straight narrow tube which passes beneath the supra-œsophageal ganglia to the hinder region of the head and thence into the thorax. In the mesothorax it increases in diameter, and becomes dilated to form an elongate *crop* (*cr.*). Lying along the sides of the hind portion of the œsophagus and the crop, and extending backwards into the meso-thorax, are the *salivary glands* (fig. 31). Each gland is accompanied by a *salivary reservoir* (*sal. res.*). The right and left salivary ducts extend forwards parallel with the œsophagus, and eventually join to form a common salivary duct, which opens in the mouth cavity on the ventral surface of the hypopharynx. Situated in the posterior portion of the metathorax, or in the beginning of the first abdominal segment, is the gizzard (*gz.*). This organ exhibits little or no outward indication of its presence, and is in reality a modification of the hinder extremity of the crop. Following the gizzard the fore-gut narrows again, and protrudes for a distance of 2·5–2·75 mm. into the cavity of the mid-gut, forming an elongate *œsophageal valve* (text-fig. 9).

(b) *The Mid-Gut.*—The mid-intestine (*m.g.*) commences in the second abdominal segment, and in its natural position completely encircles the hind-gut (fig. 30). It is a narrow tube with a uniform diameter of 0·5 mm. Behind the gizzard, and situated at the commencement of the mid-gut, are five *enteric cœca* (*ent. cœ.*). These are short finger-like diverticula, three of which are dorsal and two ventral in position. Out of 11 soldiers which were dissected, nine individuals possessed five cœca and two had four. Their size also varies somewhat, and occasionally, as seen in fig. 31, the two ventral cœca are longer than the dorsal.

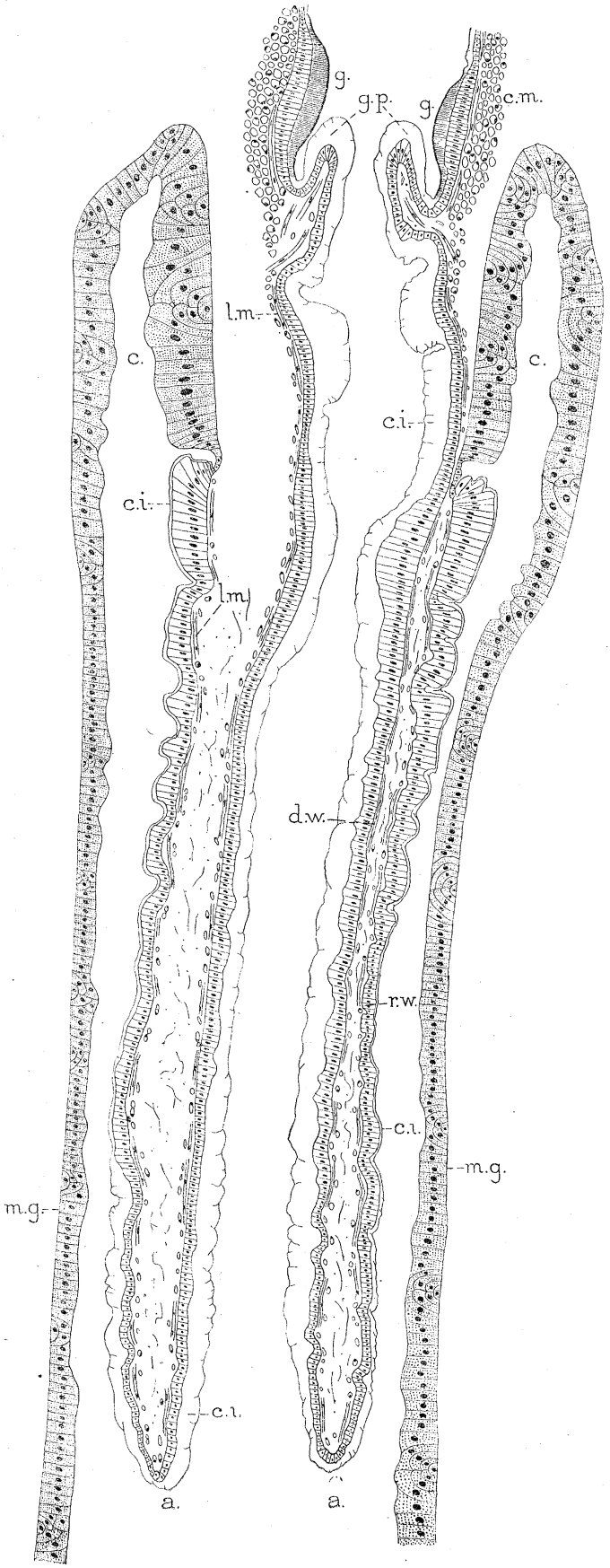
(c) *The Hind-Gut.*—This section of the alimentary canal is derived from the embryonic proctodæum, and like the fore-gut is lined throughout with chitin. It is divisible into four regions (fig. 31); the first region is extremely short, and receives the *Malpighian tubes* (*t.*). These latter organs are eight in number, arranged in pairs, evenly grouped around the gut in the form of a circlet. The second region of the hind-gut (*l.i.*) is the *large intestine*, which takes the form of a capacious sac filled with enormous numbers of Protozoa. It is markedly bent upon itself (fig. 30), the apex of the bend being situated in the first abdominal segment or in the hinder portion of the metathorax. The third region or colon (*co.*) is a short narrow tube, and is usually devoid of Protozoa. The terminal portion of the hind-gut (*r.*) is the *rectum*, which is an oval or globular sac when dilated with waste material; it opens to the exterior by means of the *anus*.

(d) *Histology of the Digestive System.*—The *œsophagus* consists of the following coats : a matrix layer (*m.l.* in fig. 37), in which the cell boundaries are either wanting or hard to distinguish. This layer is directly continuous with the hypodermis of the body-wall. Towards the cavity of the œsophagus it is thrown into a series of shallow folds, and small scattered nuclei are distributed in its cytoplasm. A layer of chitin (*c.i.*) lines the œsophagus, and closely follows the course of the folds in the matrix layer. Two distinct muscular coats are present—an inner one composed of longitudinal fibres (*l.m.f.*), and an outer coat of circular fibres (*c.m.f.*). In the anterior half of the head the muscle coats are much more strongly developed than in any other portion of the œsophagus. Between the muscles of these two layers, radial fibres pass outwards, to be attached to the walls of the head capsule and to the tentorium. A short distance behind the supra-œsophageal ganglia the wall of the œsophagus becomes noticeably thinner. The muscular coats are much less developed, and the radial muscles disappear entirely. The longitudinal muscles (*l.m.f.*) are situated in close apposition to the outer surface of the matrix layer. The circular muscles are less closely packed together, and are invested externally by a delicate peritoneal membrane (*p.m.*). In the commencement of the thoracic region the characters again change—the matrix layer becomes very much thinner, and is no longer thrown into folds. The longitudinal and circular muscles are only feebly developed, and with these histological characters the œsophagus passes into the *crop*. This is a thin-walled sac, usually filled with ligneous material, which shows through its translucent coats as a pale brown mass. Posteriorly, the walls of the crop increase in thickness—the matrix layer becomes deeper, and the muscular coats more pronounced, until the *gizzard* is reached. This organ is lined internally by a ring of 24 denticles, consisting of three kinds (figs. 34–36): (1) A circlet of six large denticles ($d._1$), 0·20 mm. long and 0·06 mm. wide ; the anterior portion of each is oblong, with a prominent tooth, or keel, projecting into the cavity of the gizzard. The posterior portion is pyriform, with the pointed end directed backwards. (2) A series of six intermediate denticles ($d._2$), shorter and broader than the previous series, but similarly provided with a median tooth or keel, though the pyriform posterior portion is absent. (3) A series of 12 narrow denticles ($d._3$), 0·15 mm. long and 0·04 mm. wide ; these are situated between the denticles of series 1 and 2, and are devoid of the median keel. The denticles are, morphologically, specially chitinised folds, and the matrix layer is reflected into them. The latter exhibit a definite cellular structure (*vide* text-fig. 9) ; the cells are columnar in form, with their nuclei packed together towards the outer aspect of the gizzard wall. The circular muscles are very strongly developed (*c.m.*), and are closely packed together, forming a close investment to the gizzard. Longitudinal muscles (*l.m.*), on the contrary, are very few and inconspicuous.

Placed immediately behind the gizzard is a ring of six ovoid cushions or pads (fig. 36), each measuring 0·19 × 0·17 mm. These structures project into the cavity of

the gut, and in transverse section appear as six prominent folds. The anterior half of each cushion is invested with imbricated, chitinous, scale-like papillæ, each carrying from one to three backwardly directed spines at its apex (fig. 34). Further backwards these scales pass, by gradual transition, into bristle-like hairs. Just in front of the denticles of the gizzard, the cuticular lining of the crop is provided with a zone of minute semi-lunar papillæ, finely dentate along their free margin (fig. 35). Behind and between the cushions just referred to is a zone of very similar cuticular papillæ, but with the dentations along their margin fewer and somewhat coarser. The gizzard and the cushions together form a mechanism for crushing and straining the food, only the smaller wood-particles gaining admission into the mid-gut. The whole structure appears to be physiologically very similar to the gastric mill and pyloric strainer of the Crayfish. Behind the gizzard the fore-gut is pushed far into the cavity of the mesenteron, forming, with the walls of the latter, an elongate *œsophageal valve* (text-fig. 9). In this region the matrix layer is composed of columnar cells for the greater part of its course, and is thrown into a series of well-defined folds, lined internally with a very deep, though soft and membranous, layer of chitin. Both longitudinal and circular muscles are present in the walls of the valve, though the former are most in evidence. At the apex of the valve, in the cavity of the mid-gut, the wall is reflected back upon itself, and carried forwards so as to almost reach the posterior border of the gizzard. This reflected layer is similarly composed of columnar epithelium, but the chitinous lining is very thin and delicate. At the junction of the fore-gut and mid-gut the transition is abrupt and sharply marked (text-fig. 9), and the chitinous intima disappears completely. Between the descending wall (*d.w.* in text-fig. 9) of the œsophageal valve, and its reflected layer (*r.w.*), muscle fibres, fine tracheæ, and connective tissue are enclosed. The outer wall, enclosing the œsophageal valve, is entirely formed of enteric epithelium, which does not differ in any essential features from that of the remainder of the mid-gut.

The walls of the *mid-gut* (fig. 33) are composed primarily of enteric epithelium, consisting of narrow columnar cells. The muscular coat is very delicate, and consists of an inner layer of circular fibres, with occasional anastomoses, and an external longitudinal layer. Both coats are composed of striated fibres; a connective-tissue membrane invests the outside and inside of the muscular layer, and is sometimes seen separated from the underlying epithelium. The characters of the cells of the enteric epithelium naturally vary according to their various phases of physiological activity. Usually, globules are to be seen in their cytoplasm, and, during the process of secretion, they accumulate in size and number, gradually causing the cell-membrane to bulge into the intestinal cavity (fig. 33). Eventually, these vesicles become constricted off by means of a narrow neck, until they are finally liberated into the lumen of the gut. In fixed preparations, cut into microtome sections, these globules are granular in appearance, and exhibit very little affinity for

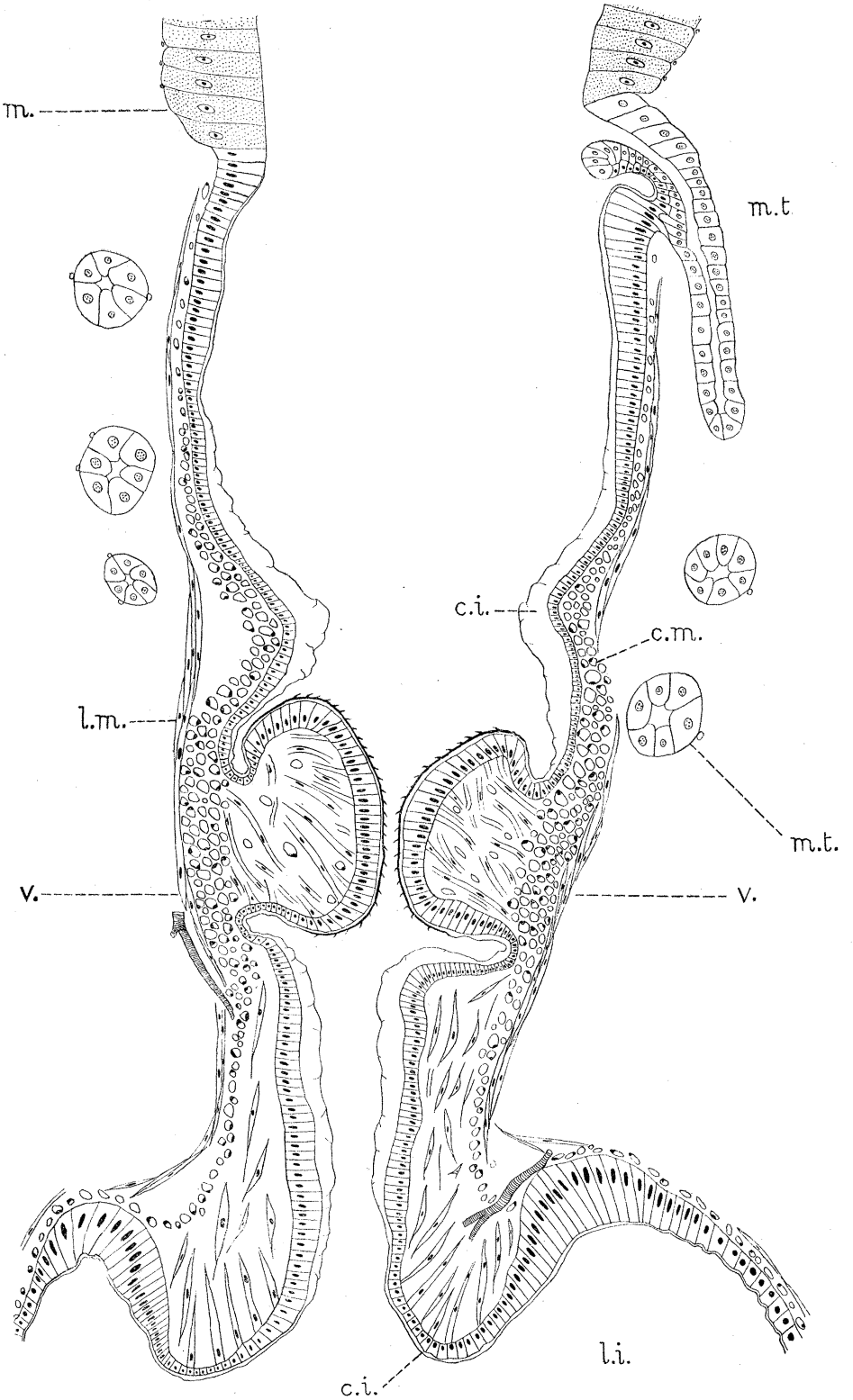


TEXT-FIG. 9. — Longitudinal section through the gizzard, œsophageal valve and two cœca of the mid-gut of the soldier. × 300. The cells of the ectodermal portion of the valve are left plain, those of the endodermal portion are dotted; *a.*, apex of œsophageal valve; *c.*, cavity of enteric cœcum; *c.i.*, chitinous lining; *c.m.*, circular muscle fibres; *d.w.*, descending wall of œsophageal valve; *g.*, teeth of gizzard; *g.p.*, pads or cushions of gizzard; *l.m.*, longitudinal muscle fibres; *m.g.*, wall of mid-gut; *r.w.*, reflected wall of œsophageal valve. (The cœcum on the left side is slightly displaced outwards, which occurred during the process of section cutting.)

ordinary staining reagents (Brazilin and various hæmatoxylin stains). In the resting phase (fig. 33), the surface of the mid-gut cells facing the central cavity is invested with a striated hem or platform (*s.h.*), as is usual among insects. The mid-gut epithelium is thrown into a series of closely packed folds, and, at the bottom of these folds, are "nests" of young cells, which are centres of regeneration. These cells actively divide, giving rise to growing daughter-cells, which eventually develop into ordinary epithelium, replacing those which become exhausted and are no longer functional. Numerous transitions in size are to be observed between the youngest cells of these "nests" and the fully formed epithelial cells, and there appears to be no doubt that they are centres of epithelial regeneration, and not of the nature of glandular crypts. The histology of the mid-gut closely resembles that of *Periplaneta*, described by MIALL and DENNY (1886, p. 121), and its epithelial layer is less deeply folded than that of *Leucotermes lucifugus*, as described by FEYTAUD (1912, p. 542, text-fig. 10).

The first portion of the *hind-gut* (text-fig. 10) is extremely short, attaining a length of only 0·9–1 mm. from the point of insertion of the Malpighian tubes to its début into the large intestine. Situated near the middle of its course is a group of three inwardly projecting folds. The chitinous lining is reflected over these folds and invested with fine backwardly directed spines (text-fig. 10). The folds are well supplied with muscle fibres, and function as a valve, which serves to open and close the passage between the mid-gut and the large intestine. At the junction with the large intestine it projects into the cavity of the latter in the form of a papilla, composed of four groups of deep columnar epithelial cells. The latter are very narrow and attenuated, and their nuclei form a closely compacted zone placed near the outer surface of the epithelium (nearest the muscular coat). The points of origin of the Malpighian tubes sharply demarcate the hind-gut from the mid-gut. The second region of the hind-gut is the *large intestine* (fig. 39), which is a greatly distended thin-walled sac. Internally it is lined with a delicate chitinous intima (*c.i.*), in direct continuity with the cuticle investing the outer surface of the body. The matrix, or cellular layer (*m.l.*), varies considerably in thickness in different individuals, and in some examples it is reduced to the condition of a thin membrane-like stratum. No definite cell boundaries are to be detected, its cellular nature only being evident by the presence of nuclei. The matrix layer rests externally on a basement membrane (*b.m.*), and outside the latter is a double muscular coat. The inner coat consists for the most part of circular muscle fibres (*c.m.f.*), but here and there longitudinal fibres (*l.m.f.*) interlace with the circular muscles, and in places rest directly upon the basement membrane. In these instances the circular muscles lie external to those of the longitudinal coat (fig. 39). The muscle layer is separated from the body space by a peritoneal membrane (*p.m.*).

The next region, or colon, is an extremely short tube of narrow calibre, measuring, on an average, only 0·48 to 0·52 mm. in length. Histologically it shares the



TEXT-FIG. 10.—Longitudinal section through the commencement of the hind intestine of the soldier. × *circa* 400. The cells of ectodermal origin are left plain, those derived from the endoderm are dotted; *c.i.*, chitinous lining; *c.m.*, circular muscle fibres; *l.i.*, large intestine; *l.m.*, longitudinal muscle fibres; *m.*, wall of mid-gut; *m.t.*, malpighian tube; *v.v.*, valve of hind gut.

characters of both the large intestine and the rectum. Its innermost lining is composed of slightly thicker chitin than that of the preceding region, and the matrix layer does not differ in any important features, the outer striated zone, which is characteristic of the rectum, not being in evidence. The muscle coats are strongly developed and resemble those of the rectum rather than the corresponding layers of large intestine. Physiologically they form a well developed valve situated between these two regions. Outwardly directed radial fibres arising from the chitinous layer are present, the circular muscles form a compact coat consisting of four to five layers, and external to these is a layer of longitudinal muscles.

The rectum (fig. 38) closely resembles in structure that of *Leucotermes lucifugus* described by FEYTAUD (1912, p. 551). The matrix layer (*m.l.*) is very thick, with large nuclei, for the most part elongate oval or pyriform in shape; cell boundaries are to be discerned with some difficulty, and its outer layer (*p.c.s.*) has a remarkable striated or fibrous appearance; externally it is invested by a basement membrane (*b.m.*). The chitinous inner lining (*c.i.*) varies in appearance in different individuals, the differences apparently being due to the length of time which has elapsed since ecdysis has taken place. In an example which had newly cast its chitinous cuticle and inner linings, this layer was relatively thin, having a thickness of less than one-tenth of that of the striated zone already referred to. In another specimen which had not recently undergone ecdysis this layer exceeded in thickness that of the striated zone as is seen in fig. 38. Both the matrix layer and the chitinous lining are thrown into a series of folds and sulci on the lumen side of the gut wall. A well-developed muscle coat is present, the inner layer being composed of circular fibres, and the outer layer arranged longitudinally. Between the muscle coats and the matrix layer there are frequently spaces occupied by numerous small tracheal branches and capillaries (*trh.*), the rectum being exceptionally well supplied in this respect. A small amount of connective tissue is also present. Groups of powerful radial muscles are very prominent and pass outwards to be attached to the neighbouring body-wall (fig. 62). When filled with waste material, the rectum is capable of a large amount of distension, which is due to the fact that, at definite locations, there are deep folds in its walls. The latter are much thinner and more flexible at these positions than elsewhere, and allow either for the rectum to be distended when full, or to remain in a flattened or collapsed condition, when empty. Around the anus the structure of the rectal wall undergoes alteration. The matrix layer becomes much thinner, the prominent striated zone is no longer in evidence, and only slight indications of foldings are present. Both radial and circular muscles are to be distinguished, the latter forming a definite sphincter ani.

(e) *Histology of the Organs Associated with the Digestive System.*—The *salivary glands* (fig. 31) consist of a variable number of lobules, each of which is composed of an aggregation of secretory cells which discharge their products into the duct of the lobule. The latter opens into the main salivary duct of its side; in some cases it

opens directly, while in others the ducts from several lobules unite, and the common duct thus formed conveys the secretion into the main salivary duct. The minute histology of the glands agrees very closely with HOFER'S account (1887) of the salivary glands of *Periplaneta orientalis*. The gland cells are for the most part very much vacuolated, the vacuoles being occupied by accumulations of salivary secretion. Certain of the cells contain an ovoid or pyriform capsule, each capsule being the intra-cellular terminal expansion of a ducteole. The glands are innervated by fine branches of the recurrent nerve (*r.n.* in fig. 32), which subdivide into delicate fibres distributed throughout the glands. The salivary reservoirs are elongate, thin-walled sacs composed of small flattened pavement cells, and lined internally with a very fine chitinous coat. In stained preparations the nuclei of these cells are evident in very large numbers, but the cell boundaries are not noticeable. Anteriorly, each reservoir is drawn out and continued forwards in the form of a duct. The two ducts combine in the head region to form the median common salivary duct. In a similar fashion, the two ducts from the glands combine to form a common channel, which opens into the main salivary duct, slightly anterior to the point of union of the two reservoir ducts. Both the ducts from the glands and the reservoirs are kept distended by means of spiral thickenings of their inner lining, closely resembling those of tracheæ. The two ducts of the salivary glands are of narrower calibre than those of the reservoirs, and are lined by cubical cells instead of pavement epithelium. They are clearly recognisable in sections owing to the greater thickness of their walls, and their more deeply staining properties. The median common salivary duct opens on to the ventral surface of the hypopharynx, just at the region where the integument of the latter becomes continuous with that investing the floor of the mouth cavity. Disposed around the aperture is a group of deeply staining cells which appear to be glandular in function.

The *enteric cæca* share the same general histological characters as the walls of the mid-gut and need no further description.

The Malpighian tubes.—These organs (Plate 7, fig. 40) are composed of a layer of relatively large polygonal excretory cells, averaging about eleven in number to a linear millimetre. In transverse section each tube has a diameter of approximately 0·06 mm., and from five to eight cells are visible simultaneously in such sections. The nuclei of the excretory cells are oval, and measure on an average 0·015 mm. long and 0·011 mm. in breadth. In the centre of each nucleus is a well marked clear area surrounded by a peripheral zone of deeply staining granules. Occasionally, as seen in fig. 40, bi-nucleate cells are observed very similar to those figured by BERLESE in the Malpighian tubes of the nymph of *Locusta viridissima* (1909, p. 788, fig. 975). On the side bordering upon the lumen of the tube, each excretory cell presents a kind of striated margin (*str.*) or " apparato cigliare " of Venesiani (1902), which is regarded as being composed of fine pore canals. A basal zone (*str.*) very similar in appearance, and also stated to be composed of canaliculi, is present along

the external margin of the cells and directed towards the hæmocœlic body cavity. This zone has been observed in the Malpighian tubes of several insects, but I have only been able to satisfy myself of its occurrence in *Archotermopsis* in one or two fortunate preparations. Each tube is bounded externally by a stout refractive tunic (*p.m.*), composed of a peritoneal coat overlying, and in close contact with, an inner and more delicate basement membrane. The Malpighian tubes are well supplied with fine tracheæ and tracheal capillaries, one or more of these vessels usually being evident in transverse sections (*t.c.* in fig. 40). The histological appearance of the tubes varies according to the state of physiological activity prevailing at the time of examination (when fresh tissues are used), or of killing and fixation. In the more active phases of excretion, the cells contain large numbers of highly refractive spheroidal excretory particles, which are unaffected optically by the action of staining reagents. In cells containing few, or none, of the excretory particles, the two striated zones are exhibited more clearly than during other phases of activity. Also the size of the lumen of a tube varies within very wide limits ; in some phases it is almost obliterated, the free margins of the excretory cells then being in contact with one another at one or more points. When excretion has been actively in progress, the cavity of the tubes is much larger and more evident than in the resting phases.

ii. *The Winged Sexual Forms.*

The digestive system in the winged males and females differs very little in its morphology from that of the soldier. In conformity with the smaller and more rounded shape of the head, the œsophagus is proportionately shorter than in the latter caste. The only other noticeable difference is seen in the large intestine which is, as a rule, less voluminous than in the soldier. This feature is correlated with the occurrence of intestinal Protozoa in smaller numbers, or with their absence.

iii. *Worker-Like Forms.*

In worker-like individuals of both sexes the shortened œsophagus is noticeable as in the winged forms. The large intestine varies considerably in different individuals which were dissected. In most specimens Protozoa were present in large numbers, and this region of the alimentary canal was as greatly dilated as in the soldier, and had a similar sac-like appearance. In other examples the large intestine was somewhat less voluminous, and in these instances a markedly smaller number of Protozoa was present. Altogether seven worker-like specimens were dissected : all had well-developed gonads, the females containing several nearly full-sized eggs. They were obtained from one and the same colony which contained upwards of 30 of these forms.

iv. *The Larval Soldiers.*

In soldier larvæ, measuring 9 mm. long, the œsophagus is proportionately shorter in relation to the remainder of the gut, than in the fully grown members of this caste.

Intestinal Protozoa were present in abundance, and the large intestine was much dilated and sac-like in appearance.

4. *The Fat-body.*

(a) *The Soldier.*—In the soldier the fat-body consists of a single layer of lobules situated beneath the body wall. It bounds the general hæmocœlic body cavity, which is freely bathed in blood, but no extensions of the fat tissue penetrate between the general viscera. A layer of fat-body, however, closely invests each testis and a small amount is present in association with the ovaries. The lobules are relatively small, and very loosely compacted, giving the fat-body a fenestrated appearance in a surface view. Each lobule is much vacuolated and contains numerous small spherical or ovoid nuclei ; externally it is invested by a delicate membranous coat.

(b) *The Winged Sexual Forms.*—In the winged forms, the fat-body attains a much greater degree of development; in fully-grown individuals, just prior to swarming, it is seen to occupy the greater part of the body cavity. In the abdomen it closely envelops the digestive organs, nervous system and gonads, and its lobules are larger, fewer in number, and more closely compacted together. The extensive development of the fat-body in these forms results in a great reduction in the blood-containing space, and a consequent lessening of the volume of the blood. In the thorax there is no marked increase in the fat tissue present, and only a very small amount penetrates between the thoracic muscles. A thin layer is present on the floor of the head and a more extensive deposit occurs just behind the brain, above the œsophagus.

(c) *The Larvæ.*—Only the older larvæ were examined with reference to this tissue, and in these examples it attains the same extent of distribution as in the soldier, leaving a large central blood-containing space.

(*d*) *Worker-like Forms.*—In four worker-like forms which were dissected the fat-body was extensively developed, resembling the condition found in the winged forms.

5. *The Nervous System and Corpora Allata.*

(a) *The Soldier.*—The nervous system consists of the supra- and infra-œsophageal ganglia, together with a ventral nerve cord, consisting of three thoracic and six abdominal ganglia. A visceral or sympathetic system is also well developed.

The *supra-œsophageal ganglion* (fig. 43) is situated in the extreme anterior region of the head and measures 1·12 mm. transversely* and 0·6 mm. antero-posteriorly. The *protocerebron* is extremely well developed, which is remarkable considering the fact that the eyes are imperfect organs. The protocerebral lobes form the largest part of the brain and give off the optic nerves. The latter present an unusual feature

* In all cases the transverse measurement is the distance between the roots of the two optic nerves. The antero-posterior measurement is taken from the root of the antennary nerve to the hind margin of the optic lobe of the same side.

in that they divide into three branches each of which passes to the eye. The *deutocerebron* is placed just anterior to the protocerebron, and is formed very largely by the antennary lobes, the dorsal lobes not being evident as distinct regions. The antennary nerves do not present any special features. The *tritocerebron* comprises the two tritocerebral lobes which are situated far apart from one another, and united together by means of the *post-œsophageal commissure*. From each lobe there arises a composite nerve consisting of the fibres of the *labral nerve* (*l.n.*) innervating the labrum, and the *frontal nerve* which passes to the unpaired ganglion of the same name. Arising from the tritocerebron are the *para-œsophageal connectives* which are directed nearly vertically downwards.

The *infra-œsophageal ganglion* forms a pyriform mass and, beyond the fact that paired nerves arise therefrom, it exhibits no outward indications of a paired structure. The *para-œsophageal connectives* enter close together in the mid-dorsal line, and not far from the centre of the ganglia. The mandibular nerves are large and stout, and arise in close association with one another from the anterior border of the ganglia. Nerves of the first maxillæ and labium arise a little further posteriorly.

The *ventral nerve cord* does not call for any detailed description. The *thoracic ganglia* lie one in each segment of the thorax, and from each ganglion a pair of backwardly and outwardly directed nerves pass to the legs of their segment. The *abdominal ganglia* lie one in each of the first six segments. The sixth and last ganglion innervates the remaining segments, and also gives off nerves to the anal cerci and the genital organs.

The *sympathetic nervous system* consists of a *frontal ganglion* (*f.g.*) lying over the œsophagus, a short distance in front of the brain. It is connected with the *tritocerebron* by a paired *frontal nerve* (*f.n.*), and also gives off a fine anterior nerve which, so far as I have been able to trace, passes to the anterior portion of the œsophagus. Posteriorly, the frontal ganglion gives off a backwardly directed *recurrent nerve* (*r.n.*) which passes along the dorsal aspect of the fore-gut, beneath the brain, to terminate in a *stomachic* or *ventricular ganglion* over the hinder part of the œsophagus. Situated a little distance behind the brain is a pair of *œsophageal* or *post-cerebral ganglia* (*œs.g.*), innervating the aorta or anterior prolongation of the dorsal vessel. These ganglia, together with the nerves which connect them with the brain, form the paired sympathetic system. Just behind the œsophageal ganglia are a pair of whitish oval bodies—the *corpora allata* (*c.a.*)—which are in close relation with the sympathetic system. These organs are the *corpora incerta* of MEINERT and the *ganglia allata* of HEYMONS. They are placed slightly asymmetrically with reference to each other, the right corpus allatum often being situated a little in advance of the left. In many cases they have been regarded as a pair of posterior sympathetic ganglia, a view, however, which is now being abandoned. Histologically they differ from nervous tissue, and have rather the features of glandular organs. Each corpus allatum is just visible to the unaided eye. Viewed in longitudinal section, it is seen

to consist of a number of relatively large nuclei situated in a granular matrix of protoplasm, definite cell boundaries not being evident. Scattered through the matrix are vacuoles, and the whole organ is invested externally with a thin membranous tunic. The corpora allata are intimately associated with the œsophageal ganglia, and are innervated by nerve fibres derived therefrom. The only previous observer who has referred to these organs in the Termitidæ is HOLMGREN (1909, p. 206), who has described and figured them in the sexual forms of *Eutermes chaquimayensis*. He finds that they are much smaller in the young sexual forms than in the King and Queen, but, on the other hand, they undergo hypertrophy and degeneration as they increase in size. JANET (1899, p. 321) regards the corpora allata as being morphologically the reduced and modified representations of the mandibular furca, and remarks that: "Le mode de formation de ces corpora, par invagination et émigration d'un paquet de cellules hypodermiques, et la situation de la région où ils prennent naissance, region qui est peu éloignée de la bande nerveuse médiane et qui est située entre la mandibule et la maxille, me semblent venir à l'appui de cette interprétation. Il en est de même du fait, si intéressant, mis en évidence par HEYMONS, que, chez *Bacillus*, les cellules qui constituent ces organes conservent leur pouvoir chitinogène, et que, par conséquent, elles restent caractérisées par la plus importante des propriétés du tissu qui constitue les furca. S'il en est bien ainsi, c'est l'invagination, non apparante, qui fournit les corpora allata, qui représente l'invagination tentoriale mandibulaire que HEIDER a cherché, en vain, entre la mandibule et la maxille." This interpretation is not accepted by BERLESE (1909, p. 599), who regards these organs as being glandular in function with an internal secretion. NABERT (1913), who has recently made an extensive study of the corpora allata, in representatives of most orders of insects, holds a similar opinion.

In their method of development, and their histological structure, it appears probable that the corpora allata are to be regarded as modified ectodermal glands, which have lost communication with the exterior, and become ductless organs, secreting certain hormones into the blood. The fact that they are found in all orders of insects suggests that their presence is essential to the vital economy of those organisms.

(b) *The Winged Forms.*—In the winged forms the nervous system comprises a similar number of thoracic and abdominal ganglia as in the soldier. It differs from that caste in several respects, of which the following are the most important: (1) The general morphology of the brain and cerebral nerves; (2) the much shorter connectives uniting the infra-œsophageal ganglion with that of the prothorax; (3) the presence of nerves to the wing muscles.

The *brain* (Plate 7, fig. 44, and Plate 10, fig. 61) measures on an average 1·28 mm. transversely, and 0·72 mm. in the antero-posterior direction. As a rule, it attains slightly greater dimensions than that of the soldier; the optic lobes are somewhat larger and more prominent, and the optic nerves are extremely stout with a diameter of 0·27–0·32 mm. They pass directly to the eyes, and exhibit no indications of

subdivision such as is evident in the soldier. The *sympathetic nervous system* offers no essential points of difference from the condition found in the latter caste, and any further reference is consequently unnecessary. The *corpora allata* (figs. 44 and 61) are slightly more rounded than in the soldier, but exhibit similar relations with the aorta and œsophageal ganglia. They are usually placed slightly asymmetrically with reference to one another, the left frequently being situated somewhat in advance of the right. In two instances, however, these bodies were seen to be directly opposite one another.

(c) *Larval Forms.*—Two soldier larvæ, 4 mm. in length, were dissected, and the brain thereof had a transverse measurement of 0·8 mm., and 0·32 mm. in the antero-posterior direction. Two further larvæ of similar length, and ultimately destined to produce winged forms, were also dissected, but the brain did not offer any salient differences either in size or form from that of the soldier larvæ. In all four examples the ventral nerve cord consisted of a similar number of ganglia to the adults. In soldier larvæ 6 mm. long the brain measured $0{\cdot}8 \times 0{\cdot}48$ mm., and the optic nerves were divided distally into three branches as in the fully-grown examples of that caste. A soldier larvæ 9 mm. in length had a brain measuring $0{\cdot}9 \times 0{\cdot}48$ mm., but no larger examples were dissected.

(d) *The Nymph.*—In two nymphs in the first stage, 11·5 mm. in length, with thin leaf-like wing rudiments, the brain measured $0{\cdot}96 \times 0{\cdot}48$ mm. The optic nerves were markedly stouter than in the soldier larvæ of corresponding length, but they exhibited a definite division distally into three branches, all of which passed to the eye. The division took place further from the brain than occurs in the case of the soldier larvæ, and the branches were consequently shorter.

(e) *Worker-like Forms.*—In these examples the brain resembles that of the nymphs more closely than the soldier. In a fully-grown specimen the brain had a transverse measurement of 1·1 mm. and 0·56 mm. in the antero-posterior direction; the optic nerve divided into three short branches just before entering the eye.

6. *The Circulatory System.*

(a) *The Soldier.*—The *heart* in the soldier does not offer any special characters requiring detailed description. It is clearly visible in the living insect as a linear, translucent area passing down the mid-dorsal line, from the meso-thorax to the apex of the abdomen. The first definite chamber commences in the meso-thorax, and the remainder are placed one in each of the succeeding body segments. The heart terminates in a greatly reduced chamber lying just beneath the tergum of the tenth abdominal segment. Anteriorly, it is prolonged forwards from the meso-thorax as a long, narrow, muscular tube or *aorta*, which communicates with the cephalic blood-surface by means of a slightly expanded mouth situated immediately behind the brain. The aorta lies just above the œsophagus, and passes between the corpora allata and the paired sympathetic ganglia, from both of which it receives attach-

ments. The usual alary muscles are present in association with the heart, together with linear groups of pericardial cells. BUGNION (1911, p. 386, and Plate 2, fig. 8) has described and figured the heart in the worker of *Termes ceylonicus*, and it appears to differ from that of *Archotermopsis* in possessing only eight instead of 10 chambers in the abdominal region.

(b) *Winged Forms.*—I have been unable to detect any essential features in the heart of these forms wherein it differs from that of the soldier. The aorta, however, is relatively shorter in conformity with the smaller size of the head.

7. *The Reproductive System.*

(i) *The Male Organs.*

(a) *The Soldier.*—The male organs, like those of the female, are well developed, and exhibit no indications either of degeneration or arrestation of development. They are situated in the eighth and ninth abdominal segments, and the *genital aperture* is placed between the ninth and tenth sterna. External genital armature is totally wanting. The *testes* (Plate 9, fig. 54) each measure from 0·3 mm. to about 0·53 mm. in diameter, and consist of a variable number of short digitate lobes (usually about ten), which are the counterparts of the ovarioles in the female. A thin layer of fat-body partially covers each testis, and conceals its actual form to a large extent. The size of the testes varies according to the age and size of each individual soldier, and the lobes of each testis communicate with the terminal portion of the vas deferens of their side. The *vas deferens* (*v.d.* in fig. 54) is a short tube measuring 1 mm. or a little more in length, and has an average diameter of 0·04 mm.; where it joins the testis its calibre increases to some extent. The two vasa deferentia unite to open into the base, or common portion of the vesiculæ seminales, which is prolonged into a short muscular *ductus ejaculatorius*. This latter canal opens on to the exterior of the genital aperture already referred to. The *vesiculæ seminales* (*ves. sem.*) are paired organs, each consisting of a number of short tubes which are the homologues of the utriculi of the "mushroom-shaped gland" of *Periplaneta*.

Histologically, each testis lobe consists of a thin membranous coat lined at its apex by germinal epithelium, and in the lumen are the developing sex cells which have been derived from the latter. Seen in sections, the smaller lobes of the testis combine to form larger chambers which, in their turn, communicate with the terminal portion of the vas deferens. The latter is composed of a layer of epithelial cells invested externally with a thin stratum of muscle fibres. The vesiculæ seminales closely resemble the colleterial glands of the female, both in their general form and minute structure. Their tubules differ from the vas deferens in the epithelial wall, being thicker and more glandular. The nuclei are, for the most part, disposed at the periphery of the cells, and externally each tubule is provided with a stout layer of muscle fibres. The ductus ejaculatorius is a short canal lined with very deep columnar cells, outside of which is a strongly pronounced coat of muscle fibres.

Near the apex of each testis lobe are groups of spermatogonia, and a little lower down, one meets with compact masses of spermatocytes (primary and secondary) in various phases of nuclear division. At the bases of each lobe, spermatids are evident in large numbers; these cells are usually of rounded or slightly amœboid form. No mature spermatozoa were present in the vesiculæ seminales or vasa deferentia. Although I have not had the opportunity of following the process of spermatogenesis in any detail, an examination of thin sections, stained with iron-alum hæmatoxylin, failed to reveal any indications of degeneration associated therewith. I am, therefore, led to the conclusion, which is supported by other facts, that the testes of the soldier are functional organs.

(b) *The Winged Male.*—In the fully chitinised winged male, the reproductive system resembles that of the soldier so closely that any detailed description or figures appear to be unnecessary. The testes are much enveloped in fat-body, and are consequently rather difficult to detect; on an average each testis measures 0·48–0·5 mm. long and 0·32–0·4 mm. wide. The vas deferens is a slender duct varying in length from about 0·8 to 1·2 mm.; the vesiculæ seminales did not contain any spermatozoa, and form compact tubular glands measuring about $0{\cdot}7 \times 0{\cdot}6$ mm.

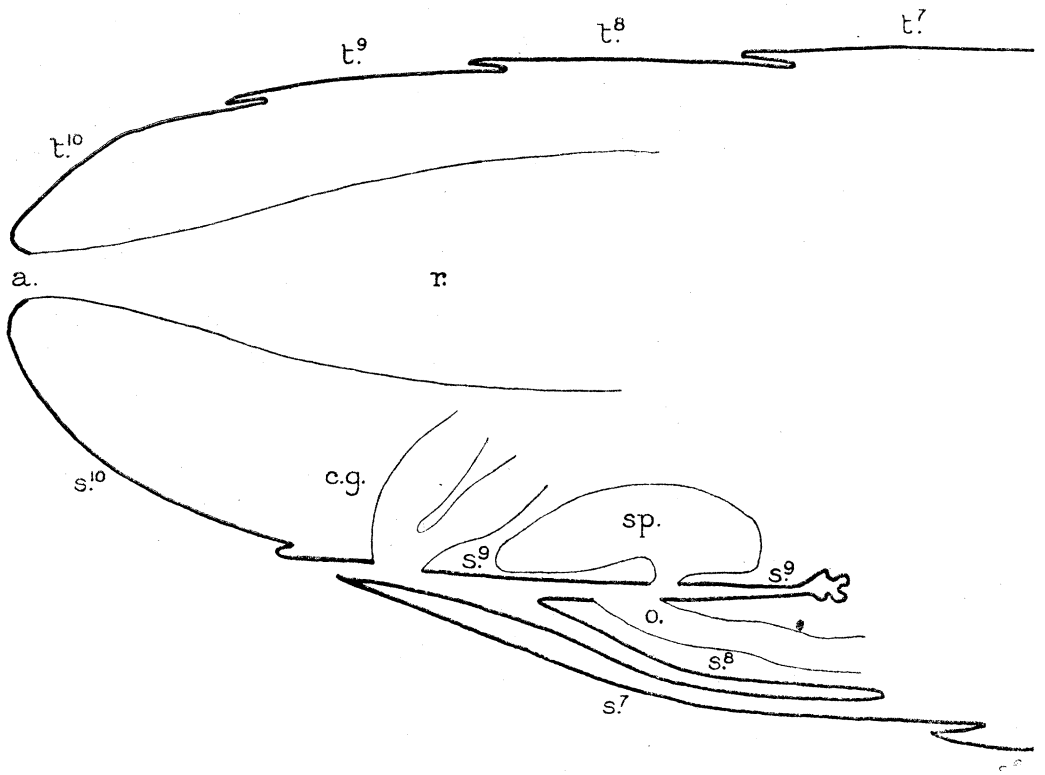
(c) *The Nymphs.*—The reproductive organs differ in no noticeable degree from those of the winged males.

(d) *Larvæ.*—Larvæ 8 mm. long pertaining to both winged forms and soldiers were dissected. The testes are markedly smaller than those of the adults, and both the vasa deferentia and the tubuli of the vesiculæ seminales are shorter. As in the case of the female genital system, the male organs similarly do not exhibit a more advanced development in the larvæ of the winged forms, than in those of soldiers of as nearly as possible the same age. In both castes the organs exhibit progressive development, and no indications of degeneration or arrestation of growth are present in the soldier larvæ.

(ii) *The Female Organs.*

(a) *The Soldier.*—The *ovaries* (fig. 46) each consist of a variable number of *ovarioles;* in five examples they varied from about 30 to 45. They overlie one another, and are closely packed together, which makes the exact determination of their number a matter of some difficulty. The ovaries extend forwards into the fifth abdominal segment; each is further prolonged into a *terminal filament* (*t.f.*), which eventually unites with its fellow of the opposite side. The median filament so formed extends anteriorly as a delicate thread, becoming lost among the fat-body of the second segment of the abdomen. Each ovary measures on an average 3 mm. in length to the base of the terminal filament, and 0·5 mm. in greatest breadth. The *oviducts* (*od.*) measure 0·9–1 mm. or more in length, and the two unite just before opening on the eighth sternum (text-fig. 11). In their histological structure the ovaries closely agree with those of the unfertilised female, and also with BRUNELLI'S

description of the ovary of *Termes lucifugus* (1905). They exhibit no indications of degeneration, and are in every respect perfect organs. In structure they belong to the simpler or panoistic type, in which special nutritive cells are absent, the yolk being elaborated within the ova themselves. At the apex of each ovariole (fig. 41) is a group of small undifferentiated germ cells (*gm.*), forming a *germarium*, and, as the length of the ovariole is traced backwards, the ova are seen in various stages of development. In the upper portion of the egg-tubes the young ova are seen with their nuclei exhibiting, what appear to be, mitotic division of their chromatin. In



TEXT-FIG. 11.—Diagrammatic reconstruction from serial sections taken through the apex of the abdomen of a female soldier, showing the relationship of the reproductive system to the abdominal sterna. *a.*, anus; *c.g.*, ducts of colleterial glands; *o.*, oviduct; *r.*, rectum; $s.6$-$s.9$, sixth to ninth sterna; $s.^{10}$, podical plate (10th sternum); *sp.*, spermatheca; t^7.-t^{10}., seventh to tenth terga.

this region the cells are disposed for the most part in a double series; their nuclei are large, measuring 0·007–01 mm. in diameter, and the cytoplasm contains a quantity of, what I believe to be, vitelline granules. These are markedly eosinophilous, staining bright red with methyl blue eosin. Similar granules have been described by BUGNION and POPOFF in the developing ova of the queen of *Termes horni* (1912, p. 226, fig. D), and he mentions that they stain violet-red with hæmalum-eosin. Further backwards the ova increase, in size, and are arranged in a single series within the ovarioles. In the posterior third of the latter, each egg lies within its own follicle, entirely surrounded by a definite *follicular epithelium*. A

typical follicle is seen in fig. 42, which represents a transverse section of an ovariole; measurements thereof were as follows :—

	mm.
Diameter of follicle	0·076
,, ovum	0·060
,, nucleus	0·038
,, nucleolus	0·007

In the basal portions of the ovarioles the follicular epithelium is no longer in evidence, and the ova are seen lying free. The latter are oval in shape, and the largest examples that were observed measured $0{\cdot}28 \times 0{\cdot}09$ mm.

Opening on the ninth sternum, a short distance behind the aperture of the oviducts, are the *colleterial* or *sebaceous glands* (Plate 9, fig. 53). Each gland consists of a rather complex group of convoluted tubuli, varying in diameter from 0·026 to 0·038 mm., and whitish in colour. They are situated in the body cavity beneath and at the sides of the rectum; they have occasional attachments to the latter, and also to the fat-body and Malphigian tubes. The tubuli of each gland converge and open into a very short tube of larger calibre, which, in its turn, unites with its fellow, to open into a main *common duct* (*m.c.d.*). This duct averages 0·5 mm. in length, and varies from 0·07 to 0·13 mm. in diameter, the greater diameter being nearest its opening on to the exterior. It is lined by very elongate and narrow *epithelial cells*, which appear in sections cut at various angles (Plate 8, fig. 50). Externally, these cells rest on a *basement membrane* (*b.m.*), while the lumen of the duct is lined by a *chitinous intima* (*c.i.*). On the outside of the basement membrane is a layer of *circular muscle fibres* (*c.m.*), which decreases in thickness, and disappears on approaching the points of origin of the tubuli of the glands. Histologically the latter closely resemble the duct in structure, in that they consist of elongate *epithelial cells* resting externally on a *basement membrane* (fig. 51). The lumen of each tubule is extremely small, and is bounded by a delicate *chitinous intima*. Muscle fibres, however, are entirely absent in the tubuli.

These glands are homologous with the colleterial glands of *Periplaneta*, and, in the latter genus, they secrete the substance out of which the egg capsule is formed (Miall and Denny, p. 170). From their size and completeness of development they are evidently, in *Archotermopsis*, important organs. They contained at the time of examination little or no secretion and, unless fertilisation takes place, their function apparently remains in abeyance.

Opening on the ninth sternum, in close proximity to the aperture of the oviduct, is the *spermatheca* (text-fig. 11 and Plate 9, fig. 53); this organ is folded upon itself, the bend being directed posteriorly. Histologically it consists of a layer of deep, narrow columnar cells with very elongate nuclei. Internally it is lined by a thin *chitinous intima* and, externally, the epithelial cells rest upon a *basement membrane*.

Outside the latter is a loose *muscular coat* which, however, is not continuous over the entire spermatheca (Plate 8, fig. 52).

The remarkable feature of the female reproductive organs of the soldier is their large size and the completeness of their development, there being but little difference from the condition present in the unfertilised winged female. MULLER (1873, p. 336) mentions that in *Calotermes canellæ* the reproductive organs in the soldiers similarly closely resemble those of the winged caste. The ovaries and colleterial glands, however, differ in being slightly smaller in size, and there is no spermatheca. In *C. nodulosus* and *C. rugosus* the ovaries are also well developed, but the spermatheca is likewise absent in both species.

In *Termes lucifugus*, according to LESPÈS (1856, pp. 240 and 244), the female organs in both workers and soldiers exhibit obvious signs of degeneration. In the workers he states that, under a high magnification, no trace of eggs were to be observed, only globules of "graisse liquide," often very voluminous. In the soldiers the ovaries are still less developed, and there are no associated organs.

In *Eutermes monoceros*, Koen., BUGNION (1909, pp. 276 and 278) states that he has been unable to discover any traces of sexual organs, either in the soldiers or the workers.

It is evident, from these remarks, that in the soldiers (and also the workers) of the higher Termites (*Termes* and *Eutermes*), the female reproductive organs are degenerate or wanting. Whereas in the more primitive forms (*Calotermes*) they are present in a well developed condition, attaining their least modified form in *Archotermopsis*. There is reason to believe, as is discussed on p. 142, that in the latter genus the soldiers are not infrequently fertile, and it is likely that all the individuals of that caste are potentially capable of reproduction. This feature would account for the unmodified condition in which these organs are found in *A. wroughtoni*. Unfortunately, we know nothing concerning the internal anatomy of the soldier in *Mastotermes*, but it is probable that the reproductive organs are present in a condition equally primitive to *Archotermopsis*.

(b) *The Winged Female.*—The reproductive organs of the winged female were examined in seven specimens, all of which had attained their full chitinisation, and were apparently ready to issue from the nest. In each instance the gonads were observed to closely resemble those of the adult soldier, both as regards size and histological characters (Plate 8, fig. 45). The spermatheca and colleterial glands presented a similarly close resemblance to their counterparts in that caste. Each ovary is composed of a variable number of ovarioles; in one case only 12 were present, but 22 and even more is a common number. In dimensions the ovary varied from 1·6 to 3 mm. long, and from 0·56 to about 0·6 mm. in maximum breadth. The oviduct is narrower and more contracted than in the queen and, measured from its point of union with its fellow of the opposite side, to the base of the lowest ovariole, it attains an average length of 0·8 mm. In breadth it measures from 0·11 to 0·19 mm.

At its apex the ovary is prolonged forwards as far as the terminal filament which joins that of its fellow in the second abdominal segment. The common thread thus formed becomes attached to the fat-body in the meso-thorax, where it appears to terminate. Follicular epithelium was present to all ova exceeding about $0{\cdot}6 \times 0{\cdot}8$ mm. in dimensions, and the size of the most mature follicles varied from 0·51 to 0·56 mm. in length, and from 0·17 to 0·24 mm. broad. They are thus larger than any found in the soldier, owing to the slightly more advanced development of the eggs.

(c) *The Queen.*—In the queen the most striking feature is the great size of the ovaries, which occupy the major portion of the dorsal half of the body cavity in the abdominal region. The ovarioles can be clearly seen through the tergal shields of the abdomen, and differ markedly from those of the winged unfertilised females in their much greater length. The oviducts are also much broader, thus allowing for the free passage of the eggs; the spermatheca is larger, and the colleterial glands are filled with a milky secretion which imparts to them a glistening white appearance.

(d) *The Nymphal Stages.*—Among eight first stage nymphs which were dissected, the ovaries (Plate 8, fig. 49) varied in length from 1·2 to 0·3 mm. This wide range of variation appears to be due, to some extent, to the age of the individual. The developing egg-cells, however, did not in any of these examples attain a greater size than $0{\cdot}2 \times 0{\cdot}07$ mm., and were thus smaller than the largest ova found either in the winged females or the soldiers. In the second stage nymphs, the gonads and egg-cells had attained slightly larger dimensions.

(e) *Worker-like Forms.*—Eleven worker-like females were dissected with special reference to the gonads. The latter (Plate 8, fig. 47) do not differ from those of the winged female, except that in several specimens they were considerably larger, owing probably to the fact that the individuals dissected were nearer sexual maturity than the latter. In length each ovary varied from 2·5 to 5 mm., the oviduct averaged 1 mm., and the number of ovarioles varied from about 32 to 48. Eggs attaining a length of 0·05 mm., and over, in most cases had their follicles evident; in several instances the longest eggs attained a measurement $1 \times 0{\cdot}48$ mm., thus exceeding in size any found in the winged females. I may add that these examples contained abundant intestinal Protozoa.

(f) *Larvæ.*—In the larvæ the gonads (fig. 48) are markedly smaller in size than in the adults. The tubuli of the colleterial glands are shorter, and the spermatheca is smaller and more difficult to detect. A good deal of variation in the size of the sexual organs was observed in larvæ of apparently nearly the same age. Furthermore, it was found that in larvæ of the winged forms, the reproductive organs do not exhibit a more advanced stage in development compared with those of the soldiers or worker-like forms. The following measurements were made on various larvæ all taken from the same colony.

Type of larva.	Length.	Length and breadth of ovary.	Length of oviduct.	Size of largest egg-cells.
	mm.	mm. mm.	mm.	mm. mm.
Soldier	8·5	1·2 × 0·22	0·83	0·05 × 0·04
„	8	0·7 × 0·2	0·37	0·04 × 0·03
„	6·5	0·72 × 0·2	0·8	0·05 × 0·04
Winged female	8	0·8 × 0·15	0·8	0·04 × 0·03
„ „	8	0·64 × 0·12	0·65	0·04 × 0·03

(iii.) *The Ova.*

The eggs of *Archotermopsis* are whitish in colour with a smooth glistening surface. They are laid in groups of from 10 to 25, each group placed in a small rounded chamber, which was gnawed out of the side of one of the galleries in the centre of the wood. The chambers are roughly circular in outline, and measure about 8–9 mm. in greatest diameter. The eggs are laid close to one another, but are not held together by means of any secretion. Each egg is ovoid in form, and averages 0·95 to 0·98 mm. in length and 0·45–0·5 mm. in diameter; the chorion is quite smooth, and when examined under a high power magnification, no sculpture or pattern is to be detected on its surface. The eggs laid by the worker-like forms are similar in form and size to those deposited by queens.

(iv.) *General Remarks on the Reproductive System.*

The most important deduction to be derived from a study of the reproductive system of *Archotermopsis* concerns the soldier caste. These organs show a gradual progressive development, from the condition seen in the young larvæ to that attained in the adult soldiers. Neither degeneration nor arrestation of development is to be detected at any period, and a study of the histology of both ovaries and testes lends strong support to their being *functional* organs in that caste. The gonads and the associated parts attain as large a size, and are as completely developed, as in the winged males and females prior to leaving their nest. It has already been pointed out that it is possible to select a series of species in which the gonads of the sterile castes exhibit progressive stages in reduction, until we reach the condition found in *Eutermes monoceros*, where they are apparently wanting altogether. This fact itself affords strong evidence in support of the conclusion that caste production is not in any way associated with the condition of the gonads.

E. Observations on the Biology of the Species.

So far as known this Termite is restricted in the distribution to the North-West Himalaya and Kashmir. I have found it at elevations ranging from 4000 to

9000 feet, and it may possibly occur a little below the lower elevation also. It selects the dead wood of *Pinus excelsa* and *P. longifolia* to serve for its food and habitation, and Mr. BEESON has recently discovered that it also utilises *Picea morinda*, *Abies pindrow*, and *Cedrus deodara*. It is not unlikely that *Cupressus torulosa* may also subserve this same function, but the insect has not so far been discovered to utilise the wood of that species of conifer. It attacks dead trees, stumps, and fallen trunks, selecting those in which the process of decay has already become evident (text-fig. 1). Although I have searched for *Archotermopsis* on a number of occasions, I have never found it in living or sound felled timber, and most probably the large amount of resin contained therein acts as a deterrant. Any structure which might be designated a termitarium or nest is absent, and the bulk of the members of a colony are to be found in irregular chambers situated in the decayed portions of a tree trunk. The wood is perforated in various directions by large galleries or tunnels. Certain of these passages pass outwards in a radial direction terminating just beneath the bark, if the latter be present. The majority, however, run in a longitudinal direction following the grain of the wood (text-fig. 12). The insect does not construct tunnels of cemented material on the surface of the tree trunk or the ground, as is the custom among a very large number of Termites. There is usually, therefore, no outward manifestation of its presence, which probably accounts for the insect having so long remained a rarity. When necessary, however, it closes up crevices by means of a cement of masticated ligneous material, or of excrementous matter held together by salivary secretion. The centre of a colony is occupied by the ova and very young larvæ, and in their immediate vicinity the queens and kings are to be found. I have, on several occasions, come across three or four queens associated with a single large colony of ova and larvæ, which probably represent several colonies which have become confluent. It is almost impossible to determine the limits of a colony, as a large tree trunk may contain 20 or 30 groups of ova and larvæ and several queens. Also, one colony may unite by numerous tunnels and galleries with another. These groups are surrounded by older larvæ and nymphs, while the soldiers are most numerous towards the periphery. Winged sexual forms remain near the centre of a colony until their wings attain their mature size, but are afterwards to be found in the tunnels leading to the exterior.

The food of this species consists of moist decaying wood, solid excretory matter ejected through the anus by their fellows, fluid diet afforded by the older larvæ, cast off exuviæ, and occasionally they devour dead members of their colony. I may add that these Termites will also imbibe drops of water, sprinkled near their tunnels, when in captivity. Larvæ 4 mm. long and upwards, the nymphs, and worker-like forms feed mainly on decaying wood and solid excretory material. The soldiers, owing probably to the form of their mandibles, appear to prefer the softest and most decaying portions of the wood. The unfertilised winged adults take much less food than the nymphs. The very young larvæ (under 4 mm. in length), and the kings

TEXT-FIG. 12.—Portion of a dead log of Deodar (*Cedrus deodara*) showing the galleries excavated by *Archotermopsis wroughtoni*, running parallel with the grain of the wood. The outer zone of the sap-wood is seen on the right-hand side, and new galleries are being extended into the undecayed wood on the left. (From a drawing lent by the Zoological Branch of the Forest Research Institute, Dehra Dun, India.)

and queens, are fed upon a fluid substance provided by the older larvæ and worker-like forms. Whether this is regurgitated from the mid-gut, or the product of the salivary glands, as is commonly believed, I am unable to say.

At times certain of the members of a colony exhibit convulsive movements. When in captivity these movements mostly occur after the individuals have been disturbed. The whole body undergoes a kind of quivering motion which is repeated at irregular intervals. They appear to serve as warning signals to their fellows, indicating alarm or danger.

The queens deposit their ova during a large part of the year, for young larvæ 3 mm. in length have been met with during the months of February and July. The medium sized larvæ of soldiers and winged forms are found in abundance during the month of February and, at that time, a few early nymphs may be met with, but I did not come across any specimens of the later nymphs or winged adults. During June and July late larvæ and nymphs occur in abundance, and also winged adults. Swarming appears to take place at irregular intervals during the monsoon season of June to August. The actual stimulus which causes the winged individuals of a densely populated colony to forsake the nest and enter the outer world is, I believe, a sufficiently high temperature together with a requisite degree of humidity. On one occasion I observed, near Bhowali (Kumaon), a swarm of winged individuals emerging from a log of *Pinus longifolia* during the hot weather season. This swarming took place about two weeks before the monsoon arrived, and in this respect was exceptional. It is noteworthy, however, that a heavy local rain shower of about half an hour's duration had just fallen. For a few hours the relative humidity of the atmosphere and superficial soil was very high. The winged individuals commenced to issue almost immediately after the rain had ceased, and I believe that there is no doubt that the swarming took place as a direct response to the sudden rise in humidity. I may add that I have observed similar "premature" swarming in a species of *Termes*, after local showers, both at Allahabad and Dehra Dun. Normal swarming of *Archotermopsis* was seen on two occasions during the monsoon season, the insects issuing from tree trunks, on the slopes of the hill sides, during the afternoon. The swarm on both occasions flew up the hill, the insects not alighting on the ground until they nearly attained the summit about 500 vertical feet distant. Some 30 individuals of one swarm were captured, and were found to consist of both males and females. Furthermore, I have reared in Cambridge a small swarm comprising individuals of both sexes. Four large colonies were also examined during the period of the year when swarming takes place. They contained a large number of fully developed winged forms of both sexes, males being in the majority. Snyder (1915, p. 72) observed in *Leucotermes flavipes* and *virginicus* individuals of both sexes swarming together, no evidence of separate swarming of the sexes being noted. His observations were conducted both on captive colonies and in the forest at Falls Church, U.S.A. Grassi and Sandias (1897, p. 278), state that in *Calotermes*

flavicollis the sexes swarm separately, the males invariably taking flight two or three hours later than the females. Those same authors also mention (p. 310 *et seq.*) that in *Leucotermes lucifugus* the sexes swarm separately. FEYTAUD (1912, p. 512), on the contrary, states that he has observed swarming in these species on numerous occasions, and that he found the swarms to consist of both males and females. FULLER (1915, p. 333), with reference to South African Termites, mentions that in two species many individuals have been observed to mate, and at once to seek shelter, within 6 or 8 feet of the spot from which they had just issued. He further adds that, at times, vast numbers of one or other species, or several kinds together, take to the wing simultaneously, over a great area of country, and it is on such occasions as these that sexes of different parentage meet.

The primary reasons for the occurrence of these swarms of winged Termites are, I believe, to ensure that the sexes may meet, and a sufficient number of individuals survive for the purpose of continuing the race, and that new colonies may not be founded in the immediate proximity of the parent colony. The mortality from birds, lizards, and other animals during the swarming is enormous, and the prodigality of winged Termites has its analogy in certain fishes, for instance, which produce vast numbers of eggs on account of the wholesale destruction which they suffer. It seems perfectly clear that in the above instances, at any rate, the phenomenon of swarming among Termites is not for the purpose of preventing inbreeding, as is often supposed.

It is noteworthy that, during the months of December to February, snow falls occur in the pine forest areas frequented by *Archotermopsis*. I have observed fallen tree trunks containing colonies of this Termite covered with some three inches of snow. On the other hand, in this same locality in June, the shade temperature not infrequently attains 90° F. The insect is consequently capable of withstanding a much wider range of temperature variation than is usually associated with such heat-loving forms as Termites.

Worker-like forms are of irregular occurrence—the majority of the colonies were without examples which could unhesitatingly be referred to that category. One colony near Bhowali (Kumaon Himalaya) contained, however, over forty specimens of these forms, and another contained about thirty. In both instances they were found during May and June, and possibly their appearance may, to some extent, be seasonal. The great development of the gonads in the examples dissected, and the fact that one worker-like form laid eggs in captivity, indicates that they are also gynæcoid forms. True neoteinic queens or kings were not found, although they are known to occur in *Termopsis angusticollis*. It is not unlikely that it may fall to future observers to discover them, but the possibility of the gynæcoid worker-like forms subserving the same function should not be overlooked.

F. Intestinal Protozoa, with Descriptions of New Species.

Living within the lumen of the posterior intestine of *Archotermopsis* is to be found an abundant Protozoan fauna. It occurs principally in the older larvæ, soldiers, nymphs, and worker-like individuals, less abundantly in the younger larvæ, and only occasionally and scantily in the winged reproductive forms. Whenever the Protozoa are present, evidence thereof can be detected by the fact that the contents of this portion of the digestive system appears brown to the unaided eye. The large intestine is greatly enlarged and distended (Plate 10, fig. 62), in order to harbour the truly enormous fauna which it contains. It is noteworthy that no special sac-like outgrowth of the gut is present for the reception of these organisms, such as is found among certain other Termitidæ. If a small drop of this brown, turbid contents of the intestine be transferred to a slide, and examined in normal saline solution under the microscope, a truly remarkable spectacle greets the eye. It is seen to consist almost entirely of vast numbers of actively moving Protozoa, only an insignificant quantity of ligneous or other material being present. The fauna is, on the whole, richest in numbers of species and individuals in the worker-like forms.

For the purpose of investigating these organisms, both fresh and stained preparations were utilised. Frequently, when examined in normal saline solution, their activities proved too vigorous to admit of detailed examination. This disadvantage was effectively overcome by first smearing the surface of the slide very thinly with egg albumen, similar to that used for fixing the organisms to the slide for purposes of staining. For making out details of cytological structure acetic methyl-green proved useful for certain features. The best results were obtained after fixation with hot Schaudinn's sublimate-alcohol, to which a trace of acetic acid had been added. Several other fixatives were utilised, but their effects proved less satisfactory. For purposes of staining Heidenhain's iron-alum hæmatoxylin was principally used, the objects being first heavily stained, and then gradually decolourised, until the required depth was attained.

The following species of Protozoa occur in *Archotermopsis wroughtoni* :

1. *Trichonympha* (*Holomastigotoides*) *pristina sp. nov.*

This species is the largest representative of the intestinal Protozoa occurring in *Archotermopsis*, and measures from 167μ to 280μ in length, and from 57μ to 144μ in breadth. It is present in great abundance in the hind intestine of the worker-like individuals, forming a very large proportion of the conspicuous brown contents of that portion of the digestive canal. It is also found in a similar situation in the larvæ and nymphs, but appears to be less common in the soldier, and rare in the winged sexual forms.

In its form and structure this species agrees extremely closely with the form A of *T. hertwigi*, Hartmann (1910, p. 345), mainly differing therefrom in being shorter

and broader, in the absence of any differentiation into ectosarc and endosarc, and in the simpler structure of the "cephalic organ." It is, in all respects, the most primitive member of the Trichonymphidæ yet discovered.

The organism is elongate-oval in general form, widening posteriorly (Plate 9, figs. 56 and 57). It is, however, somewhat plastic and constantly exhibits slight changes of form during life. At its anterior end is a collar of prominent, actively vibrating, flagella (fig. 57). The remainder of the body is uniformly covered with shorter structures apparently of the nature of cilia (?). The flagella forming the anterior collar move independently of the cilia investing the general body surface, and are often to be seen still in activity after the movements of the latter have ceased. The organism propels itself forward by means of an elegant gliding motion, nosing its way among the hosts of its confrères, and other Protozoa, which densely populate the field of the microscope. The protoplasm exhibits no demarcation into ectosarc and endosarc, and neither have I been able to detect any trace of a contractile vacuole. Over the anterior one-fourth to one-fifth of the body the protoplasm is clear and contains no ingested particles or granular inclusions (*c.z.* in fig. 56). In many specimens this clear zone exhibits faint longitudinal striæ, disposed at a distance of about 0·002 mm. apart. They are superficial in position and are probably cuticular in origin. As a general rule, the nucleus is situated at the junction of the clear and granular areas, but in some cases it is entirely enclosed within the latter. In the living organism it averages 0·019 mm. in diameter, and in its most usual condition, contains a dense skein of chromatin (fig. 56). During certain phases of life the chromatin fuses up into a dense compact amorphous mass devoid of any nuclear membrane. But, notwithstanding the fact that I have examined some hundreds of specimens, stained by various reagents, I have never observed the poly-energid nucleus, distributed into secondary nuclei scattered through the cytoplasm, as described and figured by HARTMANN (Plate 29, fig. 38) for *T. hertwigi*. In one or two specimens I have observed the nuclear membrane wanting over a portion of the circumference with a slight extrusion of the contained chromatin —a condition which closely resembles HARTMANN'S fig. 32. In a few specimens I have also noted the protoplasm of the anterior portion of the clear zone of the organism somewhat contracted, leaving a hyaline outer layer surrounding a denser inner mass, suggesting a differentiation into ectosarc and endosarc (*cp.* HARTMANN'S Plate 28, fig. 15). This appearance is so rare that it cannot be regarded as characteristic of this species and, for this reason, I believe it to be merely an artifact, due to the physical action of reagents. There is no trace of a micronucleus or cytostome, and I believe the method of feeding described by HARTMANN to be substantially correct. If a cell mouth be present, it can scarcely be situated very far forwards as claimed by KENT (1885), for I have never, on any occasion, observed any solid particles within the anterior zone of clear protoplasm.

At the extreme anterior end of the body is a remarkable structure termed by

HARTMANN the "Kopforgan," and it is from this region that the anterior collar of flagella takes its origin. It appears to consist of a minute cuticular cylinder, closed anteriorly by a cap. The contents of the cylinder exhibit very varied reactions to stains. When Heidenhain's iron-alum hæmatoxylin is the reagent employed sometimes the whole inner substance of the cylinder stains densely black. On rare occasions the apical part of the contents alone absorbs the stain, or the peripheral zone only becomes coloured. The inner stainable contents I am inclined to regard as a modified blepharoplast, and the outer enclosing cylinder as a mechanical structure, one of whose functions is to give rigidity to the anterior extremity of the organism. This latter function is evident when observing the living *Trichonympha* pushing its way among other organisms, with its anterior extremity never flattened, but always presenting a rigid apical point. The outer sheath, or "Glocke" of HARTMANN, appears to be completely absent in *T. pristina*.

2. *Trichomonas termitis sp. nov.*

This flagellate is extremely abundant in the soldiers, nymphs, and worker-like forms, and in the living state it varies from 30 μ to 88 μ in length (excluding the flagella), and from 13 μ to 57 μ in greatest breadth. From measurements made on 10 fixed and stained examples, the length varied between 30 μ and 83 μ, and the maximum breadth between 15 μ and 64 μ; averaged size specimens measured approximately 64 $\mu \times 38$ μ. The higher measurements refer to divisional forms. When in full activity the organism constantly changes its form; at times it is extended to the fullest degree, and a few seconds later it may be contracted into an ovoid or almost spherical object. The undulating membrane (*v.m.* in figs. 58–60) is in constant motion the whole time, and is thrown into a series of about 11 to 17 curves, with corresponding sinuses between them, which appears to be a much higher number than is figured for most species of *Trichomonas*. This very constant feature is also well exhibited in stained preparations (figs. 59 and 60). The movements of the membrane pass from the flagella end to the posterior extremity in an unceasing, rapid, series of ripples or undulations. Only two free flagella are present, and in this respect the present species differs from other members of the Polymastigina and, therefore, is only provisionally relegated to the genus *Trichomonas*. The two flagella are relatively stout and short and of equal length. A third flagellum is adherent along the outer edge of the undulating membrane, and in many living examples its extremity is prolonged posteriorly beyond the termination of that membrane (fig. 58). A cytostome (*cyt.*) is present and situated very far forwards. An axostyle (*ax.*) is likewise evident, but I have been unable to detect it in living specimens, except when it is partially extruded at the hinder end of the body; it is abruptly pointed and tolerably slender (fig. 58). The cytoplasm of the living animal is slightly granular, a few vacuoles are present, and there are

numerous ingested particles of various sizes, some attaining relatively considerable dimensions.

In fixed and stained preparations the most conspicuous feature is the thick chromatinic basal rod (*ch.l.* in figs. 59 and 60). It extends from near to the cytostome to the posterior end of the body, where it usually curves somewhat inwards. In large, well-developed examples this rod may attain a thickness of 0·002 mm. KOFOID and SWEZY, in their recent work on "Trichomonad Flagellates" (1915, p. 302, *et seq.*), regard this structure as being the homologue of the parabasal body of JANICKI (1911). In close association with the anterior extremity of the chromatinic basal rod is a well-defined blepharoplast (*bp.* in fig. 59); the flagella are intimately related thereto, and a rhizoplast* (*rh.*) may sometimes be seen passing from it to the nucleus. The latter structure (*n.* in fig. 59) is ovoid in form, enclosed by a definite membrane, and is usually seen with a central karyosome and several scattered granules of chromatin. A small number of chromidia are often to be observed between the nucleus and the anterior end of the chromatinic basal rod. The two free flagella are occasionally observable in stained preparations, and the marginal flagellum is deeply stained along its whole course of attachment to the undulating membrane. Its free posterior portion, however, does not appear to absorb staining reagents, and I have not been able to detect it after examining many hundreds of stained specimens.

Divisional forms are extremely abundant, and in some cases all the films made from an individual Termite contain such specimens in large numbers, and very few examples in the vegetative phase. In these instances it appears as if an epidemic of fission had set in and spread to most of the individuals. Binary fission alone was observed, multiple fission described by KOFOID and SWEZY (1915) not being seen. In typical instances of binary fission the chromatinic basal rod, the blepharoplast, flagella, and undulating membrane are all duplicated (*vide* fig. 60), while the nucleus appears to be the last to undergo complete division, though mitotic phases are already being passed through. Certain of the earlier phases of nuclear division are difficult to detect, owing to the presence of what KOFOID and SWEZY term the "intranuclear chromidial cloud." It fills the nucleus, and the latter appears uniformly deeply stained, and the stain is very difficult to remove by decolourising reagents. According to these authors the chromidial cloud has only previously been observed by BENSEN and by ALEXIEFF. It is not until the daughter nuclei have been formed that the fission of the body of the organism commences. The chromidia increase in number in the cytoplasm (*ch.g.* in fig. 60), and may extend along about half the length of the organism, following the course of the chromatinic basal rods. The behaviour of the axostyle during fission has not been followed in the present instance.

* This is best observed in slightly macerated examples, a feature also mentioned by KOFOID and SWEZEY (p. 301).

3. *Treponema termitis*, Leidy (emend. Dobell).

This species has been found by DOBELL (1910) in *Calotermes militaris* in Ceylon. A "Spirochæte," which I have provisionally referred to this same species, occurs in large numbers among the other micro-organisms which populate the large intestine of *Archotermopsis*.

In addition to the above organisms, at least two other forms of Protozoa were found in the hind intestine of the soldiers and worker-like forms. As my material of these was in some cases scanty, or the technique of fixation and staining less successful than with the other species, I shall content myself with brief descriptions only. A much more extended study than I have been able to devote is necessary before generic or specific determinations could be justified. Both forms are apparently quite new.

Species α.—This organism was found abundantly in all individuals of *Archotermopsis* containing other Protozoa. In length it measures from 27 μ to 39 μ, and from 2 μ to 3 μ in greatest breadth. When alive it is elongate fusiform, drawn out to a point at its two extremities. In virtue of its attenuated form the sides appear almost parallel for the greater portion of their length. Arising from the anterior extremity are two or more flagella, the number varying in different examples. In some specimens, two flagella, one much longer than the other, were observed; in others, three or often four flagella were noticeable. The surface of the organism is seen to be marked with several irregular longitudinal lines or striæ. When examined alive, in salt solution, the animal undergoes almost constant movement by means of its flagella; its body, however, remains stiff and rigid, and was never observed to bend or curve upon itself in any way. On many occasions, *Treponema termitis* was observed attached singly, or in groups, to one or other extremity of this species, sometimes giving the latter a tufted appearance. It is noteworthy that GRASSI and SANDIAS (1898, p. 51) mention what appears to be a *Treponema*, attached in a similar manner to *Dinenympha gracilis*.

When fixed and stained with iron-alum hæmatoxylin a prominent deeply staining sinuous line reveals itself. It varies in length, and may extend more than half-way down the organism. From its behaviour towards staining reagents it appears to be of chromatinic nature. The cytoplasm is clear, and contains no woody or other conspicuous injested particles, though one or more vacuoles may be present. I have been unable to discover a cytostome and, what appears to be the nucleus, takes the form of a small deeply staining spherical body, situated just behind the insertion of the flagella. In several preparations I have observed the latter directly attached to one or two very minute granules, which may possibly be of the nature of blepharoplasts. If this organism is a member of the Polymastigina it appears to be totally distinct from any other species yet described.

Species β.—This form occurred very sparingly, and for the most part in the intestine of worker-like individuals in company with *Trichonympha pristina*. It varies in length from 114 to 159 μ, and from 49 to 95 μ in maximum breadth. Usually it is broadly pyriform in shape, and is invested with long vibratile cilia which project beyond the extremity of the body. Anteriorly, there is a group of much longer cilia which exhibit a vigorous backward and forward lashing motion. These longer cilia arise from a well-marked peristomial groove. The cytoplasm is granular, and contains a number of non-contractile vacuoles and numerous ingested particles of ligneous matter. A single anteriorly placed nucleus was observed, and near the surface of the organism a number of oblique striæ take their origin, in close proximity to the peristomial groove. I have been unable to detect a micro-nucleus, and there does not seem to be very much doubt that this species is a flagellate and possibly a member of the Hypermastigina.*

G. Affinities.

In certain primitive features of its morphology *Archotermopsis* occupies a unique position among living Termites. These are : (*a*) the presence of 6–8 joints to the anal cerci ; (*b*) the relatively long sub-anal styles, which project beyond the apex of the abdomen ; and (*c*) the large size and reniform shape of the eyes in the sexual forms. In addition to these characters, there are also a number of other generalised features associated with *Archotermopsis*, which, although not peculiar to the genus, serve to emphasize its position near to the ancestral stock of the Isoptera. These are—

(1) The well marked external differentiation of the sexes in the soldier caste.

(2) The retention in each caste of an incomplete second joint on the inner aspect of the tarsi, making five joints in all.

(3) The presence of well-developed terminal and lateral spines to the tibiæ.

(4) The presence of definite pigmented vestigial eyes in the soldier caste.

(5) The greatly branched condition of the radial vein, the retention of a small rudiment of the anal area in anterior pair of wings, and a vestige of the anal vein in the posterior pair.

(6) The presence of apparently functional gonads in the soldier caste, exhibiting a degree of development similar to that found in corresponding organs of the sexual forms. Also, the absence of any histological features suggesting degeneration, or arrestation of development in those organs.

(7) The presence of cœcal outgrowths from the mid-gut, a feature common to the Blattidæ and other Orthoptera. (These organs have not hitherto been

* Since writing the above I have received a further supply of living Termites from India. Their Protozoa are now being studied in detail by Mr. D. W. Cutler, M.A.

discovered in any other Termitidæ, but may possibly occur in certain allied species.)

(8) The frequent presence of several royal forms, in one and the same colony, and the absence of any increase in size or other modification in the queen. Also the occurrence of worker-like forms, which are to be regarded as rudimentary members of the worker caste.

(9) The complete absence of anything in the nature of a true nest or termitarium.

Archotermopsis appears to be more closely related to fossil members of the genus *Termopsis* than to recent Termitidæ. These were described many years ago by HEER (1849, p. 23, Plates 2 and 3) from strata of tertiary date, and only winged forms were discovered. Judging from HEER'S descriptions, however, they do not appear to be sufficiently well preserved, apart from the neuration of the wings, to enable any detailed comparisons to be made. Living members of the genus *Termopsis* exhibit greater specialisation than *Archotermopsis*, and differ from the latter in the following among other characters.

(1) The more reduced condition of the eyes in the soldier caste.

(2) The presence of never more than four or five joints to the anal cerci and the short sub-anal styles.

(3) The rounded form of the eyes in the sexual forms.

(4) The weaker teeth to the mandibles in the soldier caste.

(5) The pronotum in the soldiers being straight instead of convex in front.

The soldiers in *Termopsis* probably similarly exhibit external sexual differentiation, but this feature has not so far been studied.

The only other genus of the Termopsinæ is *Hodotermopsis*, Holmg., from Tonkin and Japan. Any detailed comparison with this genus is scarcely possible, as the winged forms are at present unknown. According to HOLMGREN (1911, p. 38) the cerci in the soldier are 4–6 jointed, and lateral spines are absent from the tibiæ except in the hind pair of legs. HOZAWA (1915, pp. 14–17), on the other hand, states that the cerci in the soldier of *H. japonicus*, Holmg., are obscurely 3-jointed, and, in referring to the tibial spines, this writer makes no mention of their being confined to the hind pair of legs. *Hodotermopsis* is apparently the most specialised member of the sub-family, and more nearly related to *Termopsis* than to *Archotermopsis*.

Mastotermes darwiniensis, Frog., is the sole member of SILVESTRI'S family of the Mastotermitidæ. *Mastotermes* is remarkable in that it possesses a well developed anal lobe in the hind pair of wings, the tarsi have five complete joints, ocelli are present, and sub-anal styles occur in both sexes. These primitive characters are wanting in *Archotermopsis*. On the other hand, in the possession of 6–8-jointed cerci, longer sub-anal styles, and reniform eyes in the winged forms, the latter genus retains generalised features which are not found in *Mastotermes*. These two genera are to be regarded as divergent offshoots from the primitive Isopteran stock.

As further evidence of the primitive nature of *Archotermopsis*, it is noteworthy

that the only other member of the genus so far discovered is *A. tornquisti*, von ROSEN (1913, p. 300, Plate 29, fig. 18), which occurs as a fossil in Prussian amber.

III. GENERAL OBSERVATIONS ON THE ISOPTERA.

A. EXTERNAL SEXUAL DIFFERENTIATION IN THE SOLDIERS.

That the soldiers of Termites comprise individuals of both sexes was discovered by means of dissection by LESPÈS (1856) in *Termes*, and MÜLLER (1873) in *Calotermes*. It has been since confirmed from a study of longitudinal and transverse sections by GRASSI (1898).

External manifestation of the sexes, however, is only present in the soldiers of *Mastotermes* according to HOLMGREN (1911, pp. 32 and 33). He remarks (p. 33): "Unter den Soldaten besitzen die meisten Exemplare (3) einem männlichen Hinterleib mit normalen Sterniten, während ein Exemplar weiblich ist mit einem Hinterleib, der mit demjenigen eines weiblichen Arbeiters* vollständig übereinstimmt." HOLMGREN further adds that: "*Mastotermes* ist meines Wissens die einzige Art, welche bei Soldaten und Arbeitern unzweideutige Geschlechtscharactere aufweist, und dies ist offenbar eine sehr ursprüngliche Eigenschaft." This statement, however, must be modified, because FRITZ MÜLLER (1873, pp. 336–37) has shown that in *Calotermes nodulosus*, Hag., and *C. rugosus*, Hag., male soldiers are distinguishable from the female soldiers by the structure of the eighth sternum. He adds that: "Bei den männlichen Soldaten ist wie bei den geflügelten Männchen der Hinterrand dieses Schildes zwischen den Afteranhängen kaum merklich ausgebuchtet, bei den weiblichen Soldaten dagegen tief ausgeschnitten und der dunkle dicke Chitinrand ist in der Mitte dieses Ausschnitts durch dünnere Haut ersetzt—der erste Schritt zu dem Zerfallen dieses Schildes in zwei seitliche Platten, welches die geflügelten Weibchen zeigen." It is remarkable that HOLMGREN does not quote MÜLLER's important researches, though he can scarcely have been ignorant of them. Also, as has been pointed out (p. 18), *Archotermopsis* similarly exhibits external sexual differences among the soldiers. With the exception of these three instances the sex of the soldiers in Termitidæ, so far as I am aware, can only be revealed after a dissection of the internal sexual organs, all traces of external differences having been lost.

It will be necessary, therefore, under these conditions, to modify the diagnostic characters given by HOLMGREN in his "Übersicht" of the families of the Termitidæ (1911, p. 13). The occurrence of soldiers, externally differentiated with reference to their sex, has been shown to be by no means peculiar to the Mastotermitidæ, as

* Described by SILVESTRI (1909).

HOLMGREN thought; the principal character which separates the soldiers of that family from those of the remainder of the Termitidæ is the presence of five complete joints to the tarsi.

B. On the Occurrence of a Resting Period in the Ontogeny of Termites, and its Possible Bearing on the Origin of the Pupal Stage among Insects.

In two fortunate instances I have observed that the larval soldier in *Archotermopsis*, after the penultimate moult, lies in a helpless condition for a period of at least 24 hours. It betrays no indications of movement unless disturbed. When touched with a camel-hair brush it moved its limbs in response to the irritation, but afterwards soon settled down again in the quiescent condition. It will be readily understood that it is rather a matter of good fortune to come across the insect in this stage. For this reason I am unable to say if a similar resting period is present in the ontogeny of the winged sexual forms. No such lengthy resting stage has been noted after any of the earlier moults, either in the larval soldier or among those destined to produce sexual forms.

On making a survey of Termite literature, it is evident that a more highly evolved, and unmistakable resting stage, has been described in several species. The earliest account with which I am acquainted is HOLMGREN'S description and figure (1906, p. 521), of the early development of the South American *Rhinotermes taurus*. In this insect the resting stage has only been observed in the worker larvæ immediately after an ecdysis, and is stated to last from one hour to three days! In describing this stage, HOLMGREN remarks: "Wenn sich eine Larve häuten will, so legt sie sich auf die Seite, Kopf, Beine, Antennen werden nach hinten gezogen und der ganze Körper gegen die Bauchseite gekrümmt. Bei dieser Krümmung biegt die Haut auf dem Rücken und wird über die Seiten des Leibes und den Kopf gezogen, dass sie an den Antennenspitzen und Beinen hängen bleibt. Dies geschieht in wenigen Minuten. . . . Man sollte nun glauben, dass die Larve, sobald die Haut ausgezogen ist, fertig wäre, um das nächste Stadium durchzumachen. Dies ist aber nicht der Fall. Denn nach der Häutung liegen die puppenähnlichen Larven eine verschieden (einige Stunden bis drei Tage) lange Zeit ruhend da und werden von den Arbeitern getragen und beleckt. Während dieses Ruhestadiums gehen deutlich die inneren Veränderungen, die mit den äusseren korrespondieren, vor sich." ESCHERICH (1909, p. 22), who quotes these same remarks of HOLMGREN, adds that the resting stage in *Rhinotermes* is to be regarded physiologically as a pupal condition, since internal changes also occur simultaneously. STRICKLAND (1911, p. 257) has also described a quiescent stage in the development of *Leucotermes flavipes*, Kollar. He states that: "The mature nymph becomes very sluggish, and

finally all movement ceases; it then falls on its side, and the head is bent down till it lies on the ventral side of the body, along which also the antennæ and legs are extended in a backward direction, while the wing pads are bent downwards till they lie laterally along the sides of the body. It will be at a glance noticed that, while in this position, the nymph is, to all appearances, a quiescent *pupa libera*. There does not appear to be an ecdysis immediately prior to this quiescent period, however, so I would hesitate to describe it as a true pupal period, though it undoubtedly has the same physiological function." This observer states that the quiescent stage in this species lasted from four to nine hours, and that it has only been observed in the period intervening between the nymph and adult in the sexual forms, and then for the greater part before ecdysis. Bugnion (1912, p. 1091; 1913, p. 213) states that in *Termes redemanni*, Wasm., *T. obscuriceps*, Wasm., and *T. horni*, Wasm., the workers and soldiers pass through a stage of immobility or hypnosis. They lie on their side for seven or eight days, with the head bent on the thorax, and the legs and antennæ extended backwards. In this condition they pass from the larva to the adult. In the soldiers of *Eutermes lacustris*, Bugn., this observer mentions that the head is not flexed upon the thorax, and the phase of immobility is less pronounced. He further adds that this latter condition also obtains in species of *Coptotermes* and *Calotermes*. Escherich (1911, p. 43) has also observed a resting stage in *T. obscuriceps*, Wasm. The most recent writer is Snyder (1913, p. 164, and 1915, p. 41), who has conducted observations on two North American species of *Leucotermes* and on *Termopsis angusticollis*, Walk. In these species a quiescent period is present rather late in larval life. In *Leucotermes virginicus*, Bks., and *L. flavipes*, Kol., differentiated nymphs of the first and second forms (Lespès), measuring 2–5 mm. in length, were noted to pass through a quiescent stage in their final moult. The larvæ of the soldiers and workers also pass through a similar stage in their development. The same happens in the case of nymphs of the first form and the soldier larvæ of *Termopsis*. It is after the final moult and quiescent stage that the nymphs of the first form in *Leucotermes* and *T. angusticollis* acquire their mature pigmentation and become colonising individuals ready for flight. At the same time, nymphs of the second form in these species acquire a characteristic pale pigmentation and develop into neoteinic reproductive forms. In these species, during the quiescent stage, both the larvæ of the soldiers and the nymphs of the winged forms lie on one side with the head bent down on to the ventral side of the body. The antennæ and legs also lie extended in a backward direction.

It is, therefore, evident from the preceding remarks that a quiescent or resting stage is of tolerably general occurrence among Termites. It differs, however, in various genera in the exact period in the life-history when it manifests its presence, and its duration appears to vary between very wide limits. Two stages in its evolution can be recognised.

1. In this, the more primitive condition, the head is not flexed ventrally upon the

thorax, and the phase of immobility is but little pronounced. It occurs in *Archotermopsis*, and species of *Calotermes*, *Coptotermes*, and *Eutermes*.

2. In this stage the resting condition is more evidently pronounced. The head is markedly flexed upon the ventral aspect of the thorax, and the limbs and other parts are immobile. It occurs in species of *Termopsis*, *Leucotermes*, *Rhinotermes*, and *Termes*.

From HOLMGREN'S account of the resting phase of *Rhinotermes taurus*, it is evident that the transition to the ordinary *pupa libera* of such forms as *Raphidia*, and the Hemerobiidæ among the Neuroptera, is relatively slight. A study of the resting phase among Termites supports, and gives added weight to, LUBBOCK'S (LORD AVEBURY) view (1895, pp. 69–70), that the inactivity of the pupal stage in insects is not a novel condition, but a prolongation of the shorter period of inaction which accompanies each ordinary moult or ecdysis. The slighter the change that takes place, as a rule, the shorter is the period of inactivity.

It may be said, therefore, that the pupal stage in insects probably originated in the first instance as a lengthened resting stage, after the last moult, prior to the appearance of the perfect insect. Among the Termitidæ, it can be seen in a condition similar to that which it most likely passed through in the initial steps of its evolution.

C. REMARKS ON POLYMORPHISM AMONG TERMITES.

In the admirable memoir by GRASSI and SANDIAS (1897, p. 362 *et seq.*, Plate 16, figs. 1 and 2), it is stated that the newly-hatched larvæ of *Calotermes flavicollis*, Fabr., are undifferentiated. When, however, they have attained an average length of 2 mm. they are divisible into two groups, one with a large head, but little narrowed anteriorly, and the other with a small head, more evidently narrowed towards the apex. The former develop into soldiers. The latter type of larvæ may develop into sexual forms, or the head may increase in size and the larvæ become soldiers. GRASSI and SANDIAS have further observed that larvæ already far advanced towards becoming winged sexual forms can be diverted, as it were, and develop into soldiers. In such cases the developing wing rudiments become more or less absorbed. The morphological differences between the castes they attribute to food and method of feeding. This view is held by SILVESTRI (1901, p. 479), and was also maintained by HERBERT SPENCER* in his well-known controversy with WEISMANN. In *Leucotermes lucifugus*, Rossi, GRASSI and SANDIAS observed that a similar differentiation into large- and small-headed larvæ takes place when the insect attains a length of 2·25 to 3·75 mm. The large-headed larvæ may develop into either soldiers or workers. In *Archotermopsis*, as already mentioned (p. 81), the differentiation into large- and small-headed types of larvæ is evident in the very young individuals, 2·25 mm. long with 12 or more joints to the antennæ. According to

* 'Contemp. Review,' 1893.

the observations of SNYDER (1913, p. 163), made on moulting larvæ of North American species of *Leucotermes* and on *Termopsis angusticollis*, Walk., polymorphism takes place during a moult and quiescent stage rather late in larval life. He states that the larvæ were, to all external appearances, undifferentiated previously. The possibility, however, must be borne in mind that, notwithstanding the fact that the larvæ are hatched apparently alike, they may contain latent differences which do not manifest their presence morphologically until later on in development. The recent observations of BUGNION (1912, p. 1092 ; 1913, p. 213), suggest that in *Eutermes lacustris*, Bugn., *Termes redemanni*, Wasm., *T. obscuriceps*, Wasm., and *T. horni*, Wasm., differentiation into the soldier caste takes place during embryonic life, instead of being subsequently developed from undifferentiated larvæ. On hatching, the castes can be definitely ascertained by the form of the head and mandibles. In these instances it is obvious that food can have no influence on polymorphism. It is extremely difficult to reconcile these observations with those of GRASSI and SANDIAS, who state that even far advanced larvæ of winged forms may have their development arrested and become converted into soldiers. On the other hand, HEATH (1902, p. 62), remarks with reference to Californian Termites : " For months I have fed a large number of termite colonies of all ages, with or without royal pairs, on various kinds and amounts of foods—proctodæal food dissected from the workers, or in other cases from royal forms, stomadæal food from the same sources, sawdust to which different nutritious ingredients have been added—but in spite of all I cannot feel perfectly sure that I have influenced in any unusual way the growth of a single individual."

If we enquire into GRASSI'S statements more fully it is evident that he places great stress upon an experiment (1898, p. 27), in which he selected a number of nymphs only and kept them in tubes containing triturated wood. He states that, after a time, the tubes contained not merely nymphs undergoing conversion into royal substitution forms, but others which were being transformed into soldiers, and distinguished by the greater size of the head and the elongation of the mandibles and labrum. He claims that certain of the nymphs, therefore, were converted into soldiers in order to make good the absence of the latter. Important as this experiment is, it does not afford certain proof that those particular nymphs would not have developed into soldiers under normal conditions in their original nest. I may add that I have kept an isolated colony of about 20 nymphs of *Archotermopsis* under observation for 11 months without any soldiers being produced, and the individuals were active and apparently healthy during that period. GRASSI further states that he has observed the newly-hatched larvæ being fed with saliva by large larvæ or nymphs. The large-headed forms (which ultimately develop into soldiers and workers) receive only a very small amount of saliva, as is shown by the woody or fæcal colour of the intestinal contents. But the narrow-headed larvæ (which develop into winged adults) continue for a much longer period to receive salivary diet. There is, however, no evidence

to indicate that the two types of larval forms arise as a direct response to the nutrition they receive—the facts are indeed to the contrary. He concludes (p. 30) that the development into soldiers and workers is consequent on the less quantity of saliva which they receive, and with this is associated the earlier appearance of intestinal Protozoa, and their constant presence in great abundance. The Protozoa, he implies, have a retarding effect on the development of the gonads. This thesis I claim is unproved and, as is fully discussed on pp. 158 and 162, there is good reason to believe that the Protozoa are mainly symbiotic in their relations to their host. It is remarkable, therefore, that GRASSI and SANDIAS should suggest (p. 24), that it is probable though not proved, that the Protozoa have an important digestive function, and yet at the same time they maintain that they are parasites! FEYTAUD also maintains that nutrition is of paramount importance in relation to polymorphism, and remarks (1912, pp. 564-65): "Si nous admettons, avec la plupart des auteurs, que les Termites, à leur naissance, ne sont pas prédestinés à devenir neutres ou à devenir sexués, et que leur avenir est subordonné à un choix de la part des parents ou des ouvriers adultes, le développement progressif des organes génitaux ou l'arrêt du développement de ces organes étant subordonné au régime alimentaire, il y a lieu de penser que la choix est fait dès la naissance et que les larves sont soumises dès le début à un régime différent suivant leur destinée.

"Il est probable que l'arrêt de développement des organes genitaux n'est pas forcement définitif, et que ces organes conservent la faculté de poursuivre leur évolution, si, à une période quelconque, l'individue est soumis au même régime que les larves de sexués. C'est dans ces conditions que pourraient se produire les formes anormales de nymphes-soldats ou de nymphes-ouvriers, dans lesquelles l'apparition des caractères extérieurs de nymphes s'accompagne d'un nouveau développement des organes génitaux.

"Ce réveil et ce développement secondaire ne seraient pas possibles si, au lieu d'un arrêt, il s'était produit une atrophie."

FEYTAUD (p. 565) does not state whether he proved by dissection that "nymphes-soldats" and "nymphes-ouvriers" do actually exhibit an increased development of the genital organs. The view that the gonads among Termite soldiers have undergone an arrestation of development is also held by PÉREZ but is not accepted by HEATH (1902, p. 62). In *Archotermopsis* the genital organs in the soldier caste normally attain as high a degree of development as occurs in the winged sexual forms when the latter are ready to leave the nest. This fact I have been able to prove by numerous dissections. There is consequently, in this instance, no evidence in favour of the theory of arrested development, and a study of their histology points to the probability of their frequently being *functional* organs. These remarks also apply to *Termopsis angusticollis*, three soldiers of which have been recorded by HEATH (1902, p. 59) as laying fertile ova. According to MÜLLER (1873, p. 336), in *Calotermes canellæ*, the reproductive organs in the female soldiers similarly closely resemble those of the

winged females. The ovaries and colleterial glands, however, differ in being slightly smaller in size, and there is no spermatheca. In *C. nodulosus* and *C. rugosus* the ovaries are also well developed, but the spermatheca is likewise absent in both species. With reference to the male gonads in the soldiers of *C. canellæ*, MÜLLER states that they are exactly like those of the winged males, the testes alone being a little more slender in form. In *Leucotermes lucifugus*, FEYTAUD (p. 564), states that in the soldiers and workers the gonads remain in the same stage of development as in the larvæ of the second stage. Histologically, the sexual elements remain in the condition of oogonia or primitive spermatogonia, as the sex may be. The gonads, he says, are not more developed in the larvæ of the soldiers or workers than in the adults, and for these reasons he considered that an arrestation of development, and not degeneration, has taken place. According to LESPÈS (1856, pp. 240 and 244), who studied this same Termite, the female organs in both workers and soldiers exhibit obvious signs of degeneration. In the workers he states that under a high magnification no trace of eggs was to be observed, only globules of "graisse liquide," often very voluminous. In the soldiers the ovaries are still less developed, and there are no associated organs. It is possible, however, that LESPÈS may be mistaken in his conclusions owing to the less perfect methods of technique which were current in his day.

Transitional forms, exemplifying various stages in the reduction of the gonads, are to be found among different genera and species of Termites, and they culminate in the condition found in *Eutermes monoceros*. In this species, according to BUGNION (1909, pp. 276 and 278), it is impossible to discover any traces of sexual organs, either in the soldiers or workers. My own researches lead me to believe that the reduction of the gonads, found in the sterile castes of all except the most primitive genera of Termites, is the result primarily of an arrestation of development, followed by a variable amount of atrophy or degeneration. The case investigated by FEYTAUD does not necessarily invalidate this generalisation, because problematical instances are liable to occur in which it is a matter of difficulty to decide whether the observed conditions are the result of slight degeneration following an arrest of development, or of the latter phenomenon only. It is, furthermore, extremely doubtful whether organs like the gonads, whose development entails a tax upon nutrition, can remain indefinitely in an arrested condition when no longer normally functional and, at the same time, exhibit no signs of atrophy.

If we are to accept the contention that nutrition is of paramount importance in caste production, are we also to conclude that it is likewise capable of determining the existence of large, intermediate, and small types of soldiers on one and the same species; that nutrition causes these three forms to be sharply differentiated from one another unconnected by any intermediate forms; that nutrition is likewise the stimulus which results in the occurrence of large and small workers in the same species? Do such contentionists maintain that the profound changes in the morphology of the head, mandibles, labium, tentorium, and nervous system, which distinguish

the soldier from the winged reproductive forms are the direct or indirect result of nutrition? Would upholders of this hypothesis further claim that dietary regime will account for the total loss of wings in the sterile castes, and also for the fact that in many species the members of those castes have lost all trace of eyes?

Summarising the foregoing portion of this chapter, I maintain that there is no satisfactory evidence conclusively proving that any particular type of nutrition, or the absence thereof, is capable of producing such fundamental changes in the external and internal morphology which characterise the soldier caste. It has also been shown that the reduction in the gonads is not an invariable attribute of the soldier, and that caste production is not in any way related to the presence of intestinal Protozoa. I believe, therefore, in order to obtain a solution of the problem of Termite polymorphism, we must endeavour to discover whether it may, or may not, be due to a more deeply-seated influence. BUGNION has suggested (1912, p. 1094) that the differentiation of the soldier caste is due to some fundamental cause analogous to that which determines sex (special mode of fertilisation or special chromosomes). This view, I believe, is nearer the probable truth than that of GRASSI and SANDIAS. As already mentioned, BUGNION has shown that in species of *Termes* and *Eutermes* differentiation into the soldier caste takes place during embryonic life. Furthermore, FEYTAUD (1912, p. 563) observes that in the first stage larvæ of *Leucotermes lucifugus*—"Il est possible que, dès cette période de l'existence des larvæ, il y ait déjà lieu de distinguer deux catégories d'individus au point de vue du développement des organes génitaux, ceux qui doivent devenir sexués les ayant plus développés." It is probable, therefore, that too much emphasis has hitherto been laid on the fact that, in the majority of Termites so far studied, the young larvæ are hatched *apparently* all alike. This fact has given rise to the belief that caste differentiation necessarily takes place during post-embryonic life, when its presence first becomes obvious.

One of the outstanding difficulties of the Darwinian theory concerns this problem of polymorphism—in other words, the question as to how the characters of the sterile soldier and worker secure representation in the germ cells of the species. WEISMANN, in one of his last writings on this subject (1909, p. 39), explains it in terms of his germ-plasm theory as follows: "If we regard the variation of the many determinants concerned in the transformation of the female into the sterile worker as having come about through the gradual transformation of the ids into worker-ids, we shall see that the germ-plasm of the sexual ants must contain three kinds of ids, male, female, and worker-ids, or, if the workers have diverged into soldiers and nest-builders, then four kinds. We understand that the worker-ids arose because their determinants struck out a useful path of variation, whether upwards or downwards, and that they continued in this path until the highest attainable degree of utility of the parts determined was reached. But, in addition to the organs of positive or negative selection-value, there were some which were indifferent, as far as the success, and especially the functional capacity of the workers, was concerned;

wings, ovarian tubes *receptaculum seminis*, a number of the facets of the eye, perhaps even the whole eye. As to the ovarian tubes it is possible that their degeneration was an advantage for the workers in saving energy, and if so, selection would favour the degeneration; but how could the presence of eyes diminish the usefulness of the workers of the colony? or the minute *receptaculum seminis*, or even the wings? These parts have therefore degenerated *because they were of no further value to the insect.* But if selection did not influence the setting aside of these parts because they were neither of advantage or disadvantage to the species, then the Darwinian factor of selection is here confronted with a puzzle which it cannot solve alone, but which at once becomes clear when germinal selection is added. For the determinants of organs that have no further value for the organism, must, as we have already explained, embark on a gradual course of retrograde development."

From an examination of WEISMANN'S earlier writings it is evident that he intended this explanation to be applicable to similar phenomena, both in other Hymenoptera and the Termitidæ. WHEELER, in his masterly discussion of the subject of polymorphism in ants (1907, p. 80), believes that the workers and soldiers in the social Hymenoptera are more often fertile than is usually supposed, and disputes WEISMANN'S statement that fertility, in these forms, is too rare an occurrence to exert any influence on the germ-plasm of the species. He also quotes GRASSI'S opinion to the effect that the phenomena of inheritance in the sterile castes of Termites can be interpreted on the supposition of the exceptional existence of workers and soldiers capable of oviposition.

There appear, however, to be only two recorded instances of fertility among the "sterile" castes of Termites. In *Termopsis*, as already mentioned, HEATH refers to the occurrence of three egg-laying soldiers. In *Termes strunchii*, W. Sör, SILVESTRI (1901, p. 480) found 40 ♀ workers and 8 ♂ workers with the genital organs as well developed as in the winged forms. He further describes other characters which distinguish these gynæcoid workers from sterile workers, but does not record any of the former laying eggs.

In certain other Termitidæ the reduction of the gonads, coupled with the absence of any accessory organs, renders it tolerably certain that fertility is no longer a possibility. The same argument applies with still greater purpose to *Eutermes monoceros*, where, according to BUGNION, the gonads appear to be completely absent. It appears evident, therefore, that occasional fertility among soldiers is a physical impossibility, for, at any rate, many species of Termitidæ. WEISMANN'S contention is, I believe, amply justified, and some other explanation is necessary to account for the phenomenon of inheritance in that caste.

Certain phases of polymorphism among social insects appear to me to admit of a relatively simple interpretation in terms of the Mendelian theory of heredity. In the present instance it is not my intention to attempt to explain the phenomenon in

any insects other than the Termitidæ. Among the Hymenoptera it is an attribute of the female sex, and has apparently evolved along somewhat different lines. According to the usually accepted biological criteria, the characters of the ancestral type among the Termitidæ are exhibited, in their least modified form, in the winged males and females. The soldiers betray obvious specialisations on the one hand, and indications of degeneration on the other. For this reason it is probable that the primitive Termites consisted solely of winged males and females, and exhibited at first no manifestations of a communal life. The prototype of the worker can be explained as having arisen as a mutation of the nymph stage, and characterised by the absence of wing rudiments, and the possession of a markedly larger head and jaws than those of the race from which it sprang. Natural selection would then come into play and favour the increased development of useful characters, and the degeneration of certain others, along lines already suggested by WEISMANN (*loc. cit.*). It is probable that the soldier caste similarly arose by a further mutation or series of mutations. The fact that transitional forms, intermediate in character between the soldier, worker, and winged castes, are practically unknown argues in favour of these mutations being inherited according to the laws of Mendelian segregation. I hope to show in this essay that such an interpretation appears to offer a more consistent explanation of the varied phenomena associated with Termite polymorphism than any hypothesis hitherto put forward.

The presence of worker-like individuals in *Archotermopsis* has a direct bearing upon the origin of the worker castes among Termites. Eleven examples of these forms were dissected, and they were found to closely resemble the nymphs in most of their anatomical characters. The chief difference was to be observed in the gonads, which are larger in size, probably owing to the fact that the worker-like forms are nearer sexual maturity. Many of the ova are also in a more advanced stage in development (*vide* p. 124). In three females the ovaries were considerably larger than in any of the winged females which were dissected. The fat-body also exhibited an extensive development, being only paralleled by the condition of that tissue found in the winged adults. On one occasion a worker-like female laid seven ova in captivity, but, unfortunately, they failed to develop, and I am unable to state whether they were fertilised or not. On account of the condition of the gonads, I was at first inclined to regard the forms as being neoteinic individuals of a somewhat unusual type. The fact that the soldiers also exhibit a total absence of any indications of inhibition or degeneration of the gonads, has contributed largely to my abandoning this belief. Furthermore, the slightly enlarged head, the general chitinisation of the body, the condition of the eyes, and the very variable occurrence of curiously shrivelled wing vestiges, all argue in favour of their being worker-like forms. I consider that they exhibit the first step in the evolution of the worker caste, a conclusion which, if correct, is in full accordance with the presence of other primitive features associated with *Archotermopsis*. At the same time they afford a

clue as to the possible origin of the worker, which appears to have arisen as a mutation of the nymphal stage and not of the winged adult. This mutation involved a slight increase in the size of the head correlated with the abortion of the wing rudiments. According to GRASSI, in *Leucotermes lucifugus* and *Calotermes flavicollis* there are four moults in the ontogeny of the soldiers and workers, while the sexual forms pass through five moults. This fact affords additional support to my contention that the sterile castes are to be regarded as modified nymphs.

The true worker is readily distinguishable from worker-like forms by the reduction or total absence of the eyes, and by the further increase in the size and degree of chitinisation of the head and mandibles. In its general morphological features the worker is clearly a less modified form than the soldier. Whether the former is phylogenetically the older type or not is uncertain. KNOWER (1896) states that the nasute soldier in a species of *Eutermes* develops from a worker-like larva, and according to GRASSI and SANDIAS the workers and soldiers in Italian Termites arise from large-headed (or worker-like) larvæ. At present, however, we have insufficient evidence to decide whether the soldier mutation arose *de novo* from the nymphal form, or secondarily as a further offshoot from the worker.

The principal distinguishing features in the external morphology of sexual forms and sterile castes concern the shape and size of the head and mouth parts, the presence or absence of wings and the condition of the eyes. Since we can have no conception, in the absence of experimental evidence, as to what the various allelomorphs are likely to be, it is necessary to consider the distinctive characters of each of the three castes *in toto* as collective entities; or, in other words, to deal with quantitative rather than qualitative segregation. Furthermore, this method of treatment receives justification from the fact that these various characters are intimately correlated and linked together. We do not find, for example, the giant mandibles unless accompanied by an increase in the size of the head and the absence of wings. Nor do we find the modified tentorium without the presence of an elongate labium, and both these features are, in their turn, correlated with the enlarged head and mandibles.

I propose to consider first a typical species of Termite comprising monomorphic soldier and monomorphic worker castes and the ordinary winged sexual forms. Let the symbols ASF represent the various allelomorphs which express themselves collectively in the winged sexual forms; F standing for the fertility determinant, and *f* for the absence of that factor. The worker mutation I would explain as having arisen by the loss of certain correlated allelomorphs, which we represent by S and their absence by *s*. Similarly, by means of a second mutation, involving the loss of another group of characters A, the soldier caste is accounted for; the absence of A we will represent by *a*. The parental forms will have the constitution A*a*S*s*F*f*, but the formula may be simplified by omitting the fertility determinant, which will be considered at a later stage, since it bears no relation to the origin of caste.

Now the cross A*a*S*s* × A*a*S*s* affords an ordinary case in which two kinds of differentiating characters are united, and the series contains nine different forms among sixteen individuals (BATESON, 1913, pp. 355 and 345). These may be classified as follows :—

Soldiers.	Winged sexual forms.	Workers.
2 A*a*SS	2 AASS	2 AAS*s*
1 *aa*SS	4 A*a*S*s*	1 AA*ss*
2 *aa*S*s*		2 A*ass*
	Sterile gametic union.	
	1 *aass*.	

The above hypothesis, involving the Mendelian inheritance of two analogous mutations, appears to offer a simple explanation of the origin of polymorphism among Termites. It, furthermore, accounts for the persistence of castes, which are in themselves mostly sterile, securing their representation in the germ-plasm of the species in each succeeding generation. It will be observed, from the above Table, that in the soldiers there is a predominance of S, and in the workers A is ascendant over S. It will also be seen that the gametic composition of both these castes varies. In certain individuals both the factors A and S are represented, or, in other words, they retain a proportion of the unmodified germ-plasm of the winged forms. This feature in itself appears to offer a reasonable hypothesis explaining certain phenomena which have never been adequately accounted for, viz., the occasional persistence among the soldiers and workers of certain features which belong *sensu stricto* to the winged sexual forms. These are : (1) the occasional presence of wing vestiges in both soldiers and workers ; (2) the fact that nymphs with well-developed wing rudiments (and apparently differing in nowise from the nymphs of the winged forms) have been observed to develop into soldiers. Hitherto, the occurrence of such individuals has been accounted for on the belief that they are nymphs of the winged forms which have become "converted" into soldiers through the agency of changed nutrition. On the other hand, I maintain that it is owing to the mixed nature of the germ-plasm of these individuals that the transitory parental characters appear in their ontogeny, before those of the caste to which they belong ultimately assert themselves.

In the primitive type, *Archotermopsis*, it has already been pointed out (p. 125) that a study of the anatomy and histology of the generative organs points to the conclusion that the soldiers in this genus are perfectly capable of reproduction. Very possibly this contention also holds good for the so-called sterile castes of *Mastotermes*, *Termopsis*, and certain of the more primitive members of the Calotermitinæ. If there be any truth in the present hypothesis, it is obvious, from the preceding diagram that, owing to differences in their gametic constitution, a certain proportion of the soldiers would *ipse facto* not breed true ; or, in other words, their offspring would comprise both soldiers and winged sexual forms or all three castes. The same,

of course, also applies to the workers. Thus, if we crossed an A*a*SSFF soldier with an *aa*S*s*F*f* soldier we should obtain soldiers, workers, and winged sexual forms among their progeny. This, as a matter of fact, has been actually recorded by HEATH (1902, p. 59) in the case of an egg-laying soldier of *Termopsis angusticollis*. He states that the development was followed for a long time, and "the young, and the nymphs and workers into which they became transformed, appeared in all respects perfectly normal."

In the greater number of the Termitidæ, however, the fertility determinant F has become lost in the soldier and worker castes, and their gametic constitution is no longer *a*SF and A*s*F, but *a*S*f* and A*sf* respectively. In the case of *Termes strunchii*, in which gynæcoid workers are recorded by SILVESTRI (1901), fertility may not have been completely lost, or it may occur occasionally as a reversion to the more primitive condition. As to which of these two possibilities approximates to the truth, I must confess it is almost impossible to hazard an opinion.

In certain primitive genera (*Archotermopsis* and *Calotermes*) the worker caste appears to be wanting. Possibly it is to be regarded as a primitive character, and may be accounted for on the supposition that the mutation, involving the loss of S, did not occur in certain cases, and consequently workers are absent.

In the higher Termitidæ it is well known that two fundamentally different types of soldiers are to be found: (1) Those with greatly elongated mandibles, which may be termed the *mandibulate type;* and (2) those with vestigial jaws, but with a conspicuous frontal rostrum, which may be designated the *nasute type*. The latter is undoubtedly the most highly modified of the two, and may possibly have arisen as a separate and distinct mutation. Both of these types may further exhibit polymorphism among themselves. Thus, many species of the genus *Eutermes* have both large and small nasute soldiers, while in *E. diversimiles*, Silv., the nasute soldiers exhibit large, medium, and small forms among themselves. Similarly, among the mandibulate type very many species are known to have both large and small soldiers, and in *Capritermes opacus*, Silv., three grades in size among the soldiers are known, with the mandibles developed in proportion. The existence of trimorphic soldiers, of two different types, adds greatly to the difficulties of accepting nutrition as being a factor influencing caste production. Furthermore, in other Termites the workers are dimorphic, and this dimorphism may coexist with dimorphism among the soldiers as in *Termes bellicosus*, Smeath., *Eutermes œconomus*, Tragh., and many other species.

This further development of polymorphism among the sterile castes may, perhaps, also be explained in terms of the Mendelian theory, if we admit the addition of a modifying factor which we will term L. The presence of L would modify the soldier or worker characters, or affect both those castes and result in dimorphism. In such cases, let the presence of the L factor result in the occurrence of the large forms of those castes and, the absence of L, namely *l*, in the presence of the small forms. This mutation, involving L and *l*, may have taken place ages after the soldiers or

workers as such were evolved, but this does not directly concern the subject under discussion. In fact, the occurrence of dimorphism among the sterile castes is confined to the more specialised genera, and this in itself suggests that it may be a phylogenetically recent acquisition.

In all cases the L and *l* factors would have no visible effect upon the AS individuals (winged sexual forms), for among them dimorphism is unknown. Now, by crossing two winged sexual forms, each of the gametic constitution A*a*L*l*S*s*, we have an instance where three differentiating factors are combined, and the series contained in their progeny comprises 27 different forms among 64 different individuals, as elucidated by MENDEL (*vide* BATESON, 1913, p. 336). The progeny of the cross A*a*L*l*S*s* × A*a*L*l*S*s* may be expressed symbolically as follows (the fertility determinant F being omitted for the purpose of simplifying the formulæ as before) :—

Large soldiers.	Small soldiers.	Winged sexual forms.	Small workers.	Large workers.
1 *aa*LLSS	1 *aall*SS	1 AALLSS	1 AA*llss*	1 AALL*ss*
2 *aa*LLS*s*	2 *aall*S*s*	1 AA*ll*SS	2 AA*ll*S*s*	2 AALLS*s*
2 *aa*L*l*SS	2 A*all*SS	2 AAL*l*SS	2 A*allss*	2 AAL*lss*
2 A*a*LLSS		4 A*a*LLS*s*		2 A*a*LL*ss*
4 *aa*L*l*S*s*		4 A*all*S*s*		4 AAL*l*S*s*
4 A*a*L*l*SS		8 A*a*L*l*S*s*		4 A*a*L*lss*

Barren gametic unions.

1 *aa*LL*ss*
1 *aallss*
2 *aa*L*lss*

In those species which possess trimorphic soldiers or workers a form intermediate in size between the large- and small-headed individuals is found. Its presence I am inclined to ascribe as being due to the occurrence of a further mutation of the soldier caste. This would involve a factor which has the effect of modifying the morphology of certain individuals and of unaffecting others. The hypotheses suggested herewith are admittedly speculative interpretations. My object has been to point out the possibility of the Mendelian inheritance of mutations being an important, and hitherto unconsidered, factor in the evolution of Termite polymorphism. The realisation of the importance of mutations, in the evolutionary process, has made vast strides during the last few years. A wide school of present-day biologists believe that saltatory variations provide the "material" upon which natural selection works and heredity transmits. I need, therefore, offer no apology for applying these views in the interpretation of the present problem. It is likely that the readers of this essay will be able to work out, to their own satisfaction, a more consistent *modus operandi* than I have suggested in the two cases selected. My primary object, however, has been to suggest a fresh point of view for dealing with caste formation, rather than to emphasise the definite lines along which the phenomenon may be presumed to have

occurred. In conclusion, the Mendelian inheritance of mutations offers a possible solution of polymorphism among Termites, and more especially affords an explanation of: (1) The absence of intermediate forms between the castes; (2) the constant occurrence in each generation of castes which themselves have become sterile; (3) the occurrence of dimorphism and trimorphism among workers and soldiers; (4) the occasional presence of wing-rudiments in members of sterile castes, and the occurrence of "nymph-soldiers" and "nymph-workers."

D. On Holmgren's "Exudation Theory" and the Supposed Existence of "Exudation Tissue."

An answer to the question as to the reason why ants exhibit such energy and pleasure in licking their true "inquilines" has been supplied by Wasmann, who has conducted a prolonged series of investigations on this subject (1903 and 1910, pp. 44 and 305–386). It has long been known that true ant guests usually bear tufts of reddish or golden-yellow hairs, which the ants lick assiduously. These are regarded by Wasmann as the most characteristic organs of the inquilines, and he has shown that they are situated on various regions of the integument, where numerous unicellular glands open, and that they have the function of diffusing some aromatic secretion. It is stated that in virtue of this "exudation" the inquilines repay their hosts for their hospitality by secreting a substance which is highly acceptable to them. The exudations are partly direct and partly indirect products of the fat-body. When they are indirect they are partly a glandular secretion and partly a constituent of the blood plasma of the inquiline.

These researches of Wasmann have led Holmgren to found his "exudation theory" with reference to the Termitidæ (1909, pp. 190–203). He states that "exudation tissues" are present in all castes, but attain their greatest development in the queen. They are situated in group immediately beneath the integument, in the region of the abdomen, and Holmgren states that, although they resemble the fat-body in general appearance, they exhibit in sections an entirely different structure. Instead of consisting of large cells, as is the case with the fat-body, they are composed of small cells of angular form, or flattened, and are grouped together in small columns, having the appearance of glandular or epithelial tissue. They are stained by hæmalum a uniform violet colour. This tissue, he states, secretes a special substance which passes to the surface of the cuticle either directly or by means of special hollow hairs ("Exsudattrichom"). Holmgren maintains in his "exudation theory" that we have an explanation of the biological reason for the licking which occurs among termites. The eager care, which is specially manifested by the workers towards the imagines and their developmental stages, is explained on the basis that the exudation secretions of the latter are particularly attractive to the former. He claims, therefore, that the brood-care instinct among Termites is a phenomenon, in every way comparable to the solicitude manifested by ants towards the guests that live in association with them.

In so far as I understand HOLMGREN, the "exudation tissue" is not derived directly from the fat-body, but it is the act of licking which determines its local transformation into exudatory tissue.

FEYTAUD (1912, pp. 536–600) has studied the "exudation tissue" in the queen of *Leucotermes lucifugus*, in the queen and king of *Termes bellicosus* and *T. natalensis*, and in the king of *Eutermes fungifaber*. He states that this tissue really represents a stage in the development of the royal adipose tissue, in the region of the abdomen, and has no such exudatory function. The adipose tissue of the royal forms is to be regarded as a new growth, formed chiefly at the expense of the original fat-body, by the penetration and proliferation therein of leucocytes. Little by little, the latter gradually replace the older tissues, the transformation taking place several years after swarming. At first the new tissue frequently assumes a columnar form, and FEYTAUD claims that HOLMGREN has mistaken the tissue in this stage for fully-formed glandular or "exudation tissue." The numerous careful figures given by FEYTAUD help to carry a conviction in favour of that author's interpretation as to the significance of this tissue.

BUGNION (1912, p. 216 *et seq.*) gives a somewhat different interpretation to FEYTAUD as to the nature of this tissue. He states that, in the queen of *Termes horni*, at the level of each abdominal spiracle is an aggregation of whitish tissue resembling fat-body, and disposed in the form of a kind of rosette. The cells thereof are arranged in "colonnettes," and between them are aggregations of leucocytes, but BUGNION states that he has not observed the latter penetrate within the cells. It is particularly well supplied with tracheæ, and he concludes from a study of sections that "le tissue en colonnettes dérive vraisemblablement d'une prolifération des gaines des trachées au sein du tissu adipeux de l'imago." HOLMGREN'S exudation hypotheses he finds difficult to accept, and, furthermore, he states that hollow "exudation hairs" are absent, though ordinary imperforate hairs are in evidence. He regards the tissue as glandular in function, possessing an internal secretion which acts upon the composition of the blood.

I have made a prolonged examination of the hypodermis and fat-body in *Archotermopsis*, with special reference to the possible presence of this tissue. Serial sections of soldiers, nymphs, and sexual forms were used for the purpose; the few royal forms available were not, however, sufficiently well preserved for needs of histology. In no instance was any structure which could be interpreted as "exudation tissue" discovered. Furthermore, the fat-body was only observed in one specimen (a winged female) to exhibit any traces of columnar structure. In this instance the indications of such structure were slight, and there seems little reason to doubt that the tissue in question was new fat-body in process of formation. It was situated beneath, and in contact with, the older fat-body, and had no connection with the exterior, either by means of cuticular canaliculi or hollow setæ.

B. The Presence of Intestinal Protozoa and their Significance.

The presence of an abundant Protozoan fauna in the hind gut of many Termites is tolerably well known, and, so far as I am aware, the earliest reference to the occurrence is in Lespès' memoir (1856, p. 237). This observer remarks, with regard to the workers of *Leucotermes lucifugus*, that "L'intestin est ordinairement rempli d'une sorte de bouille brune, vivante agglomération d'Infusoires." He also mentions that they are present in the adults ("petits rois et petites reines"), and states (p. 258) that "Le tube digestif contient rarement la bouillie brune que nous avons trouvée chez les ouvriers et les soldats ; c'est un matière de couleur beaucoup moins foncée qui le remplit. Il fourmille toujours d'animalcules que je décrirai plus tard." I am not, however, aware that Lespès ever published any account of these organisms. The next observer was Leidy (1877, p. 146), who mentions that, in the North American *Termes* (*Leucotermes*) *flavipes* the intestine of the workers, soldiers, and winged forms is distended with brown material. The latter consists of minute particles of decayed wood and enormous numbers of infusorial and other parasites, which he identified as follows: (1) *Trichonympha agilis*, Leidy, which he states to be probably related to the Turbellaria on the one hand, and by evolution with the ciliate infusoria on the other ; (2) *Pyrsonympha vertens*, Leidy, which is often more abundant than the former organism ; (3) *Dinenympha gracilis*, Leidy, the smallest and most abundant of the three ; (4) an Algoid form, which he describes under the name of *Arthromitus ;* (5) a *Spirillum*, probably *S. undula*. Leidy, however, does not state any reason as to why he terms these organisms parasitic. In his later and more detailed paper (1881, p. 529), he recognises the Protozoan nature of *Trichonympha*, with affinities between the Gregarines and Ciliates. He also records (p. 441) *Gregarina termitis*, sp. nov., which he found on one occasion among the other Protozoa, and a Nematode worm, *Isakis migrans*, which was described by Lespès* some 25 years previously. The next observer was Saville Kent (1885, p. 270), who recorded a new *Trichonympha*, *T. leidyi*, from an unnamed Tasmanian Termite. He claims to have detected an oral aperture in this genus, in the form of a transverse slit on one side of the body, at a short distance only from the anterior extremity. Associated with the *Trichonympha* was another Protozoan, apparently referable to the genus *Pyrsonympha*, together with a species of *Lophomonas*. In 1891 Frenzel (p. 301) described a new Trichonymphid genus and a species, *Leidyonella cordubensis*, out of *Eutermes iniquilinus* (?), from Argentina. It is a comparatively simple form, and furthermore, Frenzel remarks that he could find no trace of an oral aperture in that species. In 1892 Grassi published descriptions of five new genera and species of Protozoa from the gut of *Calotermes flavicollis* and *Leucotermes lucifugus*. They are also dealt with in his conjoint memoir with Sandias (1893), a translation of which was published by Blandford in 1897. In

* Lespès' species has recently (1916) been described by Merrill and Ford as *Diplogaster œrivosa*, sp. nov.

1897 PORTER published an admirable and fully illustrated account of the intestinal Protozoa of *L. flavipes*, confirming and extending the observations of LEIDY. He states that he was unable to find any trace of an oral aperture in *Trichonympha*, and believes that solid food particles become enclosed by folds of the body, and entangled in the cilia, and thereby become gradually engulfed within the cytoplasm of the organism. He further adds that he never found any food particles in the anterior nucleus-containing portion of the body. Gregarines he found to be very common, and also *Pyrsonympha vertens* Leidy, which appears to be always attached to the walls of its host's intestine—an important fact overlooked by LEIDY.

In 1904 Mlle. FOA (1904, p. 618) published some observations on the process of division in *Trichonympha agilis*, and she also studied, in conjunction with GRASSI (GRASSI and FOA, 1904, p. 241), the same process in *Jænia annectens*. In the following year this authoress (FOA, 1905, p. 542) described two genera of Flagellate parasites, *Calonympha* and *Devescovina*, each with a single species, from unnamed Chilian Termites. A few years later, HARTMANN (1910, p. 349) published a detailed study of *Trichonympha hertwigi*, sp. nov., from a Brazilian Termite, describing young forms, males and females, and methods of gamete formation. In the same year DOBELL (1910, p. 65) described the first intestinal Protozoa from Asiatic Termitidæ. His material was obtained from the workers of *Calotermes militaris*, and included *Gymnonympha zeylanica*, gen. et sp. nov., a Ciliate—*Nyctotherus termitis*, sp. nov., and *Spirochæta termitis*, sp. nov. Meanwhile, in Italy, BUSCALIONI and COMES (1910) gave an account of a series of observations dealing with the digestion of vegetable membranes by Flagellates, with suggestions as to their possible symbiotic function. COMES (1910, p. 11) also described *Lophophora vacuolata*, gen. et sp. nov., from *Leucotermes lucifugus*, and published a second paper (1910, A, p. 20), describing what appeared to be sexual dimorphism in *Dinenympha gracilis*, from the intestine of the same species of Termite. A year later GRASSI and FOA (1911, p. 725) contributed an important paper describing six new genera of *Trichonymphidæ*. These authors dispute HARTMANN'S conclusions with reference to his study of *T. hertwigi*. The young forms thereof they claim to belong to the genus *Pyrsonympha*, and the males of HARTMANN'S species they refer to the new genus *Holomastigotoides*. They further dispute HARTMANN'S contention that the Trichonymphida should be elevated to the rank of one of the main classes of the Protozoa, equivalent to the Mastigophora or the Ciliata, and relegate the group to the order Hypermastigina. It may be added that DOFLEIN (1909, p. 468) places them as the first "Anhang" of the sub-class Cystoflagellata, and MINCHIN, in his recent text-book (1912, p. 276), treats of them as two unclassified families at the end of the Mastigophora. The latter author further points out (p. 463) that their isolated position appears to express the defective state of knowledge concerning their affinities. JANICKI (1911, p. 321) has given a useful account of the remarkable parabasal apparatus found among Trichonymphida and other Flagellates. In this

paper he also includes a description of *Parajænia grassii*, gen. et sp. nov., and *Devescovina striata* Comes var. *Hawiensis* nov., from *Calotermes castaneus*, and *Stephanonympha silvestrii*, gen. et sp. nov., from *C.* (*Cryptotermes*) *grassii*.

In addition to the above-mentioned writers, BUGNION (1913, p. 3 ; 1914, p. 46), BUGNION and POPOFF (1910, p. 113 ; 1910, A, p. 132), and BUGNION and FERRIÈRE (1911, p. 103) have published a valuable series of observations dealing with the occurrence of intestinal Protozoa among various Ceylonese Termitidæ. Although they do not identify the genera or species of the Protozoa concerned, their writings greatly extend our knowledge of the distribution of these organisms among different Termites.

The most recent paper with which I am acquainted is that of JANICKI (1915, p. 573), which is an extended and more detailed study of those forms described in his earlier article, together with further observations on the significance on the parabasal body.

The following list comprises the genera and species of intestinal Protozoa known to me to occur in Termites. With regard to the Hypermastigina (Trichonymphidæ) I have followed the family divisions adopted by POCHE (1913, pp. 149–154). It is necessary to point out that several of the genera herein listed only doubtfully merit separate recognition, and very possibly will have to be sunk as synonyms in the light of future research.

PROFLAGELLATA, Doflein.

Genus : *Trepònema* Schaudinn.
Spirochæta, Ehrenburg (*pro parte*).

T. termitis Leidy (emend. Dobell).—From *Leucotermes flavipes* in N. America (Leidy) ; *L. lucifugus* in Japan (Prowazek) ; *Calotermes militaris* in Ceylon (Dobell) ; *Archotermopsis wroughtoni* in India (Imms).

T. minei Prowazek (emend. Dobell).—From *L. flavipes*, *L. lucifugus*, and *C. militaris*, as above.

For observations on *Treponema* and the synonomy of the species *vide* DOBELL (1912, p. 143).

Class : CILIATA, Butschli.
Order : HETEROTRICHA, Stein.
Genus : *Nyctotherus*, Leidy.

N. termitis, Dobell.—From *Calotermes militaris*, in Ceylon.

Class : MASTIGOPHORA, Diesing.
Order : POLYMASTIGINA, Blochmann.
Genus : *Monocercomonas*, Grassi.

M. termitis, Grassi.—From *Calotermes flavicollis* and *Leucotermes lucifugus*, in Italy.

Genus : *Trichomonas*, Donne.

T. termitis, Imms.—From *Archotermopsis wroughtoni*, Desn., in India (Himalaya).

Genus : *Foaina*, Janicki.

F. gracilis, Janicki.—From *Calotermes castaneus*, in Hawaii.

Genus : *Oxymonas*, Janicki.
(Of doubtful systematic position.)

Oxymonas granulosa, Janicki.—From *Calotermes castaneus*, in Hawaii.

Order : HYPERMASTIGINA, Grassi and Foa.
Family I.—DINENYMPHIDÆ, Grassi.
Genus : *Dinenympha*, Leidy.
Pyrsonympha, Leidy.
Lophophora, Comes.

D. gracilis, Leidy.—From *Leucotermes flavipes*, in the United States, and *L. lucifugus*, in Italy.

D. vacuolata, Comes.—From *Leucotermes lucifugus*, in Italy.

D. vertens, Leidy.—From *Leucotermes flavipes*, in the United States, and *L. lucifugus*, in Italy.

Family II : DEVESCOVINIIDÆ, Poche.
Genus : *Devescovina*,* Foa.

D. striata, Foa.—From *Calotermes grassii*, in Chili. Var. *hawiensis*, Janicki, from *Calotermes castaneus*, in Hawaii.

Family III : CALONYMPHIDÆ, Grassi.
Genus 1 : *Calonympha*, Foa.

C. grassii, Foa.—From *Calotermes grassii*, in Chili.

Genus 2 : *Stephanonympha*, Janicki.

S. silvestrii, Janicki.—From *Calotermes* (*Cryptotermes*) *grassii*, in Chili.

Genus 3 : *Microrhopalodina*, Grassi and Foa.

M. enflata, Grassi and Foa.—From *Calotermes flavicollis*, in Italy.

Family IV : TRICHONYMPHIDÆ, Kent (*Lophomonadidæ*).
Genus 1 : *Trichonympha*, Leidy.

T. agilis, Leidy.—From *Leucotermes flavipes*, in the United States, and *L. lucifugus*, in Italy.

T. leidyi, Kent.—From an unnamed Termite in Tasmania.

T. minor, Grassi and Foa.—From *Leucotermes lucifugus* (?), in Italy.

T. pristina, Imms.—From *Archotermopsis wroughtoni*, in India (Himalaya).

Genus 2 : *Leidyonella*, Frenzel.

* In his latest paper (1915) Janicki transfers this genus to the Polymastigina.

L. cordubensis, Frenzel.—From *Eutermes iniquilinus* (*?*), in Argentina.

Genus 3 : *Microjœnia*, Grassi.

M. hexamitoides, Grassi.—From *Leucotermes lucifugus*, in Italy.

Genus 4 : *Jœnia*, Grassi.

J. annectens, Grassi.—From *Calotermes flavicollis*, in Italy.

Genus 5 : *Eulophomonas*, Grassi and Foa.

E. calotermitis, Grassi.—From *Calotermes flavicollis*, in Italy.

Genus 6 : *Gymnonympha*, Dobell.

G. zeylanica, Dobell.—From *Calotermes militaris*, in Ceylon.

Genus 7 : *Parajœnia*, Janicki.

P. Grassii, Janicki.—From *Calotermes castaneus*, in Hawaii.

Genus 8 : *Mesojœnia*, Grassi and Foa.

M. decipiens, Grassi and Foa.—From *Calotermes flavicollis*, in Italy.

Genus 9 : *Holomastigotoides*, Grassi and Foa.

H. hertwigi, Hartmann.—For the female of *Trichonympha hertwigi*, Hartmann, from *Captotermes hartmanni*, in Brazil.

Genus 10 : *Pseudotrichonympha*, Grassi and Foa.

P. hertwigi, Hartmann.—For the male of *Trichonympha hertwigi*, Hartmann.

Genus 11 : *Spirotrichonympha*, Grassi and Foa.
(*Pyrsonympha*, Grassi.)

S. flagellata, Grassi.—From *Leucotermes lucifugus*, in Italy.

Genus 12 : *Holomastigotes*, Grassi.

H. elongatum, Grassi.—From *Leucotermes lucifugus*, in Italy.

Class : Sporozoa, Leuckart.
Order : Gregarinæ, Doflein.
Genus : *Gregarina*, Dufour.

G. termitis, Leidy.—From *Leucotermes flavipes*, in the United States.

The inter-relationships of the intestinal Protozoa with their host have been very little investigated, and many writers have regarded these organisms as being parasites. Grassi and Sandias (1897–98) maintain that the relative abundance of the Protozoa is in inverse proportion to the degree of development of the gonads of their host. According to them the development of soldiers and workers is consequent upon the small amount of saliva which they receive, coupled with the presence of numerous Protozoa. They further add that Protozoa are scarce in both the winged forms and the true kings and queens, and usually totally absent in neoteinic individuals. When they are abundant in the latter, the gonads exhibit imperfect

development. They remark that developing neoteinic forms are fed very largely on salivary diet and the disappearance of the Protozoa is most probably the direct result of its action. Finally, they conclude that it is a moot point whether the maturition of the gonads is solely due to salivary diet, or to the absence of Protozoa also—the latter they believe is not in itself a sufficient cause. Brunelli (1905 A, p. 718) has followed up the ideas of Grassi and Sandias, and states that in queens of *Calotermes flavicollis* and *Leucotermes lucifugus* infected with Protozoa there is a correlated destruction of the oocytes—a kind of indirect "castration parasitaire." My own observations, made upon *Archotermopsis*, lead me to the conclusion that no such phenomenon occurs. I have dissected more than a dozen worker-like females of that Termite, all of which had the hind-gut filled with Protozoa, and yet the ovaries were greatly developed and contained nearly full-sized ova ready for fertilization. Furthermore, I have also observed in five soldiers well-developed ovaries, larger than those of the sexual forms prior to swarming, and at the same time the hind intestine in these individuals was in each case filled to repletion with Protozoa. Well-preserved ovaries from both soldiers and worker-like forms have also been studied with special reference to their histology, and, although abundant Protozoa were present in those individuals from which the ovaries were taken, I was unable to detect any indications of degeneration of the oocytes, as Brunelli has described. Feytaud (1912, pp. 573–74) also joins issue with Brunelli with regard to the occurrence of "castration parasitaire." He regards those features which Brunelli interprets as signs of degeneration, as being in reality the result of histological alteration due to the action of reagents. He remarks (p. 583) that "Il est très difficile de faire de bonnes coupes à travers les gros ovules. Lorsque le vitellus est devenu abondant, il durcit, sous l'action des fixateurs, devient friable, cassant et s'effrite sous le rasoir. Dans toutes les reines mûres on peut trouver des ovules d'aspect analogue à celui de la figure donnee par Brunelli, et cela sans qu'il existe de Protozoaires dans la poche intestinale . . . .

"Le fait que des imagos parviennent à la maturité sexuelle et fondent une colonie nouvelle, tout en ayant la poche intestinale très développée et bourrée de Protozoaires, suffirit d'ailleurs à écarter l'idée d'une castration parasitaire."

My own observations and those of previous investigators make it very nearly a certainty that the presence of Protozoa, in the hind intestine of Termites, is correlated with a ligneous diet. In the young larvæ, and in the kings and queens, which receive a fluid diet from other members of a colony, no Protozoa as a rule are to be found. It is, furthermore, noteworthy that these forms do not partake of ligneous food at all. In the older larvæ, soldiers, workers, and sometimes in the winged sexual forms, Protozoa are abundant and ligneous diet is the rule. Another significant feature which argues against the theory of "castration parasitaire" is the fact that intestinal Protozoa have so far only been found among members of the families Protermitidæ and Mesotermitidæ. The members of these families are wood-feeding forms. Among the higher Termites Protozoa have not so far been discovered, and

moreover these forms do not partake of a purely ligneous diet. In Ceylon BUGNION mentions (1914, p. 46) having found intestinal Protozoa in the following genera: *Hodotermes*, *Calotermes*, *Leucotermes*, *Glyptotermes*, *Coptotermes*, *Arrhinotermes*, and *Termitogeton*, all of which pertain to the Protermitidæ or Mesotermitidæ. In the higher Termites such as *Eutermes*, *Capritermes* and *Termes*, BUGNION states (1914 A, p. 180) that he has never found any "*Trichonymphidæ*." Mr. E. E. GREEN, who possesses an unrivalled knowledge of the insects of Ceylon, informs me that with regard to the occurrence of intestinal Protozoa among Termites his experience is in close agreement with that of BUGNION.

With regard to the significance of these Protozoa almost all writers have regarded them as being parasites, and in many cases no proofs are advanced in support of this contention. My observations, however, have led me to the conclusion that their relationship with their host is mainly one of symbiosis. The correlation of the presence of intestinal Protozoa with those castes and individuals which partake of a ligneous diet directly supports my conclusion.

During the process of feeding the wood is seized by the mandibles and crushed to some extent by means of the grinding action of their molar surfaces. After being swallowed it passes down the œsophagus into the crop, and subsequently undergoes further crushing in the gizzard. On passing through the latter organ, it enters the œsophageal valve, which projects for a long distance into the cavity of the mid-gut. The food consequently has only to traverse a very small portion of the latter region before entering the hind-gut. On reaching the hind intestine the wood is in a condition of minute fragments and particles, and the greater bulk of it gradually becomes taken up and absorbed by the numerous intestinal Protozoa. By means of the phloroglucin reaction, I have been able to satisfy myself that the numerous particles included within the cytoplasm in *Trichonympha* and *Trichomonas* consist entirely of ligneous matter. Within the protoplasm of these organisms the woody material undergoes chemical changes, and, when ejected from the bodies of the Protozoa, much of it is in a condition capable of being assimilated as food by the host Termite. How and where assimilation actually takes place is a difficult physiological problem, involving a knowledge of micro-chemical methods which I do not possess. A significant fact is that the ligneous particles are not subjected to the action of the secretions of the mid-gut. Their passage through the latter appears to be very rapid, and on no occasion have I found woody matter in that region of the digestive system. The mid-gut frequently contains a thick fluid material which also extends up into the cœca. This fluid appears to be regurgitated from the hind-gut, and I believe is the product of the breaking down and "emulsification" of the wood by the action of the Protozoa. The readmission of solid particles into the mid-gut is effectually precluded by means of the pyloric valve already described (p. 112, and text-fig. 10).

An interesting experiment is afforded by enclosing half a dozen or more soldiers in a phial, unaccompanied by any wood or other available food. These individuals can

be kept alive, and apparently healthy, for several weeks, and their sole nutriment consists of rectal matter ejected by their fellows. This material is re-devoured again and again, until all nourishment has been abstracted therefrom. At this stage, unless fresh food be supplied, the imprisoned Termites die of starvation. A microscopical examination of the rectal matter, immediately after ejection through the anus, reveals the fact that Protozoa are present therein. It is, therefore, evident how these latter organisms are transmitted from one individual to another.

The work of absorbing the wood particles is discharged by *Trichonympha* and *Trichomonas* in the case of *Archotermopsis*. These larger forms of Protozoa also subserve this same function in other Termites. It is necessary to point out, however, that among the intestinal Protozoan fauna are some species which appear to be parasites. Of these, the most important are members of the genus *Dinenympha*, which are attached to the intestinal wall. The *Treponema* is probably parasitic on the other Protozoa. Only one species of Sporozoa has so far been discovered in the intestine of Termites, but this organism does not appear to be either a common or widely spread form.

The conception of the Protozoa being symbionts rather than parasites is due to Buscalioni and Comes (1910). Their valuable and suggestive researches into the economy of the Protozoa of *Leucotermes lucifugus* have been overlooked by several subsequent writers. These observers claim to have definitely established the conclusion that the association of Termites with Flagellates is one of symbiosis. They claim to have proved, with considerable certainty, that the Protozoa elaborate from the wood sugars and glycogen. They remark that from these materials "by a still more complicated physiological process which is found in the Metazoa, the Termites arrive at the fat and albuminous compounds, higher plastic substances in the continuous cycle of transformation which living matter undergoes." The authors state that they have not been able to investigate the secondary products (such as, for instance, the aldehydes and those of the aromatic series), which probably appear in the bodies of the Flagellates during the various phases of the complicated process of the digestion of the wood. They believe that the presence of Flagellates is essential to the welfare of those Termites which feed exclusively upon wood. Among other problems, they finally raise the question as to whether the symbiosis which they describe represents a primitive or a derived condition; in other words, was there a period when the Termites could digest ligneous material without the intervention of Protozoa? A decisive answer to this problem remains to be discovered, and Buscalioni and Comes admit the absence of sufficient data to supply it.

Grassi and Mlle. Foa (1911, pp. 740–41) do not accept the idea of Protozoa being necessary to aid the digestion of wood by the host Termites. They claim that the necessity of these organisms is not proved, and further add that, in many other wood-feeding insects, the intermediary Protozoa are not required. No concrete cases are quoted, however, in support of the latter statement. Grassi mentions that

he has tried reagents partly similar to those used by BUSCALIONI and COMES, advised also by the botanist BACCARINI, who was at that time his colleague at Catania. He states that he did not venture to draw any definite conclusions therefrom, especially when it is taken into account the fact that many animals take in a much larger quantity of food than they can utilise. Before this matter is passed out among the fæces it serves to nourish the Protozoan parasites. It does not follow, therefore, that the latter are necessary for the welfare of their host. GRASSI admits the difficulty of definitely proving his thesis, and adds that long and intricate physiological research is required, not only on the Protozoa, but also on the digestive processes of the Termites. He mentions an important experiment which he conducted with *Calotermes*. Pieces of wood containing individuals of this Termite (caste not stated) were enclosed in small boxes and kept at a temperature of about 35° C. The intestinal Protozoa died, sometimes all, often only the small forms remained alive. In this way he found that the *Calotermes* were without such usually plentiful forms as *Jœnia* and *Mesojœnia*. In other cases the *Calotermes* were entirely deprived of Protozoa and lived in full activity for several months.

It is evident, from the above remarks, that GRASSI and FOA regard the Protozoa as being purely coprozoic forms, which are not necessary intermediaries in the process of digestion of woody material by their hosts.

The above-mentioned temperature experiment does not appear to me to offer an invincible argument against the theory of symbiosis. We have first to take into account that under such conditions the Termites possibly subsisted upon fæcal matter only; proof is also wanting that progress in development took place. Secondly, I have observed that Termites in captivity frequently partake of a very small amount of food. For these two reasons, I can readily believe it possible for the Termites to flourish in the absence of Protozoa for a limited period of life. In my opinion a test experiment would be afforded by taking young larval Termites, and rearing them in captivity on thoroughly sterilised wood, excluding them from any association with older individuals containing Protozoa. If it is possible to rear Termites to the adult stage under these conditions, I would be prepared to abandon my belief in the existence of symbiosis between the Protozoa and their hosts. A very wide and promising field, for Protozoological research, is likely to be afforded by a study of the intestinal Protozoa of wood-feeding Arthropods, which have so far almost entirely escaped attention. LEIDY mentions (1881, p. 427) that in old stumps and decaying logs inhabited by *Leucotermes flavipes*, the Myriapod *Spirobolus marginatus* and the coleopterous insect *Passalus commutus* are also found. Both the latter species, he adds, sustain a multitude of "parasites" (as he terms them), and it is a remarkable fact that all three animals just enumerated use the same food, and, even at times, occupy the same habitation. It would be a matter of great interest to study the contents of the intestine in the larvæ and adults of many coleopterous

families which subsist upon wood, more especially the Ipidæ (Scolytidæ), Buprestidæ, Cerambycidæ, and Bostrichidæ. Among the Lepidoptera the wood-feeding larvæ of the families Aegeriiadæ and Zeuzeridæ, and the genus *Trypanus* (*Cossus*), likewise afford suitable subjects for study. PORTIER (1911) has investigated an apparent instance of symbiosis in the case of the larva of a Noctuid moth *Nonagria arundinis* F. (*typhæ* Esp.), which lives within the stems of *Typha*, devouring the pith. In the digestive tube of this larva are found great numbers of motile conidia of a fungus belonging to the genus *Isaria*, which exist among the devoured vegetable fragments. The conidia are always accompanied by a Micrococcus, which secretes a diastase capable of dissolving cellulose. It is at the expense of this dissolved cellulose that the conidia develop and multiply, and according to PORTIER, they eventually penetrate the walls of the intestine of their host, escaping into the blood. Most of them are there attacked by phagocytes, and transformed into lipoids, which serve to nourish the tissues of the host. I think it not unlikely that future research will show that in many wood or vegetable feeding Invertebrates, the preliminary processes of digestion are aided through the presence of symbiotic Protozoa, Fungi, or Bacteria.

DOFLEIN (1901) also maintains that the relationship between the Protozoa and Termites is one of symbiosis, and a similar view is held by BUGNION and POPOFF (1910, A, p. 136). These latter authors conclude that the Protozoa build up their own body substance at the expense of the ingested wood, and, at the same time, contribute towards the digestion of this substance. Reproducing daily in prodigious quantities, and dying even by thousands, the Protozoa, according to BUGNION and POPOFF, would be digested in their turn, and contribute indirectly to the nutrition of their host.

The symbiosis between the intestinal Protozoa and their host Termites finds a parallel among those Infusoria, which occur in the stomachs of certain Ruminants, notably the ox, sheep, goat, camel, and reindeer. The Infusoria mostly pertain to the genera *Butschlia*, *Isotricha*, *Dasytricha*, *Entodinium*, *Diplodinium*, and *Ophryoscolex*. Our knowledge of the economy of these genera is still meagre, but general opinion inclines towards the view that they are symbionts rather than parasites. It is believed that, by means of their action upon the vegetable matter consumed by the Ruminants, these Infusoria help to render it capable of being digested by the latter. Furthermore, Infusoria are absent from the stomachs of the young Ruminants prior to being weaned from their parents (*vide* NEVEU-LEMAIRE, 1912, p. 446). According to CERTES (1889), glycogen is present in the protoplasm of the Infusoria, and the latter perform a special *rôle* in the digestive process of the Ruminants. GRUBY and DELAFOND (1843) maintain that the protoplasm of the Infusoria is itself digested, and thereby contributes towards the nutrition of the host Ruminant. Similarly, the Infusoria inhabiting the large intestine of the Equidæ are possibly symbiotic in their relations with their host.

In conclusion, the intestinal Protozoa of Termites appear to afford an interesting case of symbiosis. By their action in breaking down ligneous matter, they contribute towards the digestion of the latter by their hosts. The contention that they are parasites or solely coprozoic forms is not, in my opinion, equally in accordance with the facts that are at present available.

F. On Termites in Captivity.

Although not generally known among biologists, many Termites are comparatively easy to retain alive in captivity, even when brought from the Tropics to England. The species most suitable for observation are those which feed within the stems and trunks of trees, and do not form any true nest or termitarium. It is further noteworthy that such Termites include the bulk of the more primitive species, and it is by conducting observations on these forms that the most light is likely to be shed upon the complex and unsolved biological problems associated with the Termitidæ. The writer brought a number of *Archotermopsis* from India, arriving in England on March 8, 1913; winged individuals of both sexes emerged between July 2 and 20, and the colony lived in captivity until December of the same year. A second consignment arrived from India on October 10, 1913, and about a third of the colony lived until March, 1915. In all cases they were confined, along with pieces of the wood of *Pinus longifolia*, in corked glass tubes, 20 or more cm. in length, and 4–5 cm. in diameter. A little water was sprinkled over the wood from time to time, and beyond keeping them in the temperature of the laboratory, which was warmed during the cold months, no further care was taken of them. In a few cases they ate their way through the corks of the tubes, but nevertheless, made no attempt to escape. This method of retaining them in glass tubes entailed the division of a colony into several groups. Probably, if large glass vessels were used, and a much greater number of individuals kept associated together, they would have flourished for a considerably longer period with less mortality.

Grassi and Sandias (1897, pp. 250–52) mention that they kept 3–20 examples of *Calotermes flavicollis* in corked tubes, 3–8 cm. long, and although many die off after a few weeks, a certain number can be kept alive for several months. The tubes were partly filled with fragments of wood, which should be neither too dry nor too moist. *Leucotermes lucifugus*, they state, does not flourish in these tubes, but drags on a feeble existence for a week or 10 days at most. They mention, however (p. 293), that a colony of that species, without king or queen, was kept alive for eight months in a jar half full of crushed-up phylloclades of *Opuntia*, and closed with a sheet of paper tied over the mouth.

Haviland and Sharp (1896, p. 589, *et seq.*) record keeping *Calotermes domesticus*, Hav., alive in England for nearly two years. The specimens were enclosed in glass tubes along with pieces of the wood upon which they subsist.

These same observers also mention keeping *Calotermes arctocarporum*, Hav., alive, under similar conditions, for nearly nine months.

Bugnion and Ferrière (1911, pp. 104–05) state that they kept a colony of *Coptotermes flavus* alive in full vigour from December 18, 1910, until March 11, 1911. They further state that species of *Calotermes*, *Coptotermes*, and certain *Eutermes* are easily retained in captivity if the following precautions be observed: "(1) placer les tronçons de bois qui les renferment sur une table à l'abri des Fourmis; (2) mettre sur la table d'autres branches à demi pourries au milieu desquelles les Termites puissent choisir à volonté; (3) arroser ces branches de temps à autre; (4) mettre à la portée des Termites quelques boîtes remplies de sciure."

Snyder (1915, p. 20) reared and observed *Leucotermes flavipes*, Kollar, and *L. virginicus*, Banks, in a large cage, 10 ft. × 6 ft., and about 7 feet high. The bottom of the cage consisted of a galvanised-iron box 1 foot deep. Loose earth was placed in the box to about half of its depth, over which was placed a shallow layer of leaf mould, for the purpose of retaining moisture. The sides of the cage consisted of wire netting supported on a framework of wood; the roof was of wood covered with tarred paper. Logs of chestnut wood and oak were placed within, and also decaying branches and boards of the former, which served for food and shelter. By means of this contrivance he was able to conduct observations on swarming and many other features of Termite biology.

Whether the true mound-forming Termites can be kept in captivity, away from their natural haunts, for any length of time, there appears to be no evidence. I am not aware that any observers have so far attempted the experiment.

G. Affinities of the Isoptera.

The Termitidæ are very widely separated from other social insects and, unlike the latter, are incontestably to be regarded as being among the more lowly organised members of their class. Their affinities and systematic position have been discussed by various authorities during the past 53 years, and very divergent views have been held. They have been variously classified among the Neuroptera, Pseudoneuroptera, Corrodentia, and also as a separate and distinct order of their own (the Isoptera). The latter view was held by Comstock (1895), and has been revived by Desneux (1904 and 1904 a), and Holmgren (1909). According to Desneux, the order Isoptera was founded by Brulle (Expéd. Sc. Morée, T. 3, Zool., Paris, p. 66) as long ago as 1832. For many years it was claimed that the Termitidæ were closely related to the Embiidæ and Psocidæ, a view which has been maintained by Packard (1883), Sharp (1895), Folsom (1906), Enderlein (1903), and others. The close affinity of the Termites with the Embiidæ has been contested by Grassi and Sandias (1898, p. 73), Desneux (1904 and 1904 a), and Handlirsch (1904). There is now

a growing opinion that they represent a distinct order of their own—the Isoptera—and that their affinities lie nearest to the Blattidæ and the Dermaptera. HAGEN stated (1868, p. 139) that the families "Termitina, Blattina, and Forficulina are co-ordinated and very nearly allied." DESNEUX has shown that the Isoptera are derived phylogenetically from the Blattidæ, and HOLMGREN (1909) maintains that the Termitidæ and Blattoidea are offshoots of the primitive group of the Protoblattoidæ, a view with which my own studies have led me to entirely concur. Additional confirmation of the Orthopteran affinities of the Isoptera has been afforded by WALKER'S discovery (1914, p. 93) of the remarkable synthetic type *Grylloblatta campodeiformis*, which he relegates to the new family of the Grylloblattidæ. The affinities of this insect have been further investigated by CRAMPTON (1915, p. 337), who regards it as an annectant link between the Dermaptera and the Isoptera, but more closely related to the former than the latter.

An examination of the primitive characters exhibited in the genera *Archotermopsis* and *Mastotermes* reveals the fact that many are also Blattid features, and these two genera throw a good deal of light upon the phylogeny of the Isoptera. My studies lead me to the conclusion that the Isoptera are more closely related to the Blattidæ than to the Dermaptera, and are only remotely related to the Embiidæ. This view is based not only upon certain features of their external morphology, but also upon the internal anatomy.

HOLMGREN (1909, pp. 208–13, and 1911, pp. 15–31) has dealt tolerably fully with the Blattid affinities of the Isoptera, laying special stress upon the wing characters of *Mastotermes*, and other features of their external structure. The affinities revealed by their internal anatomy have been less thoroughly examined, and *Archotermopsis* exhibits the following Blattid characters in the digestive and reproductive organs.

The digestive system is clearly of the Blattid type, and very closely resembles that of *Periplaneta*. The presence of cœca to the mid-gut appears to be a character inherited from the Colotasia (BORDAS, 1898, p. 191) group of the Orthoptera, and these structures have not so far been detected in any other Termite. The crop and gizzard are extremely similar, both in form and histology, though the gizzard is less strongly developed than in the Blattidæ. The Malpighian tubes alone offer any fundamental point of difference, and the fact that they are few in number in Termites, and numerous in the Orthoptera, is perhaps due to the probability that the former are more primitive in this respect than the latter. In *Archotermopsis* and, according to HOLMGREN, in *Hodotermes*, *Porotermes* (*Glyptotermes*), and *Calotermes* eight Malpighian tubes are present. It is noteworthy that these four genera belong to the generalised family of the Protermitidæ. This same number of Malpighian tubes, according to SCHINDLER (1878, p. 607), is found in the young larvæ (4–5 mm. long) of *Periplaneta* and the full number is not acquired until a later stage in development. The enlarged condition of the hind intestine, found in many Termites, is purely an adaptive character correlated with the presence of intestinal Protozoa, since it is no

longer evident where the latter are wanting. The salivary glands and their reservoirs bear a close resemblance, both in form and structure to those of *Periplaneta*. The hypopharynx closely resembles that of the latter genus, and MANGAN'S description thereof (1908) applies almost equally well to the same organ in *Archotermopsis*.

The reproductive system also bears a close resemblance to that of the Blattidæ, especially with regard to the female gonads. The ovaries and their ducts are closely alike in the two cases, the only marked difference being in the actual number of ovarioles present. In both cases the ovaries are panoistic, nutritive chambers being absent. The spermatheca and colleterial glands of *Archotermopsis* are entirely of the Blattid type, both in their structure and disposition. The general morphology of the male organs is similar in both *Archotermopsis* and *Periplaneta*. In the former, however, there is neither external genital armature nor conglobate gland. The vesiculæ seminales of the Termite offers no essential points of difference from the "Mushroom gland" of the "Cockroach."

A feature of great interest, and not devoid of phylogenetic significance, is BUGNION and FERRIÈRE'S discovery (1911, pp. 101–103, Plate 2, fig. 4) of a pair of elongate wing-like organs attached to the pronotum in the young larvæ (2–2·5 mm. long) of *Coptotermes flavus*. They are probably of a similar nature to the aliform outgrowths of the margin of the pronotum, found in young larvæ of other species of *Coptotermes* and of *Calotermes*. In view of their very early and transitory appearance in the ontogeny of these Termites, I agree with BUGNION in regarding them as being homologous with the aliform expansions of the pronotum of the Carboniferous Orthopteron *Lithomantis carbonaria* described by WOODWARD (1876, p. 60), and the prothoracic wings of *L. woodwardi* (Brongniart, 1890). They are perhaps to be regarded as vestigial structures, inherited from the extinct Protoblattoidea, and their presence affords further evidence of the latter group being the ancestors of the Isoptera.

IV. SUMMARY OF GENERAL CONCLUSIONS.

Archotermopsis wroughtoni is one of the most primitive of living Termites, and is restricted in its distribution to the North-Western Himalayas. It occurs exclusively in the coniferous forests from Kumaon through Garhwal, and Jaunsar to Kashmir. In vertical distribution it is limited to elevations varying from about 4000 to 9000 feet.

It attacks the dead and decaying wood of several species of Coniferæ, but does not affect that of any of the Angiosperms. No true nest or termitarium is constructed, the insect living in tunnels and hollows in the wood excavated for the purpose.

A fully developed colony comprises kings, queens, winged males and females, soldiers, worker-like forms and various larval stages. No true neoteinic forms were found.

The queen differs little from the winged female except in the absence of wings,

and exhibits no indications of degeneration or increase in size common to most species of Termitidæ.

Swarming takes place in response to a requisite amount of humidity when accompanied by a sufficiently high temperature. The swarms comprise individuals of both sexes, which suffer enormous mortality during flight. Swarming occurs for the purpose of ensuring the meeting of the sexes, to allow for the survival of sufficient individuals for continuing the race, and to secure the foundation of new colonies away from the immediate proximity of the parent colony. It also provides for the occasional intercrossing with individuals of other colonies.

Only a relatively small number of eggs are laid by each queen, and the numerical abundance of individuals is maintained by the occurrence of a larger number of queens than is met with in the higher Termites.

The soldiers rank among the largest known, and are chiefly remarkable in that they exhibit well-defined external secondary sexual characters, a feature which has become lost in almost all other Termites. The reproductive system exhibits no indications of degeneration, or arrestation of development, and is in a condition similar to that found in the winged sexual forms, prior to swarming.

The worker-like forms similarly exhibit well marked external secondary sexual characters. The reproductive system is fully developed, and, in all probability, most of these individuals are gynæcoid forms. In some examples nearly mature ova were present, and one female deposited seven eggs while in captivity. Only one other instance is known of oviposition by a member of a "sterile" caste among Termites.

The digestive system is chiefly characterised by (1) the presence of five enteric cœca, and (2) the vast numbers of Protozoa which occur in the large intestine of the soldiers, worker-like forms, nymphs and larvæ. These are absent from the very young larvæ and the queens, but occur in smaller numbers in the winged sexual forms. Five species of Protozoa are prevalent, and two of these, pertaining to the genera *Trichonympha* and *Trichomonas*, are described as new.

The nervous system consists of supra- and infra-œsophageal ganglia, three thoracic and six abdominal ganglia. The sympathetic system and the corpora allata are also well developed. The latter are to be regarded as ductless glands pouring a secretion into the blood. In all forms, with the exception of the later nymphs and winged individuals, the optic nerves present an anomalous condition of being distally divided into three branches, each of which passes to the eye.

The fat-body attains its greatest development in the winged forms and worker-like individuals. It is much less evident in the soldier and larvæ.

A definite resting stage occurs in the ontogeny of the soldier in *Archotermopsis*, prior to the last moult, though it is less pronounced in that form than in certain other genera. The pupal instar in insects probably originated, in the first instance, as a lengthened resting stage, after the last moult, previous to the appearance of the

imago. Among the Isoptera it can be seen in a condition similar to that which it most likely passed through in the initial steps of its evolution.

In certain primitive features *Archotermopsis* is unique among Termites, and is more closely related to the North American genus *Termopsis* than to any other living forms.

Polymorphism in Termites is not adequately explained as being the direct or indirect effects of special nutrition, nor does the theory of "castration parasitaire" explain the observed facts of the phenomenon. The Mendelian inheritance of mutations appears to offer a reasonable solution of several of the outstanding difficulties associated with the origin of polymorphism, and the inheritance of germinal characters in sterile castes.

The "exudation theory" of HOLMGREN is shown to be based upon premises which have been insufficiently established, and the presence of his "exudation tissue" has not been confirmed. The tissue to which he ascribed an exudatory function is most probably a stage in the regeneration of the sub-hypodermal fat-body.

Intestinal Protozoa are, so far as at present known, confined to wood-feeding Termites pertaining to the families Protermitidæ and Mesotermitidæ. Most observers have regarded these organisms as being parasites, but it appears more probable that they are symbiotic in their relations to their hosts. By breaking down ligneous matter, they contribute towards the digestion of the latter by the Termites.

The Isoptera are more closely related to the Blattidæ than to any other insects. They also have affinities with the Dermaptera, and, more remotely, with the Embiidæ.

Wood-feeding Termites can be tolerably easily retained in captivity for many months, and readily adapt themselves for purposes of observation and experiment.

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[*Addendum.*—Since this paper has been written I have perused GRASSI'S recent publication, "Flagellati viventi nei Termiti" (1917), but was unable to consult it in time to include any discussion of his results in the present work.]

EXPLANATION OF PLATES.

(Unless otherwise stated, all the figures relate to *Archotermopsis*.)

Reference Lettering.

a.	Anus.
a.a.	Anal area.
ab.m.	Abductor muscle.
abd.g.$_1$	First abdominal ganglion.
a.c.	Anal cercus.
a.ct.	Anterior circlet of flagella.
ad.m.	Adductor muscle.
a.f.	Anal furrow.
ant.l.	Antennal lobe.
ant.n.	Antennal nerve.
ao.	Aorta.
ax.	Axostyle.
b.c.	Bi-nucleate excretory cell.
b.l.	Basal line or suture.
b.m.	Basement membrane.
bp.	Blepharoplast.
b.r. and *b.r.*$_1$	Basal rods of the hypopharynx.
brn.	Brain or supra-œsophageal ganglion.
c.	Cardo.
c.a.	Corpora allata.
cc.	Concretions.
cd.	Condyle.
ch.g.	Chromidia.
ch.l.	Chromatinic line or basal rod.
ch.$_1$	Cushion or pad behind the denticles of the gizzard.
cl.	Clypeus.
c.i.	Chitinous lining or intima.
c.m.	Circular muscle layer.
c.m.f.	Circular muscle fibre.
co.	Colon.
c.p.	Left lateral chitinised plate of hypopharynx.
cr.	Crop.
c.s.$_1$ and *c.s.*$_2$	Lateral cervical sclerites.
cu.	Cuticle.
cu.$_1$	Cuticular papillæ.
cub. and *cu.v.*	Cubital vein.
c.v.	Costal vein.
cyt.	Cytostome.
cx.	Coxa.
c.z.	Zone or area of clear protoplasm.
d.$_1$*d.*$_3$	Denticles of gizzard.
d.ej.	Ductus ejaculatorius.

d.v. . . . . . Dorsal vessel.
e. . . . . . Eye.
em. . . . . . Epimeron.
ent.coe. . . . . . Enteric cœca.
ep. . . . . . Episternum.
epith. . . . . . Epithelial layer.
es. . . . . . Episternum.
f. . . . . . Femur.
f.e. . . . . . Follicular epithelium.
f.g. . . . . . Frontal ganglion.
fl. . . . . . Flagellum.
f.y. . . . . . Vitelline granules.
g. . . . . . Gena.
ga. . . . . . Galea.
giz. . . . . . Gizzard.
gm. . . . . . Germarium.
g.p. . . . . . Mental plate.
gs. . . . . . Ginglymus.
h. . . . . . Hypodermis.
hy_1. . . . . Modified hypodermal cells at points of muscle attachment.
hx. . . . . . Hypopharynx.
i.oes.g. . . . . . Infra-œsophageal ganglion.
l. . . . . . Labrum.
la. . . . . . Lacinia.
l.i. . . . . . Large intestine.
lm. . . . . . Lumen or central cavity.
l.m.f. . . . . . Longitudinal muscle fibres.
l.n. . . . . . Labral nerve.
$l._1n.$ . . . . . Nerve to the foreleg (right).
l.p. . . . . . Labial palp.
lpl. . . . . . Laterosternite.
m. . . . . . Meron.
m.c.d. . . . . . Main common duct of colleterial glands.
md.n. . . . . . Mandibular nerve.
m.f. . . . . . Muscle fibres.
m.g. . . . . . Mid-gut.
m.l. . . . . . Matrix layer.
M.t. . . . . . Malpighian tubes.
musc. . . . . . Muscular coat.
m.v. . . . . . Median vein.
mx.p. . . . . . Maxillary palp.
n. . . . . . Nucleus.
od. . . . . . Oviduct.
oes. . . . . . Œsophagus.
oes.g. . . . . . Œsophageal or post-cerebral ganglion (right).
o.l. . . . . . Optic lobe.
o.n. . . . . . Optic nerve.
oo. . . . . . Developing oocytes.
p.c.z. . . . . . Striated zone of matrix cells.

p.fl. . . . . . Posterior flagellum.
pgr. . . . . . Palpiger.
p.m. . . . . . Peritoneal membrane.
p.p. . . . . . Podical plates.
p.v.m. . . . . . Posterior prolongation of vibratile membrane.
p.v.n. . . . . . Post-cerebral nerve.
r. . . . . . Rectum.
$r._1r._2r._3$ . . . . . Branches of radial vein.
r.c. . . . . . Crypt or nest of young epithelial cells (regeneration cells).
r.c.d. . . . . . Duct of right colleterial gland.
rh. . . . . . Rhizoplast.
r.m. . . . . . Radial muscles of rectum.
r.n. . . . . . Recurrent nerve.
r.od. . . . . . Right oviduct.
r.s.d. . . . . . Right salivary duct.
r.sal.gl. . . . . . Right salivary gland.
s. . . . . . Stipes.
s.a.s. . . . . . Sub-anal style.
sal.res. . . . . . Salivary reservoir.
s.ap. . . . . . Aperture of main salivary duct.
s.c. . . . . . Sub-costal vein.
s.d. . . . . . Common salivary duct.
s.l. . . . . . Possible vestige of left maxillula (or supra-lingua).
sp. . . . . . Spermatheca.
st. . . . . . Sternum.
$st._6st._9$ . . . . . Sixth to ninth abdominal sterna.
str. . . . . . Inner striated zone.
$str._1$ . . . . . Outer striated zone.
t. . . . . . Testis.
t.c. . . . . . Tracheal capillary.
t.f. . . . . . Terminal filament.
$th.g._1$ . . . . . First thoracic ganglion.
th.s. . . . . . Thoracic scar (wing vestige ?).
t.l. . . . . . Tritocerebral lobe.
tn. . . . . . Trochantin.
tr. . . . . . Trochanter.
trh. . . . . . Tracheal tube.
$tg._{10}$ . . . . . Tenth abdominal tergum.
vac. . . . . . Vacuoles.
v.c.s. . . . . . Ventral cervical sclerite.
v.d. . . . . . Vas deferens.
v.m. . . . . . Vibratile membrane.
ves.sem. . . . . . Vesiculæ seminales.
w.o. . . . . . Wall, or investing membrane, of ovariole.

DESCRIPTION OF PLATES.

PLATE 3.

Fig. 1.—An adult soldier (male). × 6.

Fig. 2.—A mature second stage nymph (male) drawn just before the final ecdysis into the winged form. × 11.

Fig. 3.—A fully developed winged form (male) caught while issuing from the nest during a "swarming" period at Bhowali (Kumaon Himalaya). × *circa* 4.

Fig. 4.—A fully grown worker-like form (male). On the right side of the meso- and meta-thorax are irregular scars suggestive of abortive wing vestiges. × 10.

PLATE 4.

Fig. 5.—A young soldier larva, 6 mm. long. × *circa* 15.

Fig. 6.—A late larval soldier (female) in the last stage prior to assuming the adult form. × 7.

Fig. 7.—A queen taken from a colony near Dharmoti (Kumaon Himalaya). × *circa* 8.

Fig. 8.—Basal sclerites of the hind leg (left) of the soldier. × *circa* $16\frac{1}{2}$.

Fig. 9.—Basal sclerites of the fore leg (left) of the soldier. × *circa* $16\frac{1}{2}$.

Fig. 10.—Cervical sclerites of the soldier. × 27.

Fig. 11.—Left first maxilla of the soldier. × 24.

Fig. 12.—Labrum and clypeus of the soldier. × 22.

Fig. 13.—Basal sclerites of the middle leg (left) of the winged form (male). × *circa* $16\frac{1}{2}$.

PLATE 5.

Fig. 14.—Second maxillæ (labium) of the soldier seen from its ventral or pharyngeal aspect. × 24.

Fig. 15.—Lateral and slightly dorsal view of the hypopharynx of the soldier, together with the associated parts of the second maxilla. × *circa* 85.

Fig. 16.—Fore and hind wings of the right side (from an adult female). × $5\frac{1}{2}$.

Fig. 17.—Base of the fore wing showing roots of the nervures and the vestigal anal area. × 17.

Fig. 18.—Basal joints of left antenna of a winged female. × 41.

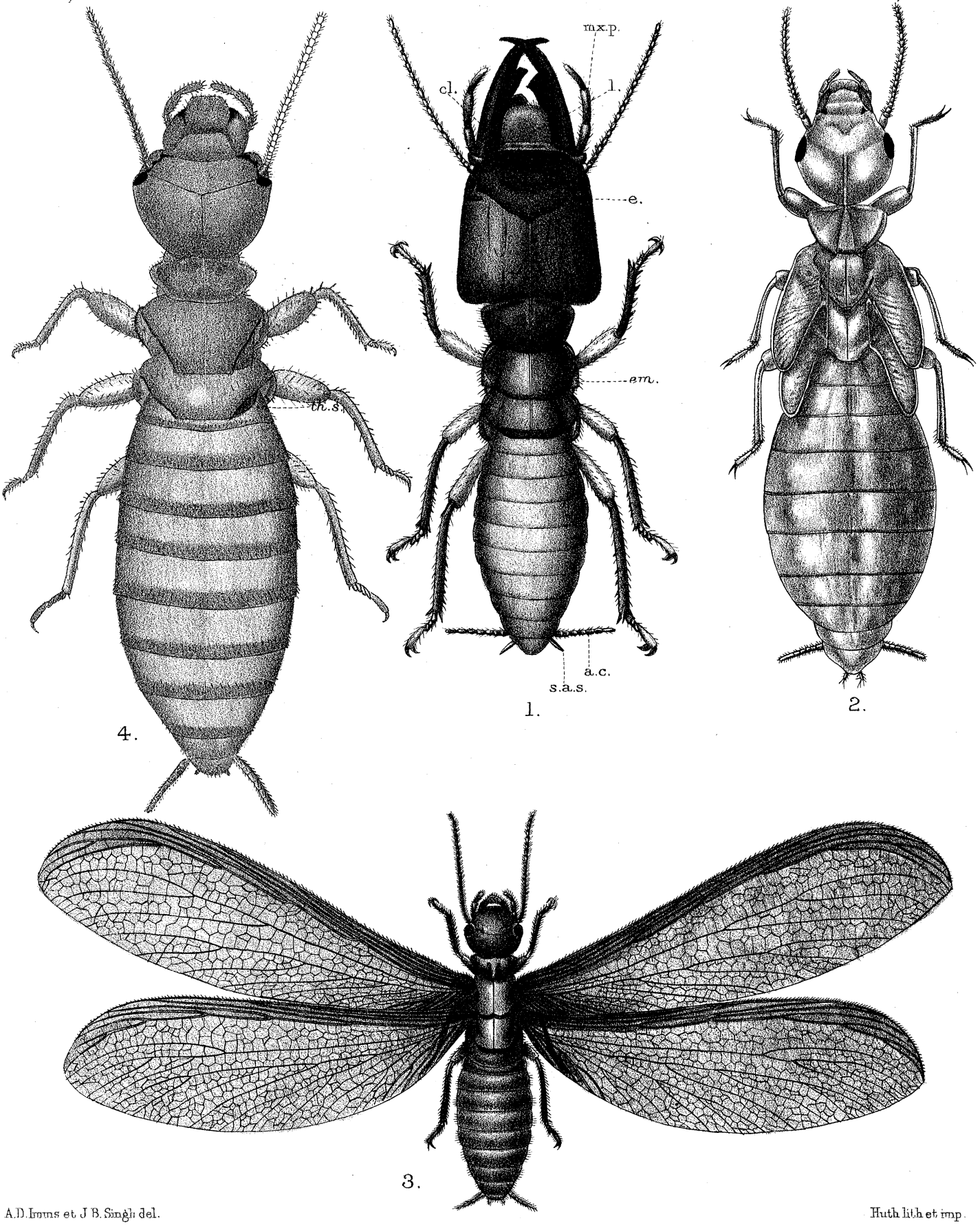
Fig. 19.—Basal joints of left antenna of a late larval soldier. × 41.

Fig. 20.—Dorsal view of the metathorax of a young soldier larva, 8·5 mm. long. × 20.

Fig. 21.—Dorsal view of the metathorax of a larva of a sexual form, showing developing wing rudiments. × 20.

Fig. 22.—Apex of the abdomen of a winged female (ventral aspect). × 18.

Fig. 23.—Apex of the abdomen of a winged male (ventral aspect). × 18.



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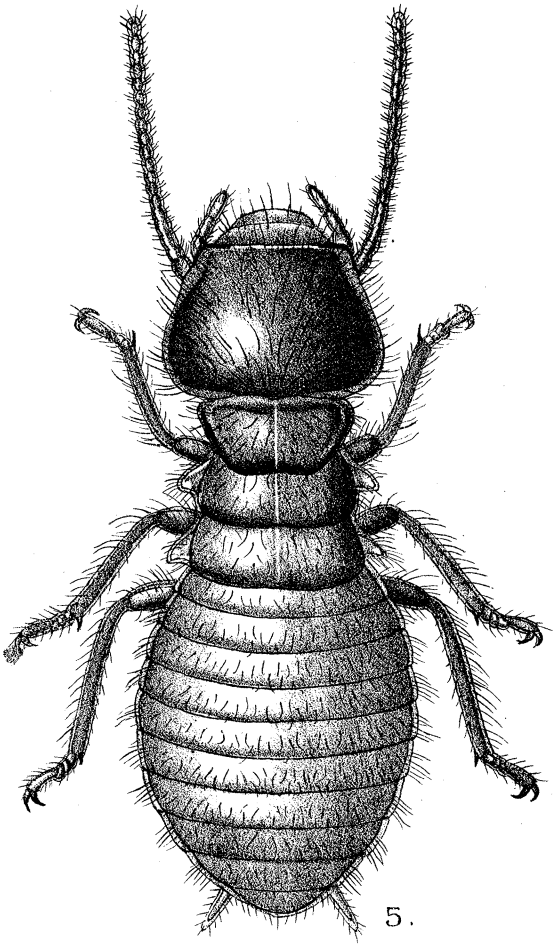

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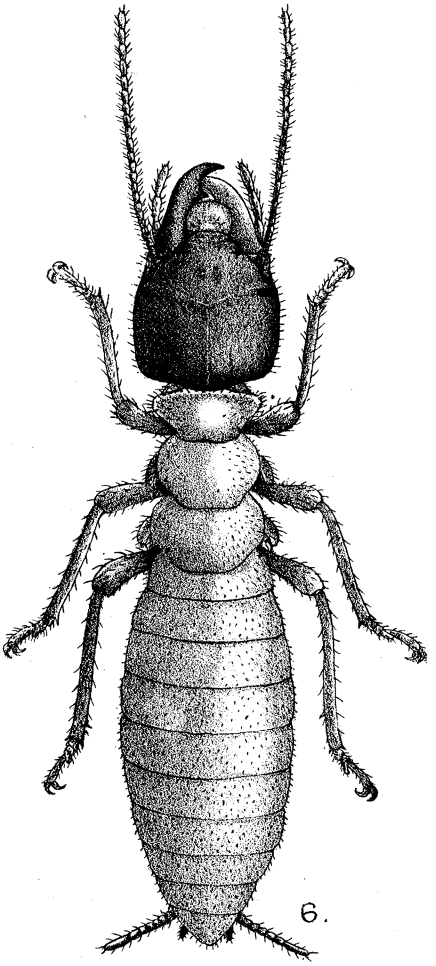

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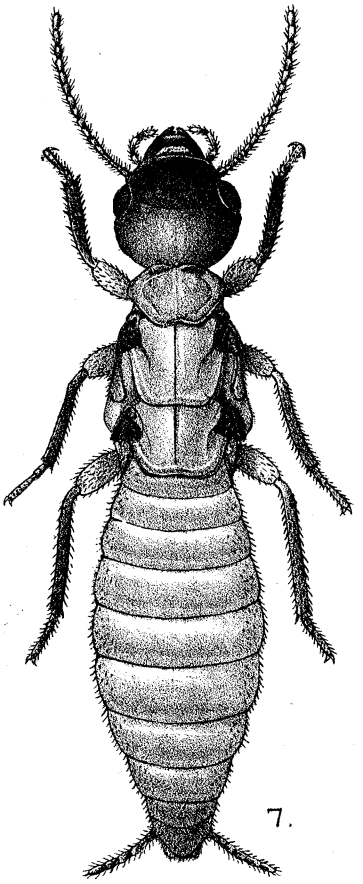

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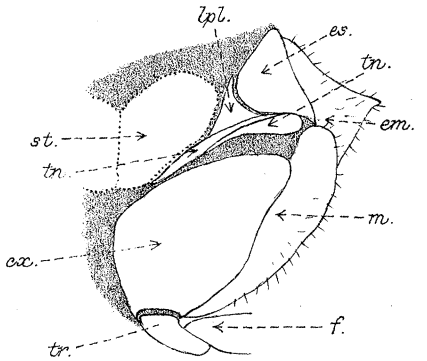

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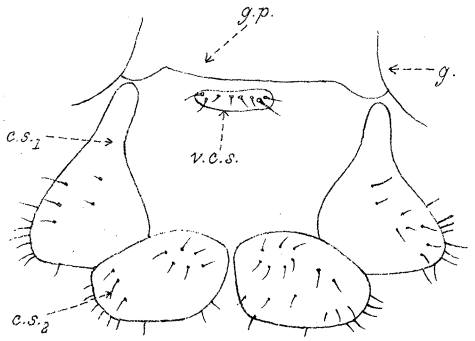

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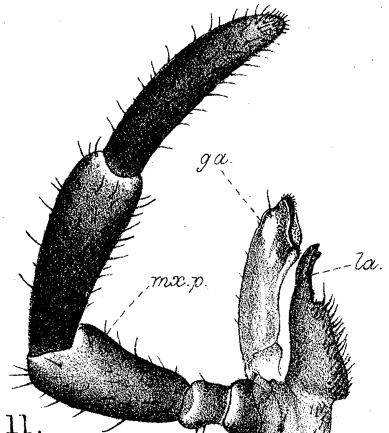

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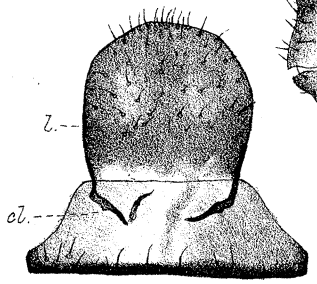

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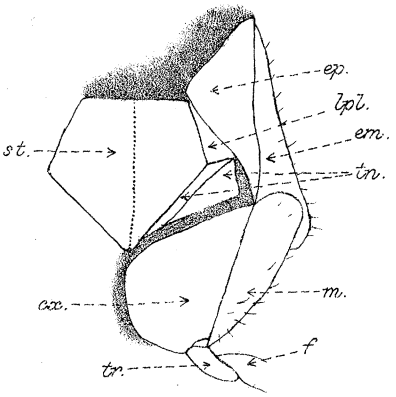

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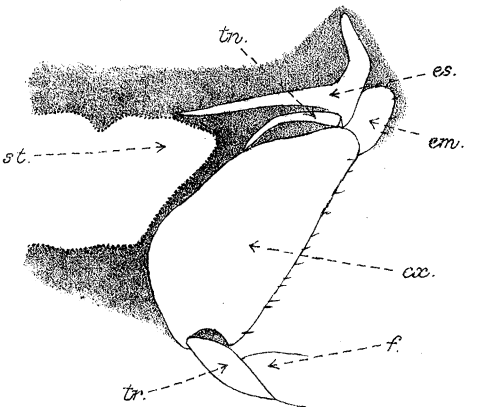

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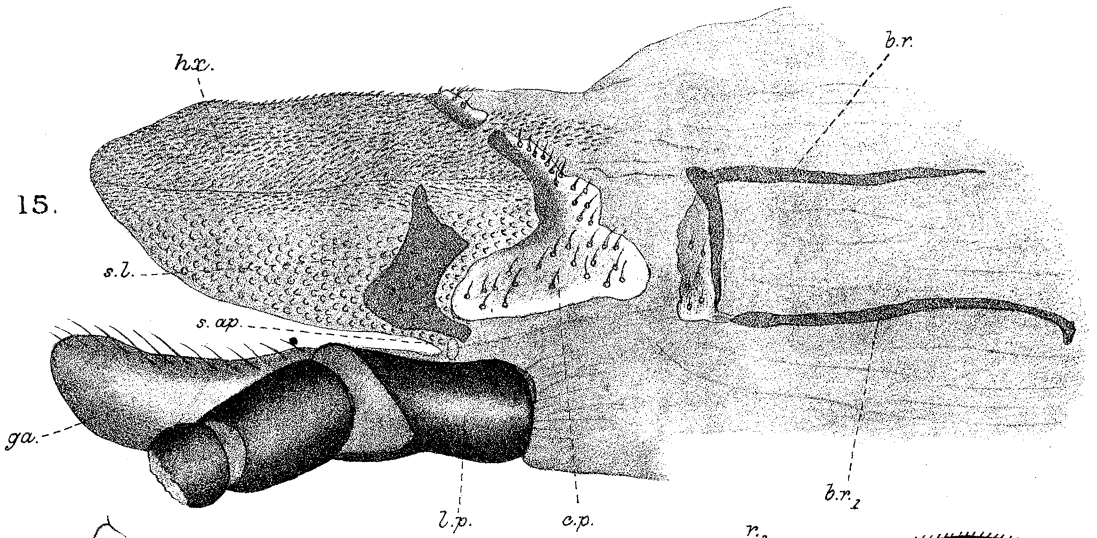

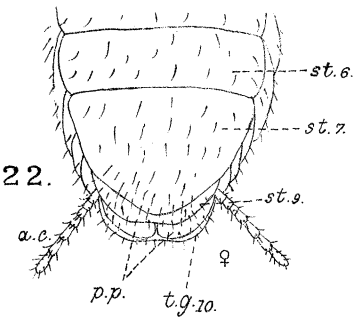

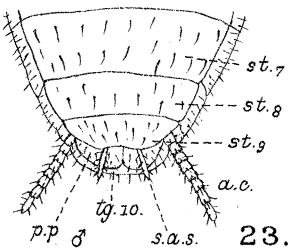

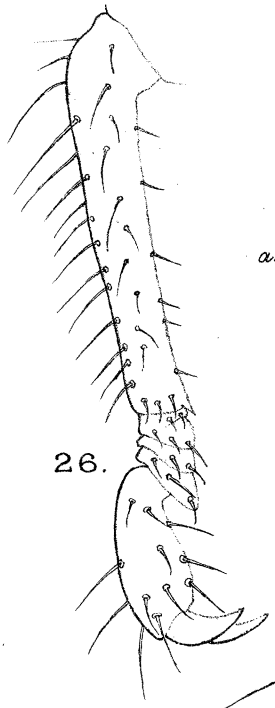

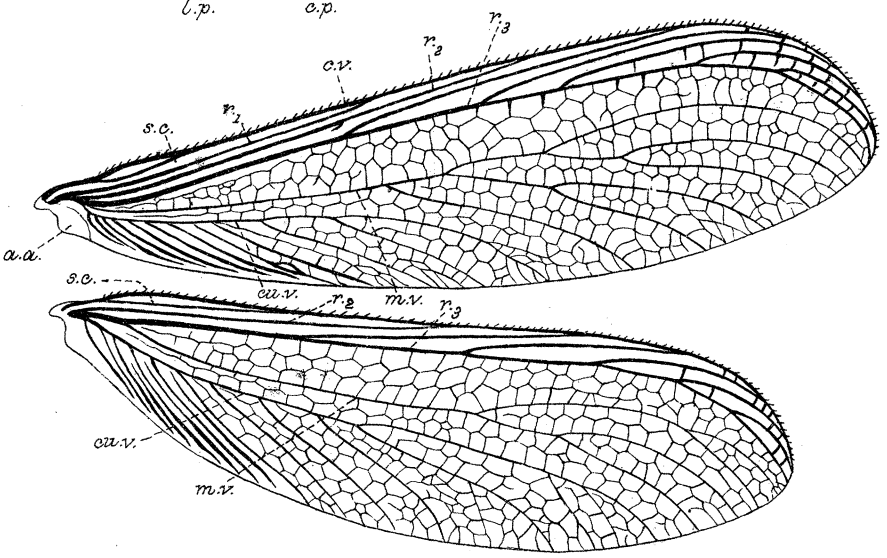

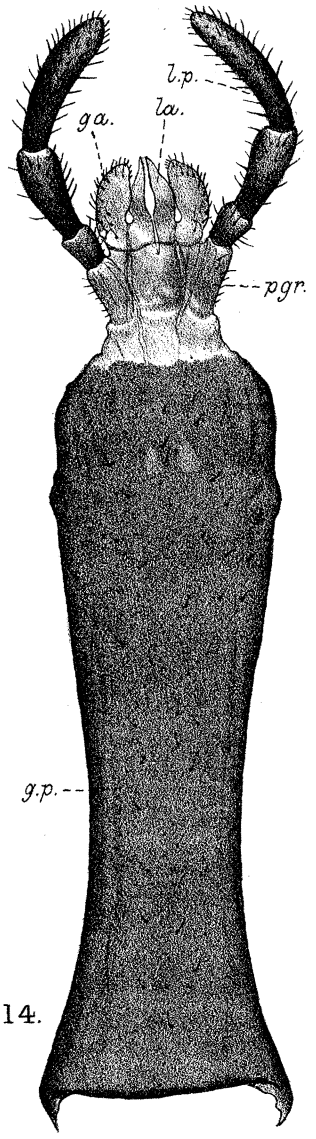

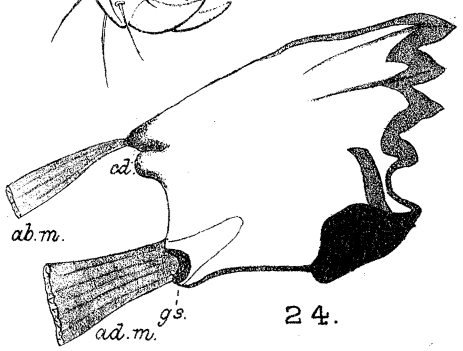

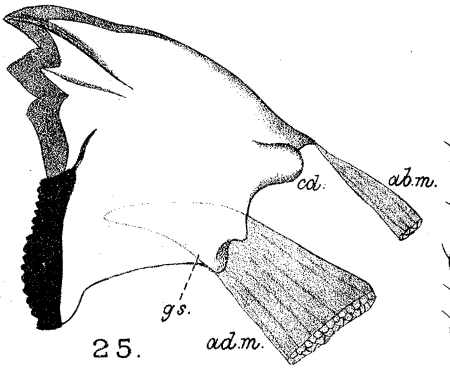

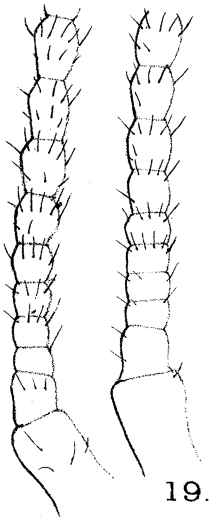

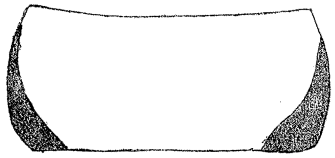

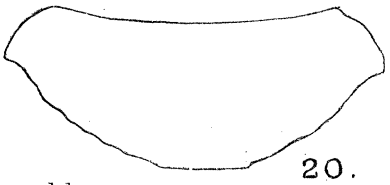

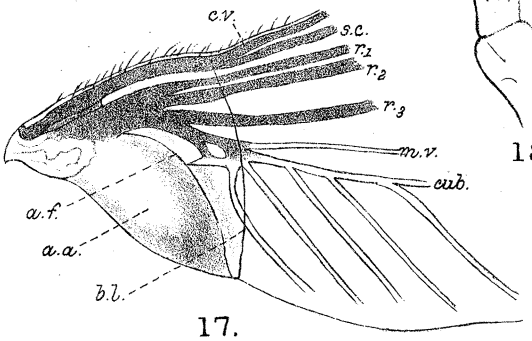

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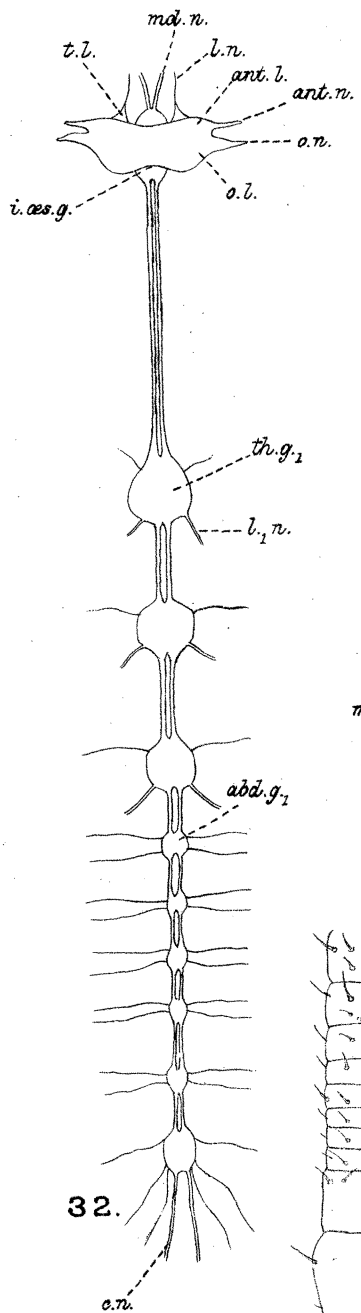

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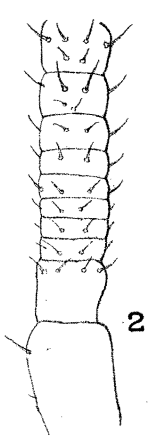

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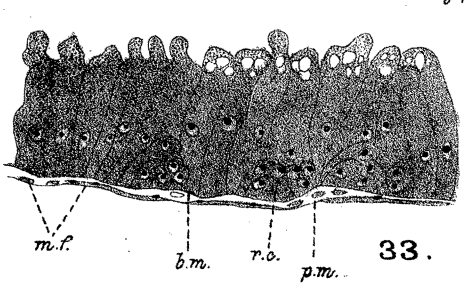

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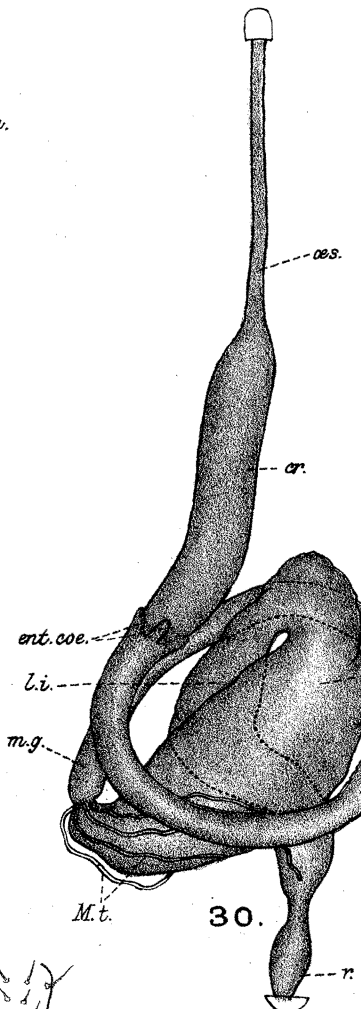

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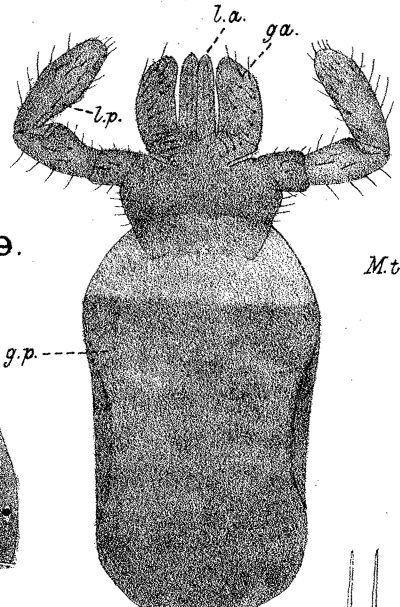

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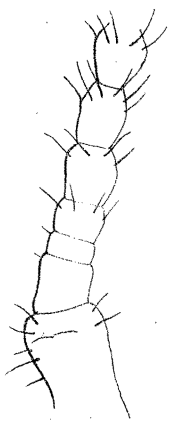

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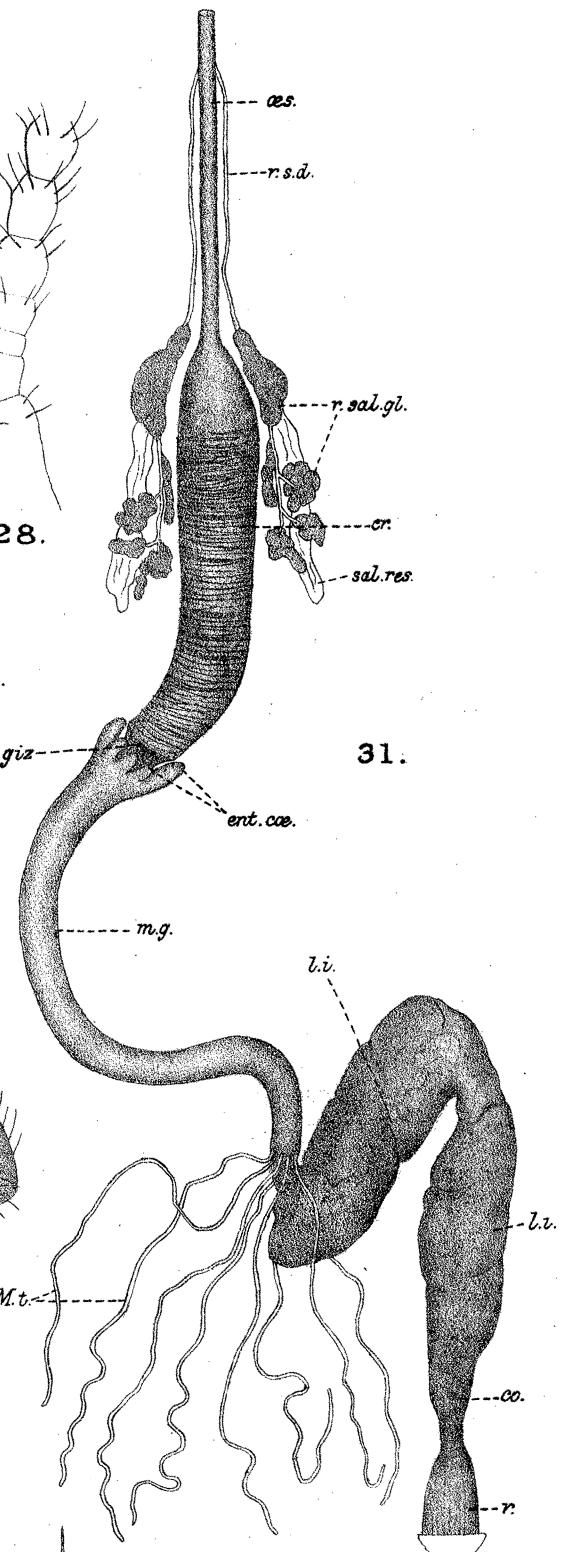

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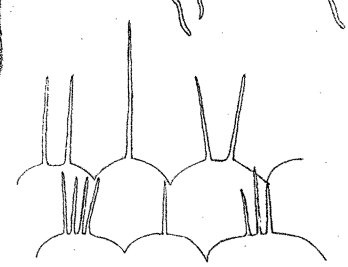

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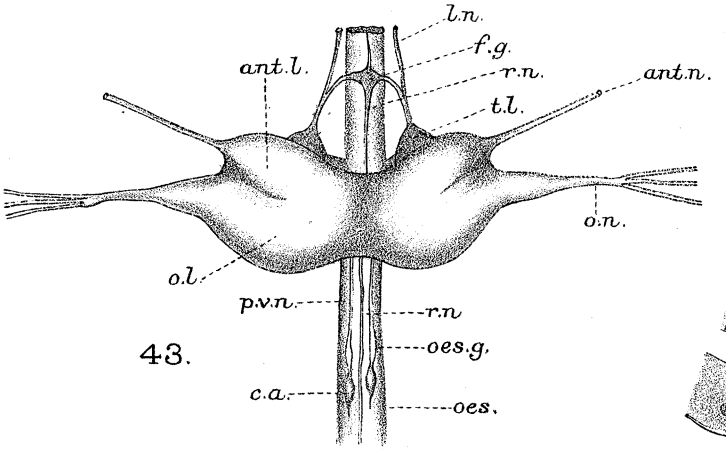

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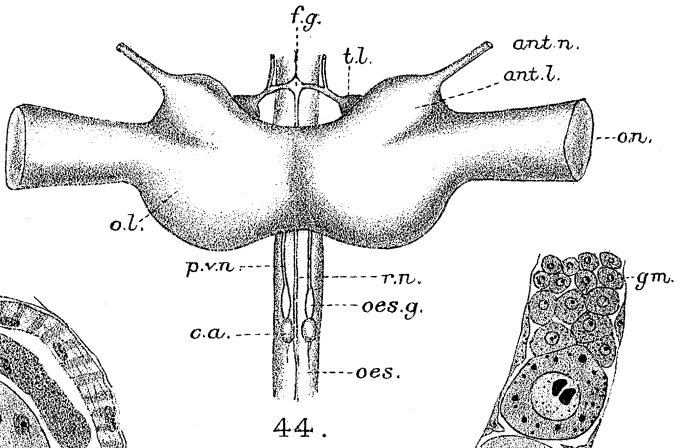

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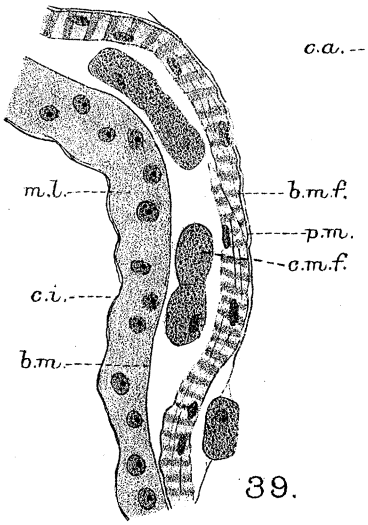

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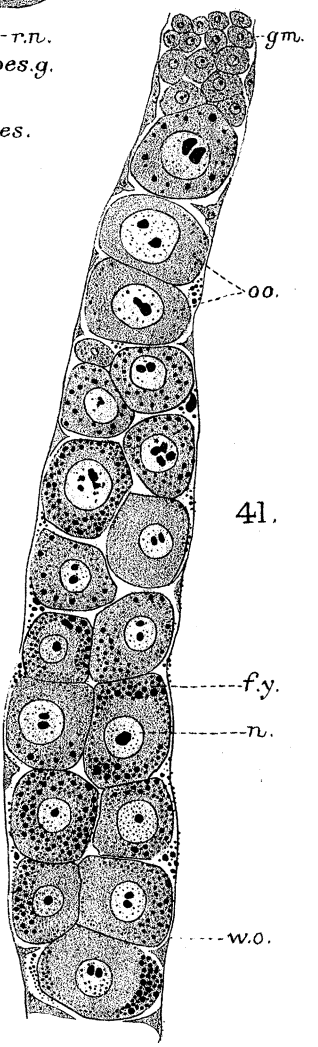

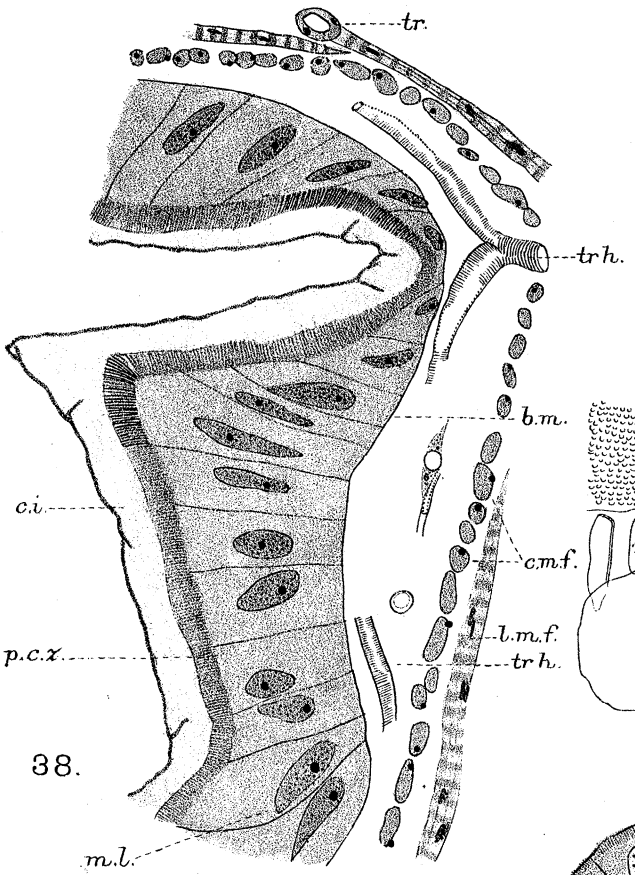

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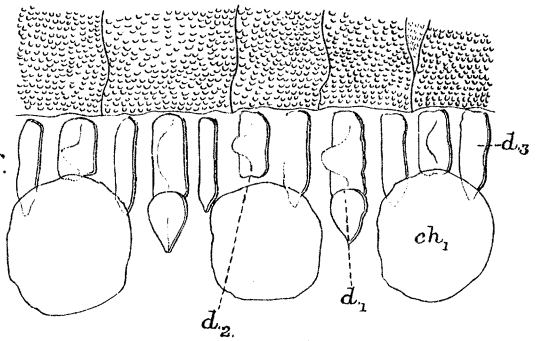

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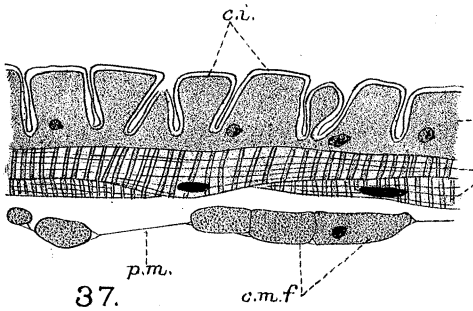

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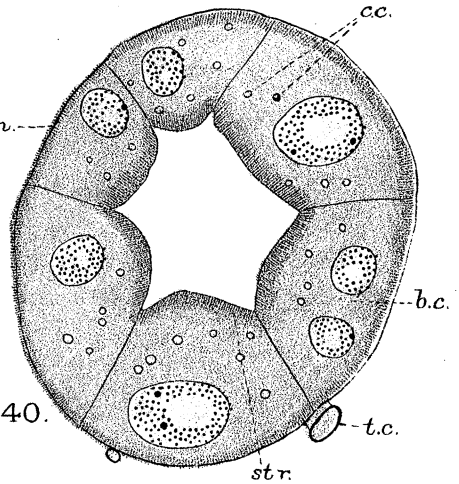

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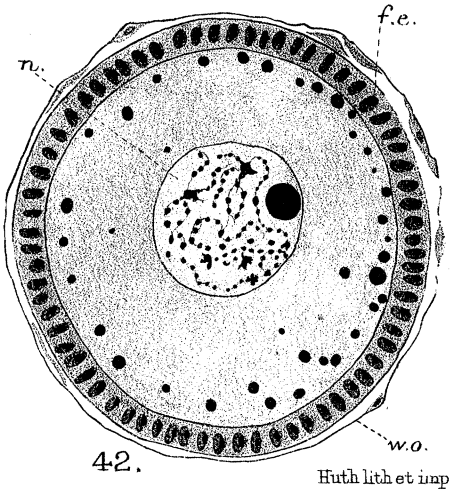

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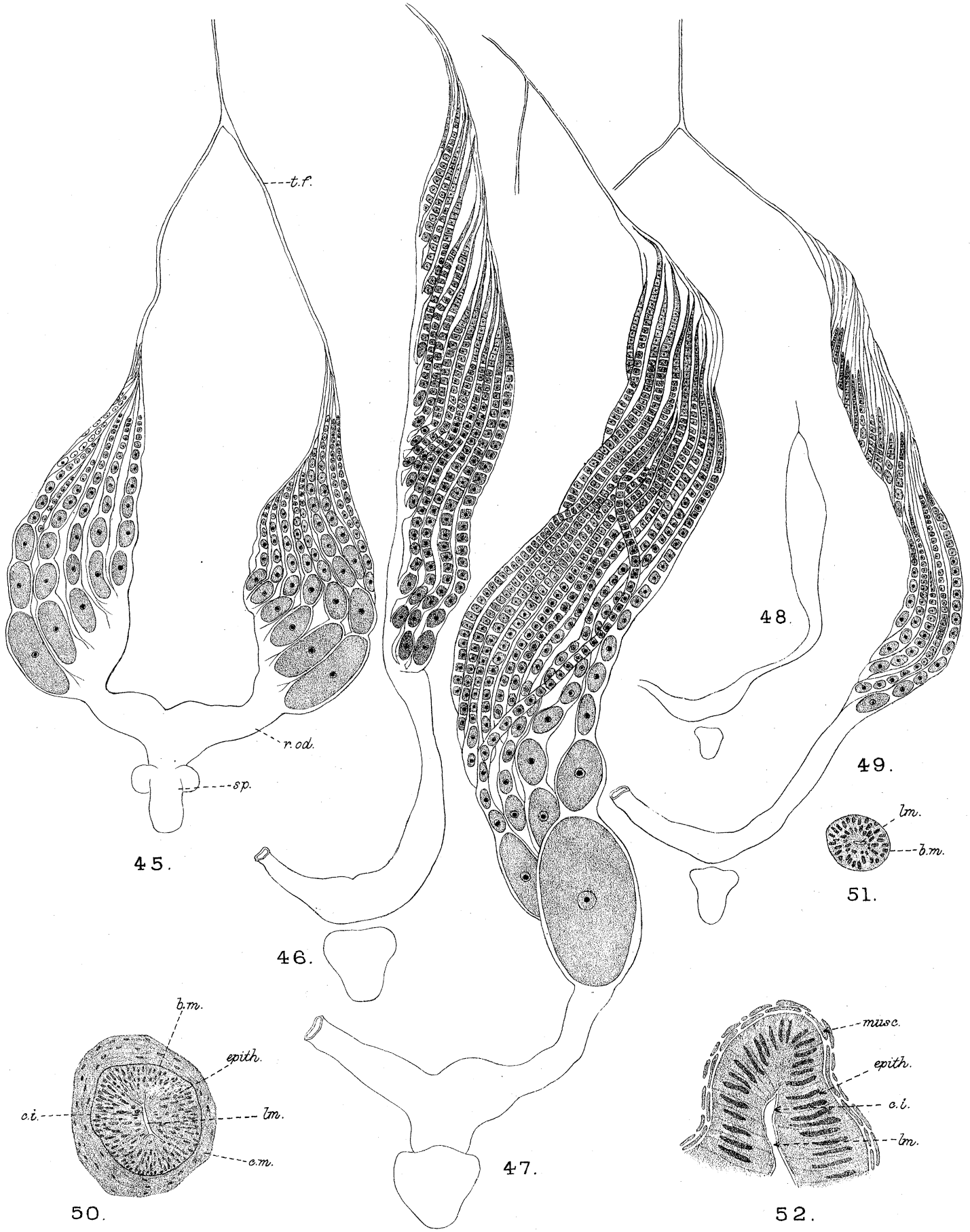
ARCHOTERMOPSIS WROUGHTONI DESN.



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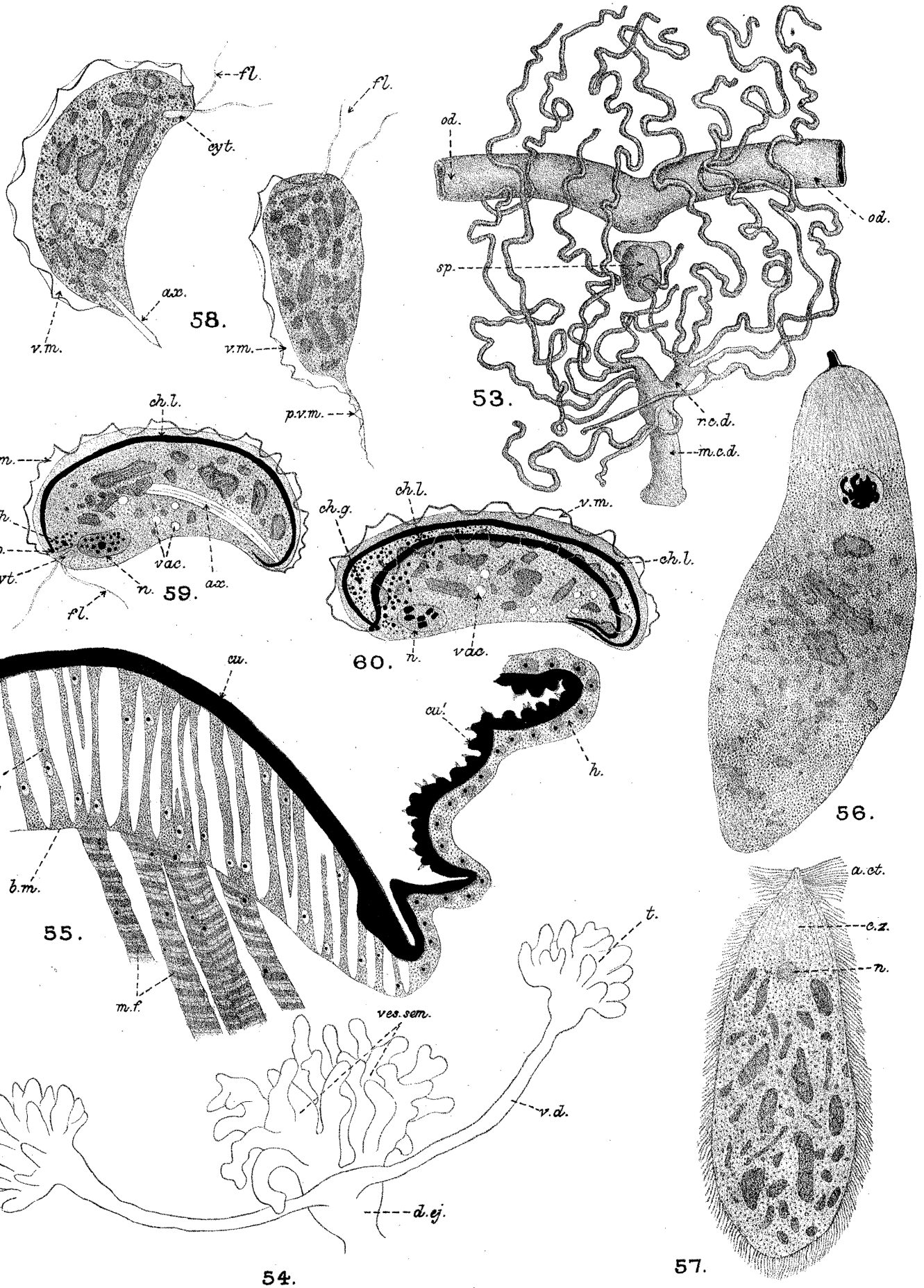

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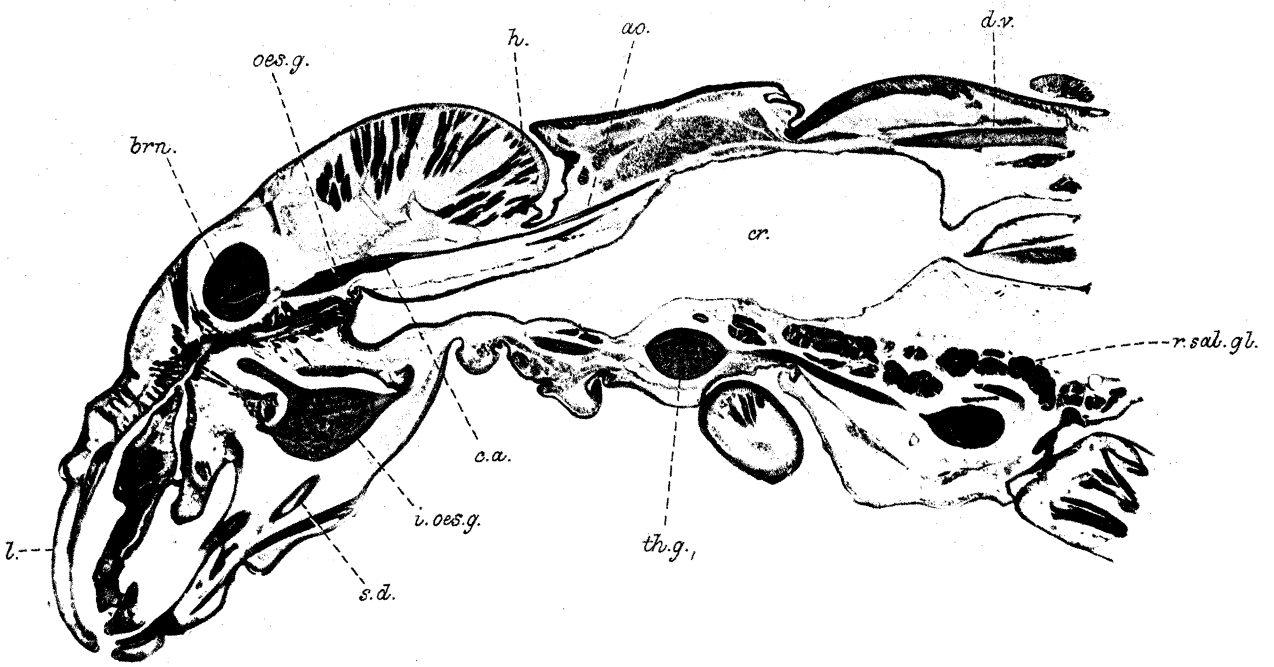

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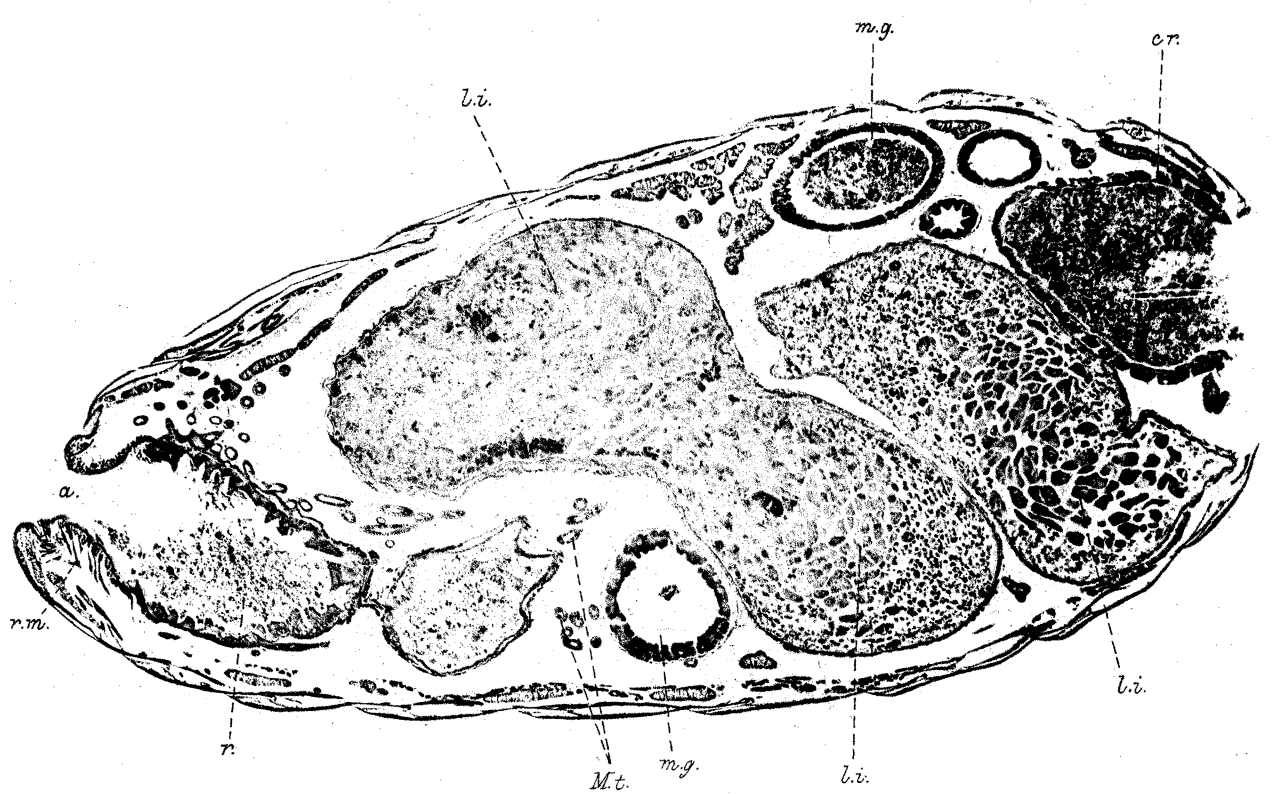

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Huth coll.

ARCHOTERMOPSIS WROUGHTONI DESN.

Fig. 24.—Left mandible of a winged female (dorsal view). × 38.

Fig. 25.—Right ditto. × 38.

Fig. 26.—Right hind leg of a larval soldier, 3 mm. in length (inner aspect). × 95.

Plate 6.

Fig. 27.—Second maxillæ (labium) of a winged female. × 35.

Fig. 28.—Basal joints of left antenna of an adult soldier. × 41.

Fig. 29.—Basal joints of left antenna of a larva 3 mm. long. × 95.

Fig. 30.—Digestive system of the soldier, showing the organs *in situ*. × *circa* 10.

Fig. 31.—Digestive system of the soldier, showing the organs unravelled and extended. × *circa* 10.

Fig. 32.—Central nervous system of the soldier. × *circa* 10.

Fig. 33.—Longitudinal section through the wall of the mid-gut of the soldier (Ehrlich's hæmatoxylin). × 500.

Fig. 34.—Scale-like papillæ armed with spines from the circlet of cushions or pads situated immediately behind the gizzard (adult soldier). × 1800.

Fig. 35.—Semi-lunar papillæ of the inner lining of the crop immediately in front of the gizzard. × 950.

Plate 7.

Fig. 36.—A preparation of a portion of the chitinous inner lining of the gizzard mounted in glycerine. Just in front of the gizzard teeth the wall of the crop is seen to be invested with minute semi-lunar papillæ (vide also Fig. 36).

Fig. 37.—Longitudinal section through the wall of the œsophagus of the soldier (posterior region). × 820.

Fig. 38.—Longitudinal section through the wall of the rectum of the soldier. × 500.

Fig. 39.—Longitudinal section through the wall of the large intestine of the soldier. × 920.

Fig. 40.—Transverse section of a Malpighian tube of the soldier. × 920.

Fig. 41.—Upper portion of an ovariole of the adult soldier stained with Mann's methyl-blue-eosin. × 550.

Fig. 42.—Transverse section through the lower portion of an ovariole and an egg follicle of the soldier. × 550.

Fig. 43.—Brain of the adult soldier, together with the sympathetic nervous system and the corpora allata. × *circa* 33.

Fig. 44.—Ditto of winged female. × *circa* 34.

Plate 8.

Fig. 45.—Ovary of an unfertilised winged female, 13 mm. long. × 32.

Fig. 46.—Ditto of an adult soldier. × 32.

Fig. 47.—Ditto of a gynæcoid worker-like form. × 32.

Fig. 48.—Ditto of a young larval soldier, 8·5 mm. long. × 32.

Fig. 49.—Ditto of a first stage nymph. × 32.

Fig. 50.—Transverse section across the main common duct of the colleterial gland; stained with brazilin. × 240.

Fig. 51.—Transverse section across a tube of the colleterial glands; stained with brazilin. × 240.

Fig. 52.—Longitudinal section through a portion of the spermatheca; stained with brazilin.

Plate 9.

Fig. 53.—Colleterial glands, spermatheca and proximal portions of the oviducts of an adult soldier. From a preparation stained with Mann's methyl-blue-eosin and mounted in euparal. Owing to the extension of the abdominal sterna during mounting the spermatheca appears slightly further behind the oviducts than occurs in the living insect. × 46.

Fig. 54.—Male reproductive organs of the adult soldier. × 48.

Fig. 55.—Section through the body-wall in the head of a winged male near the position indicated by *h* in Plate 10, fig. 61.

Fig. 56.—*Trichonympha pristina* Imms. sp. nov. from a specimen fixed in hot Schaudinn's fluid and stained with Heidenhain's iron-alum hæmatoxylin. × 400.

Fig. 57.—*Trichonympha pristina* Imms sp. nov. from a living specimen examined in salt solution. ×

Fig. 58.—*Trichomonas termitis* Imms sp. nov. Two living specimens examined in salt solution. ×

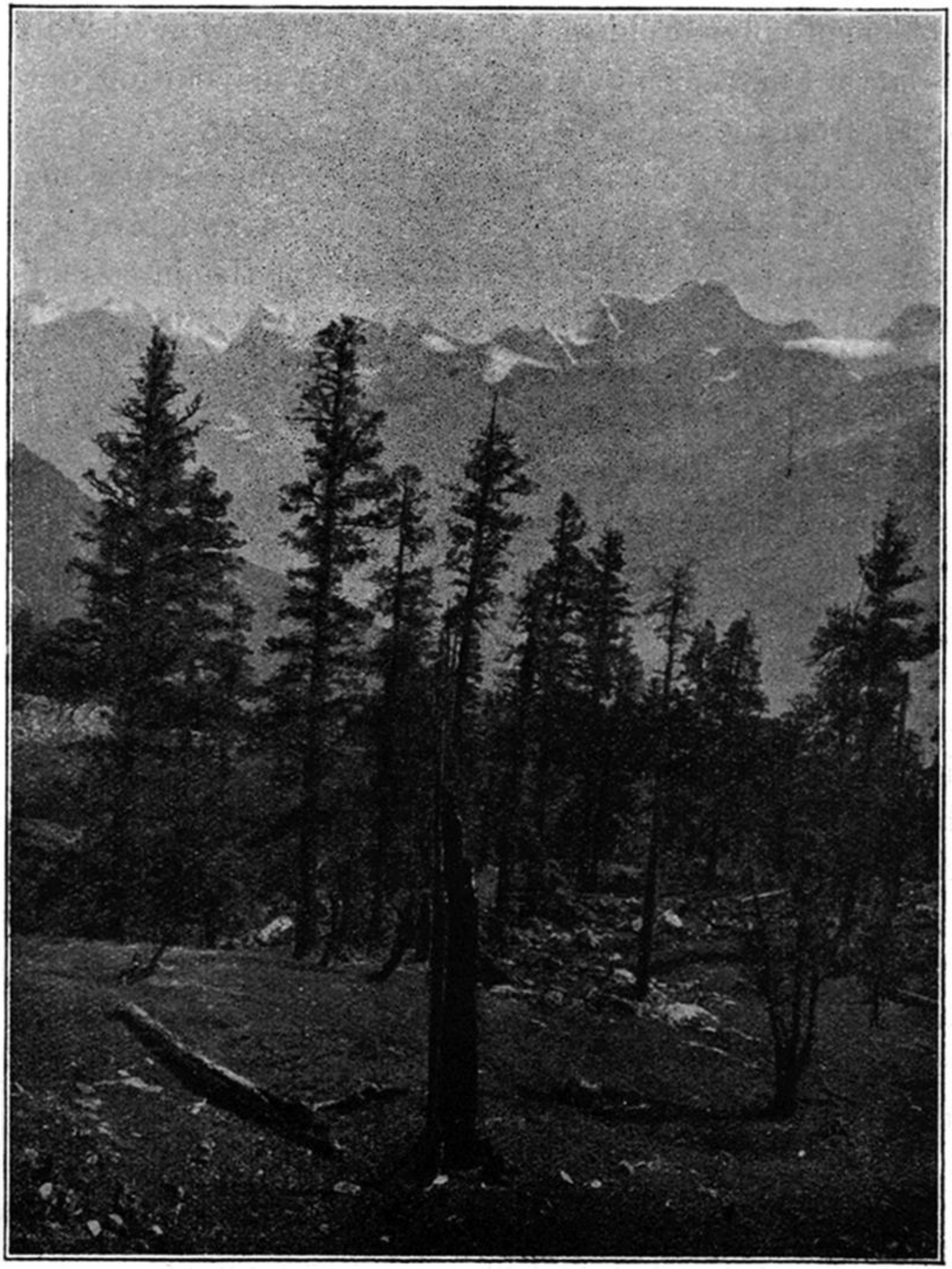
Fig. 59.—*Trichomonas termitis* Imms sp. nov. from a specimen fixed in hot Schaudinn's fluid and stained with Heidenhain's iron-alum hæmatoxylin. × 1000.

Fig. 60.—Ditto ditto undergoing longitudinal fission. × 1000.

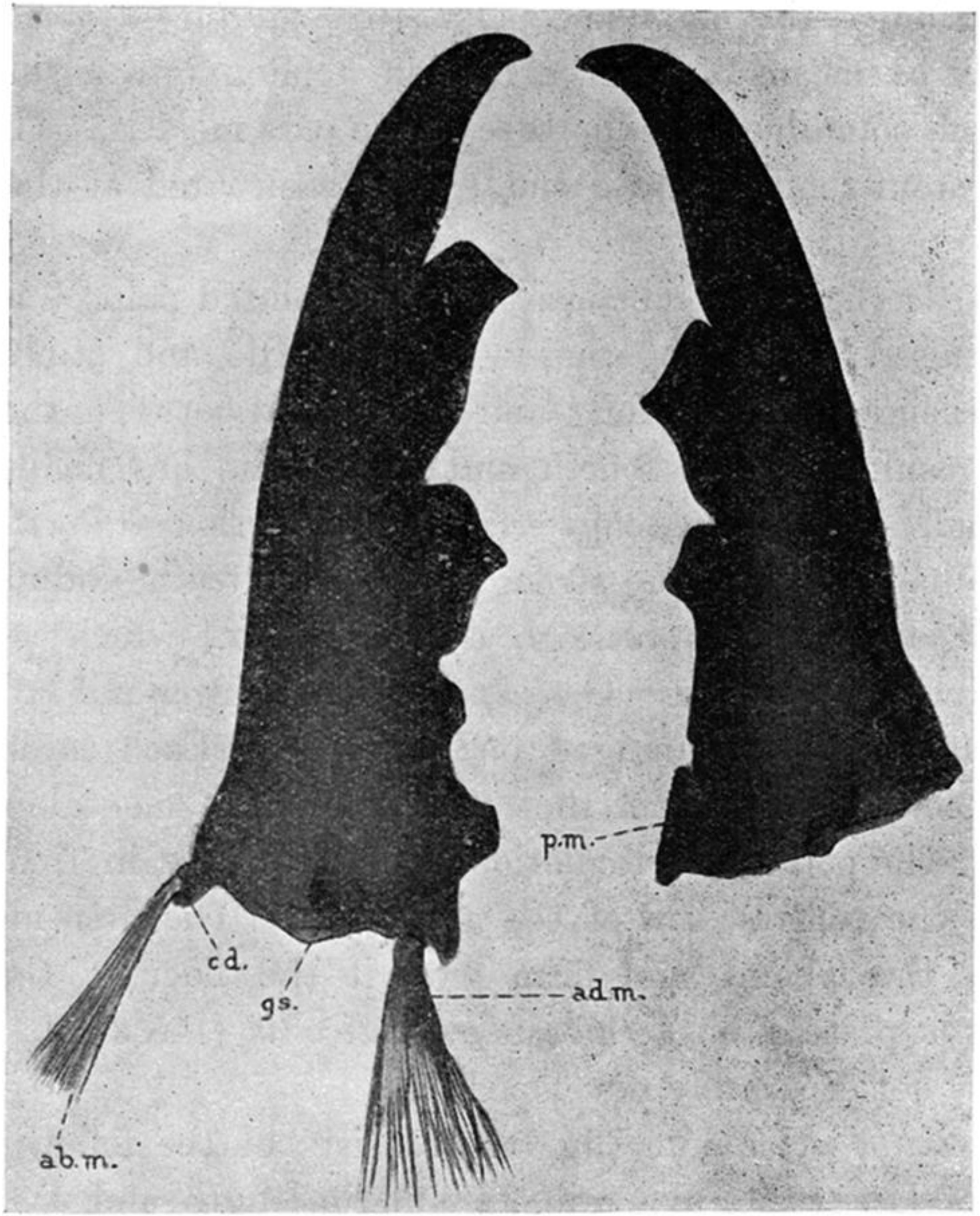
Plate 10.

Fig. 61.—Longitudinal section through the head and thorax of a winged male stained with Heidenhain's iron-alum hæmatoxylin. (Enlargement from a photograph taken by Mr. J. T. Wadsworth.) × 30.

Fig. 62.—Longitudinal section through the abdomen of an adult soldier (female), showing the distension of the large intestine owing to the presence of great numbers of Protozoa. (Enlargement from a photograph taken by Mr. J. T. Wadsworth.) × 26.



TEXT-FIG. 1.—View in a coniferous forest near Ramni (Garhwal, Himalaya). The fallen log in the fore-ground contained extensive colonies of *Archotermopsis wroughtoni*. A. D. IMMS photo.



TEXT-FIG. 2.—Right and left mandibles of the adult soldier. × 26 ; *cd.*, condyle ; *gs.*, ginglymus ; *ab.m.*, abductor muscle ; *ad.m.*, adductor muscle ; *p.m.*, pars molaris.

TEXT-FIG. 12.—Portion of a dead log of Deodar (*Cedrus deodara*) showing the galleries excavated by *Archotermopsis wroughtoni*, running parallel with the grain of the wood. The outer zone of the sap-wood is seen on the right-hand side, and new galleries are being extended into the undecayed wood on the left. (From a drawing lent by the Zoological Branch of the Forest Research Institute, Dehra Dun, India.)

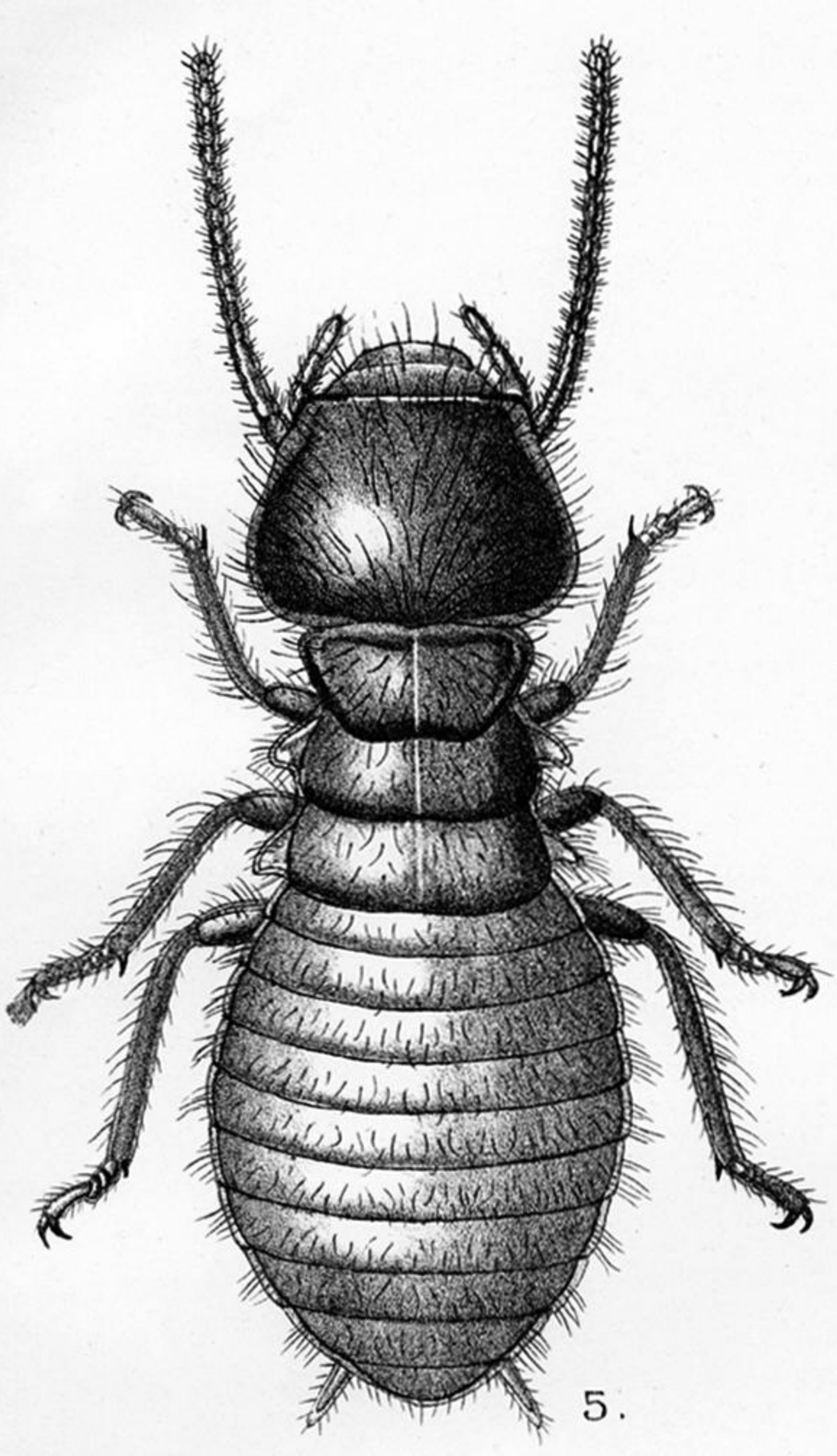
Plate 3.

Fig. 1.—An adult soldier (male). × 6.

Fig. 2.—A mature second stage nymph (male) drawn just before the final ecdysis into the winged form. × 11.

Fig. 3.—A fully developed winged form (male) caught while issuing from the nest during a "swarming" period at Bhowali (Kumaon Himalaya). × *circa* 4.

Fig. 4.—A fully grown worker-like form (male). On the right side of the meso- and meta-thorax are irregular scars suggestive of abortive wing vestiges. × 10.



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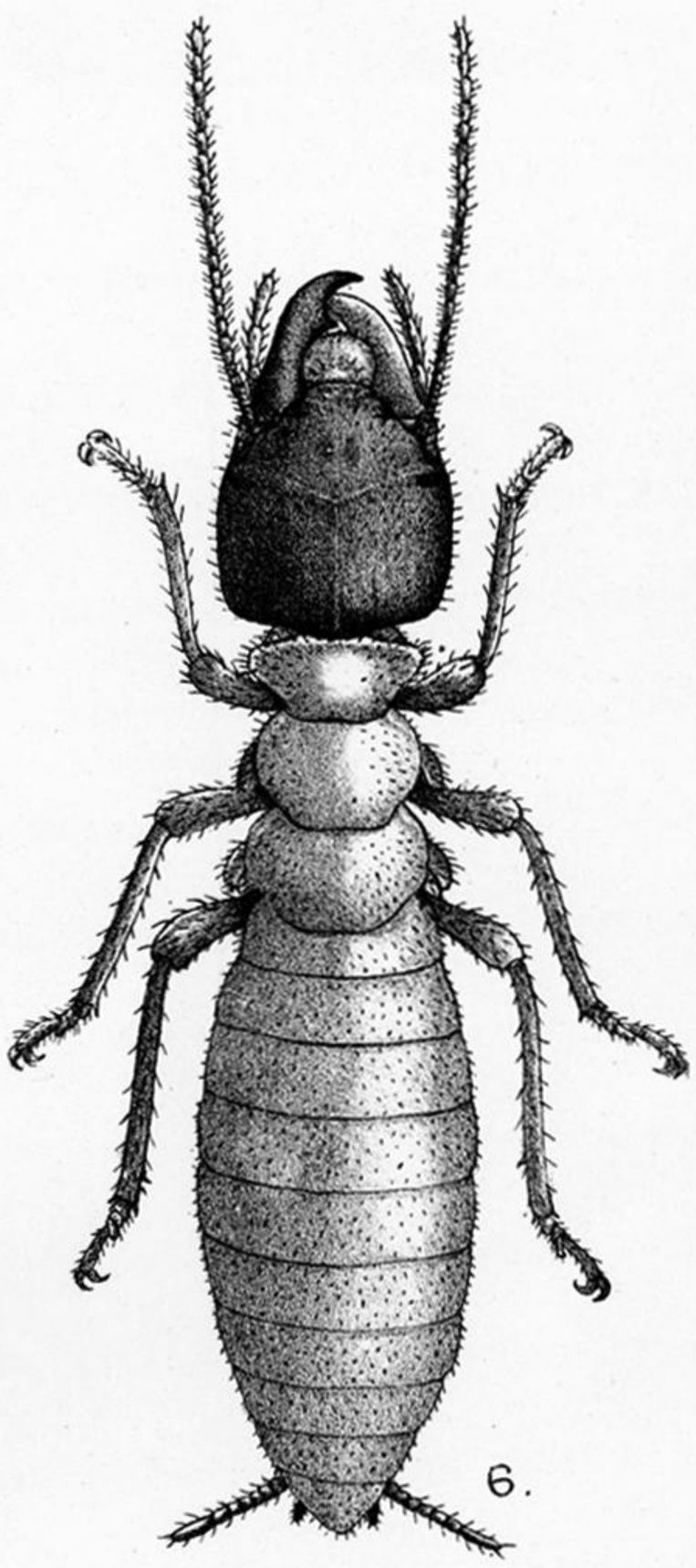

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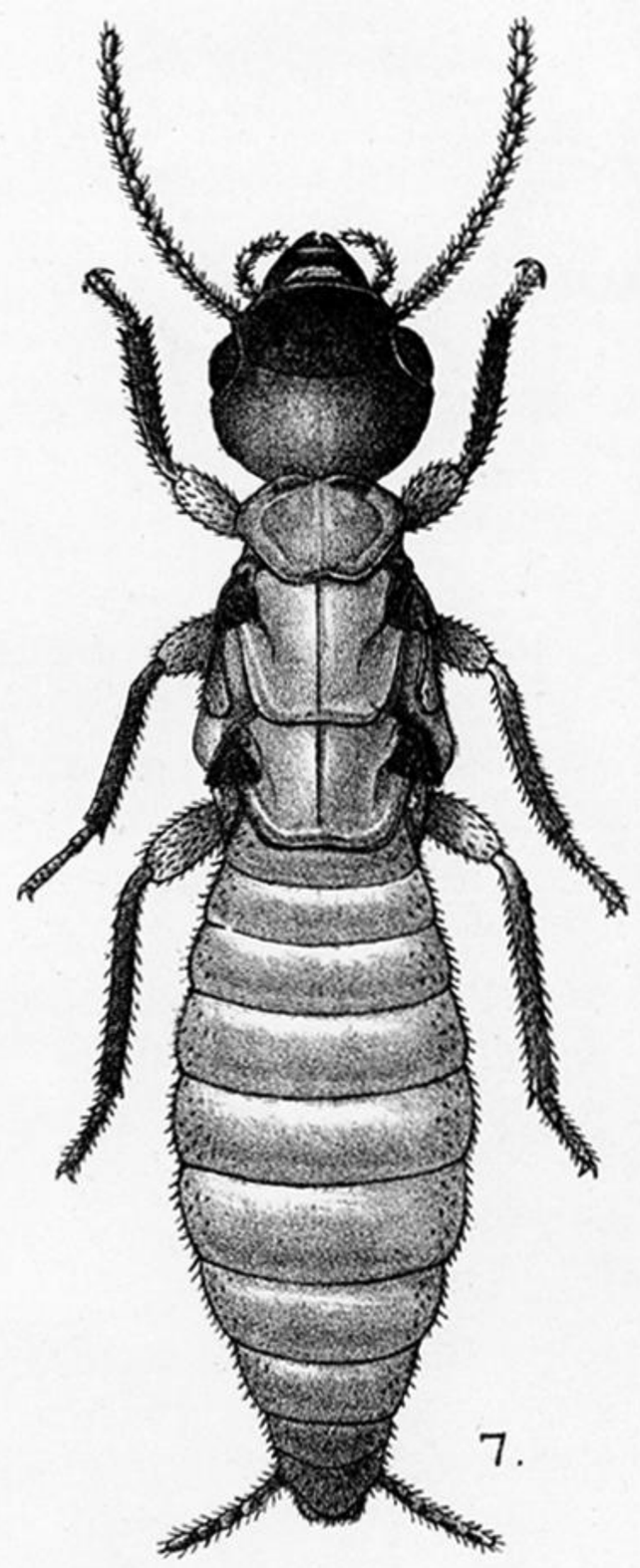

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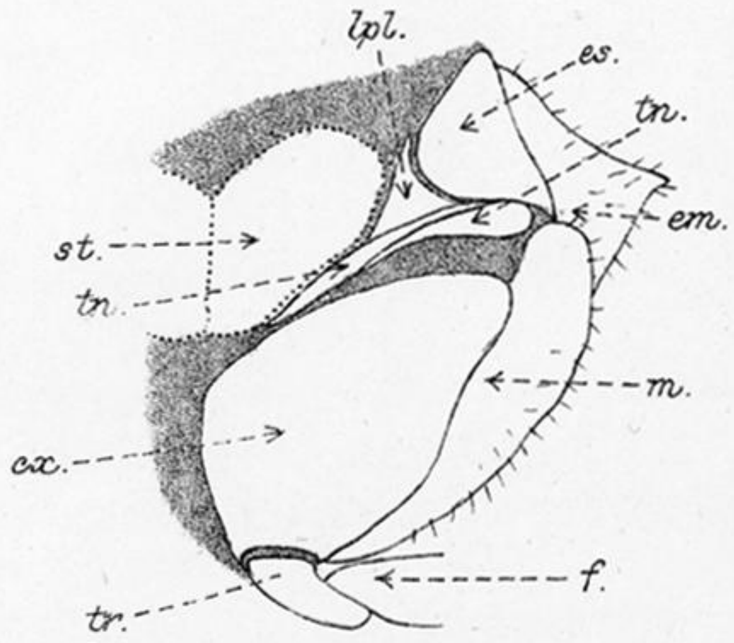

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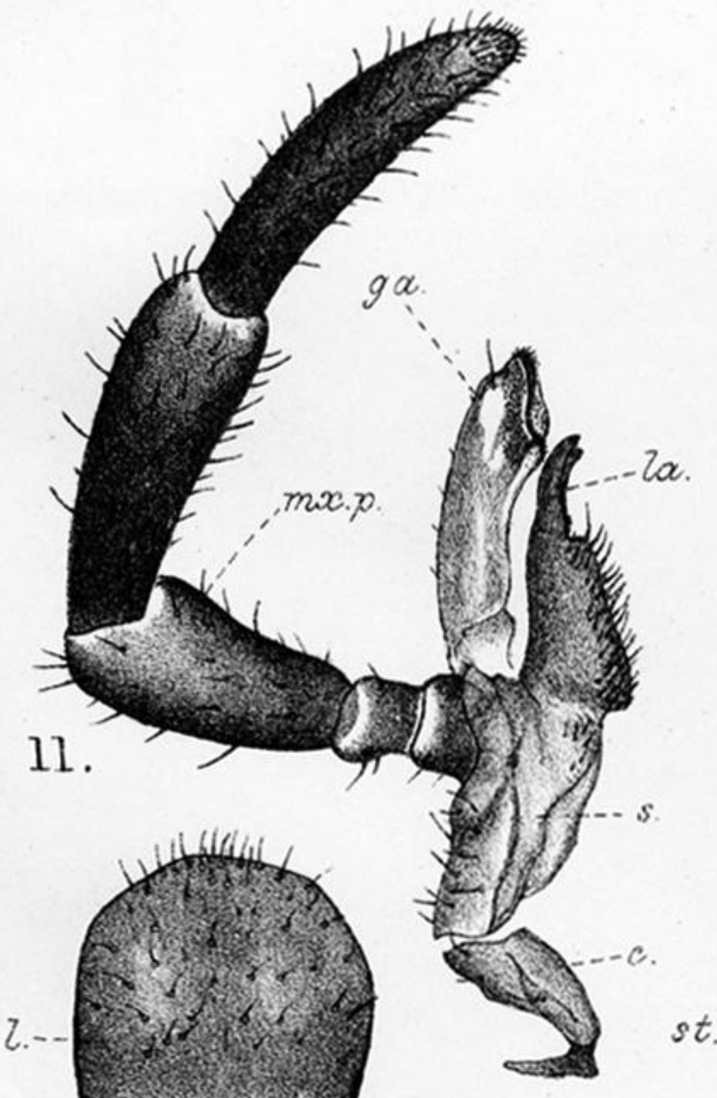

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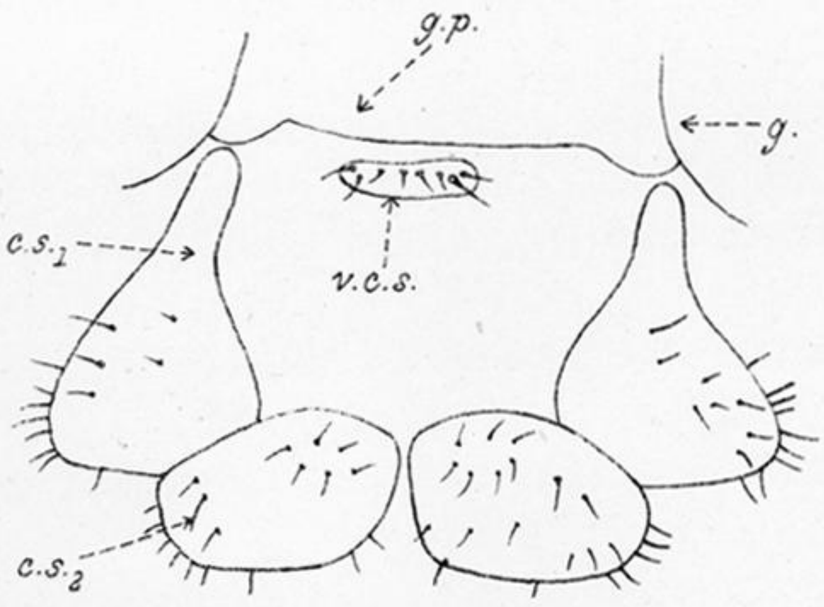

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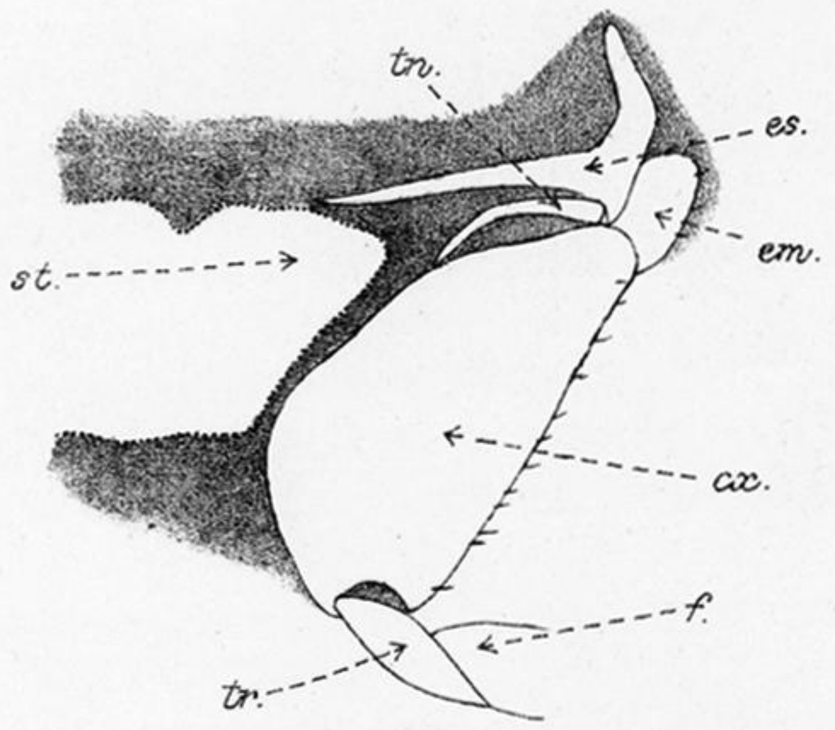

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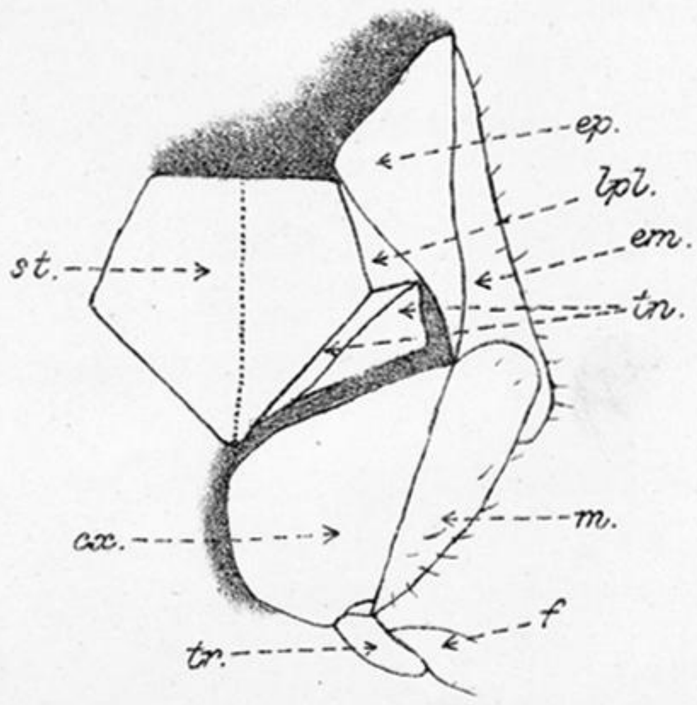

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ARCHOTERMOPSIS WROUGHTONI DESN.

PLATE 4.

Fig. 5.—A young soldier larva, 6 mm. long. × *circa* 15.

Fig. 6.—A late larval soldier (female) in the last stage prior to assuming the adult form. × 7.

Fig. 7.—A queen taken from a colony near Dharmoti (Kumaon Himalaya). × *circa* 8.

Fig. 8.—Basal sclerites of the hind leg (left) of the soldier. × *circa* 16½.

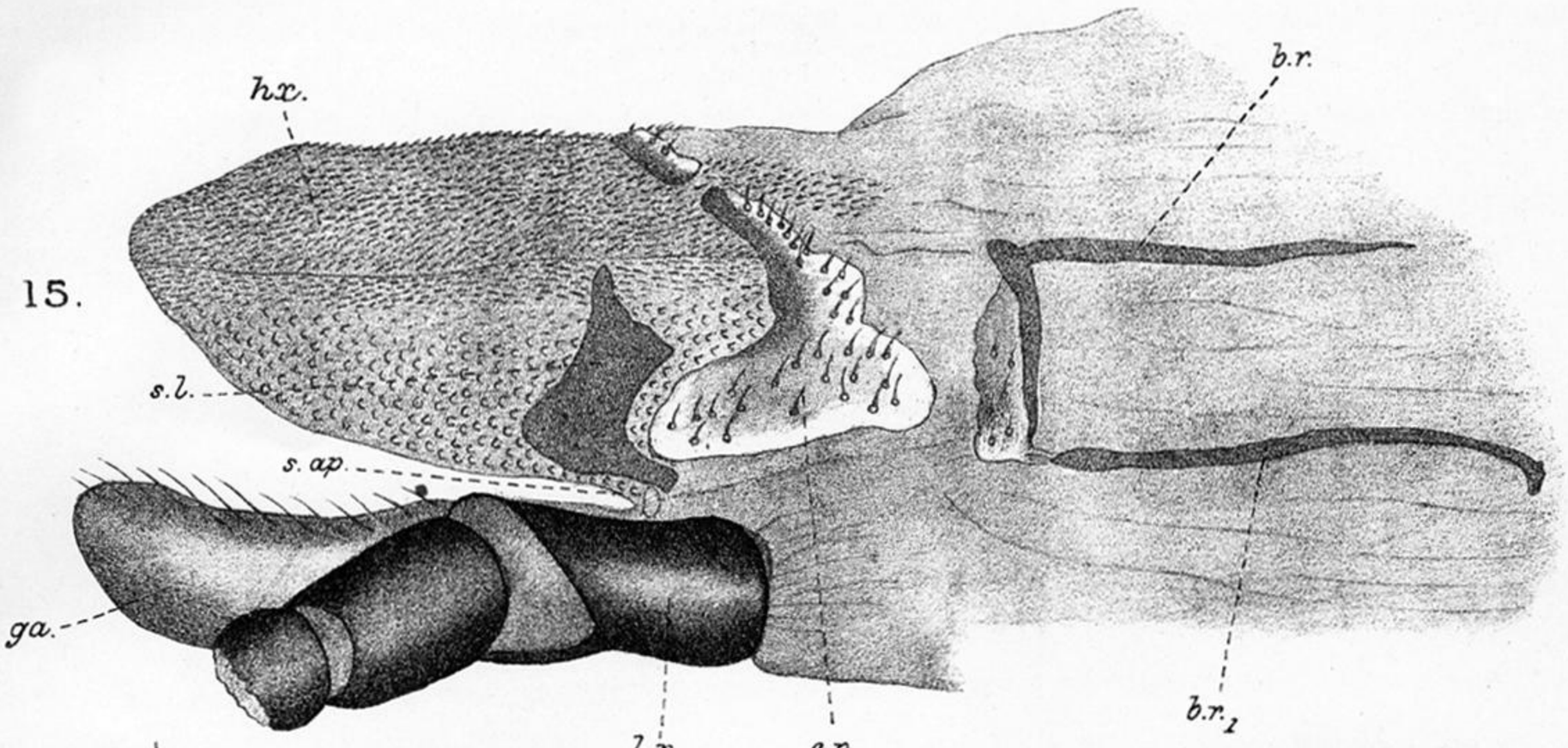
Fig. 9.—Basal sclerites of the fore leg (left) of the soldier. × *circa* 16½.

Fig. 10.—Cervical sclerites of the soldier. × 27.

Fig. 11.—Left first maxilla of the soldier. × 24.

Fig. 12.—Labrum and clypeus of the soldier. × 22.

Fig. 13.—Basal sclerites of the middle leg (left) of the winged form (male). × *circa* 16½.



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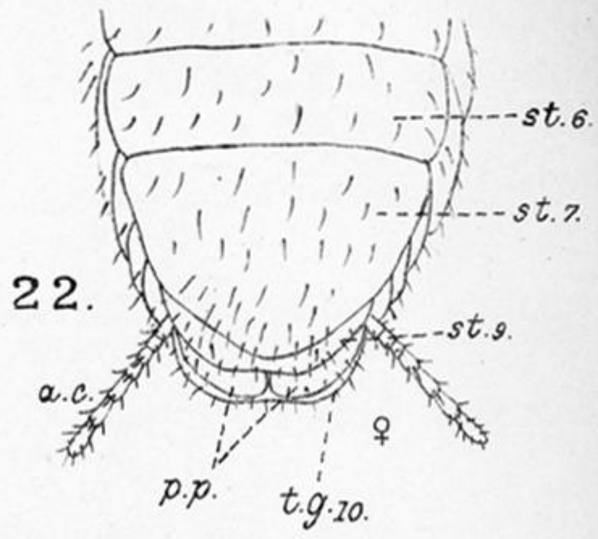

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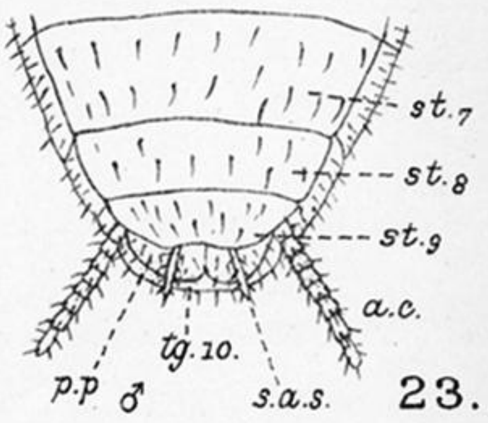

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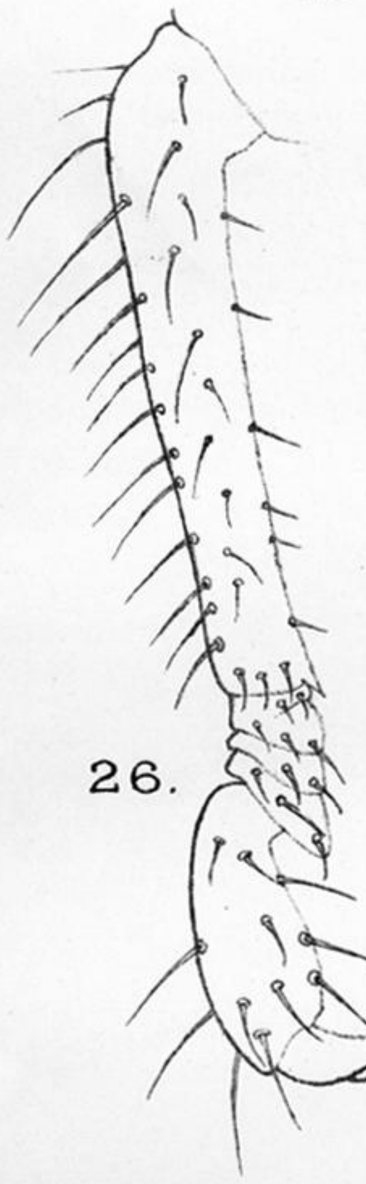

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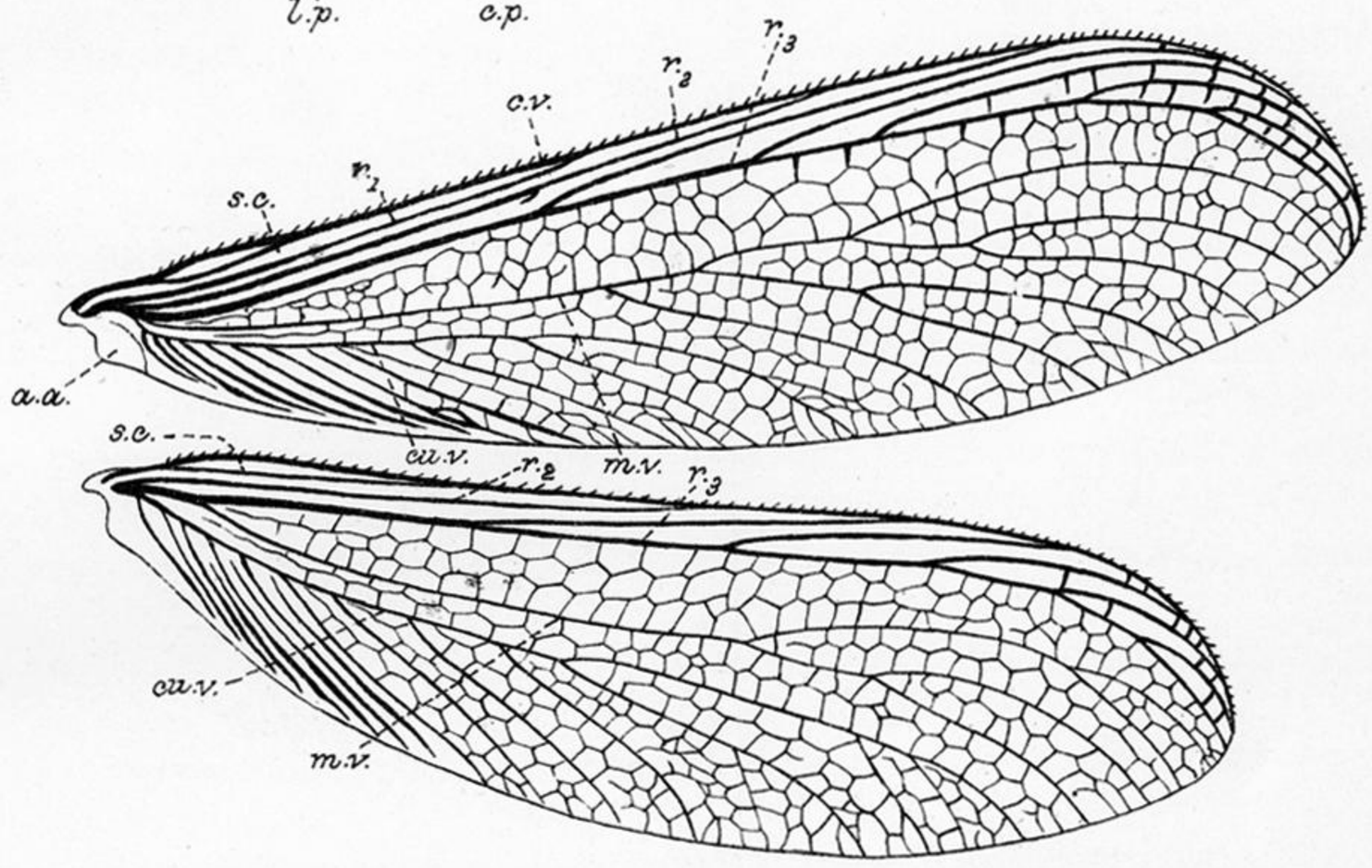

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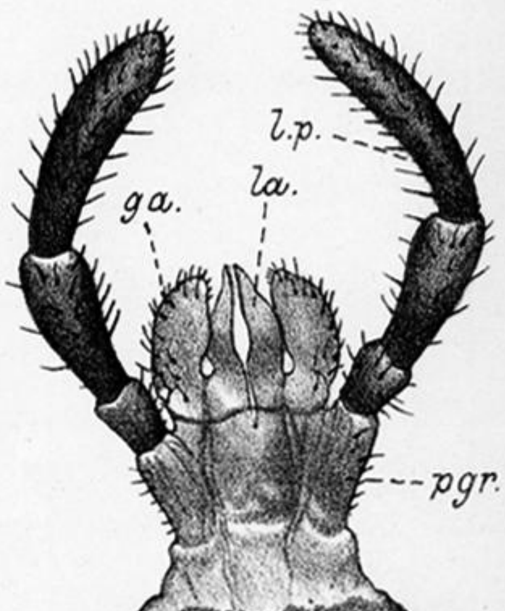

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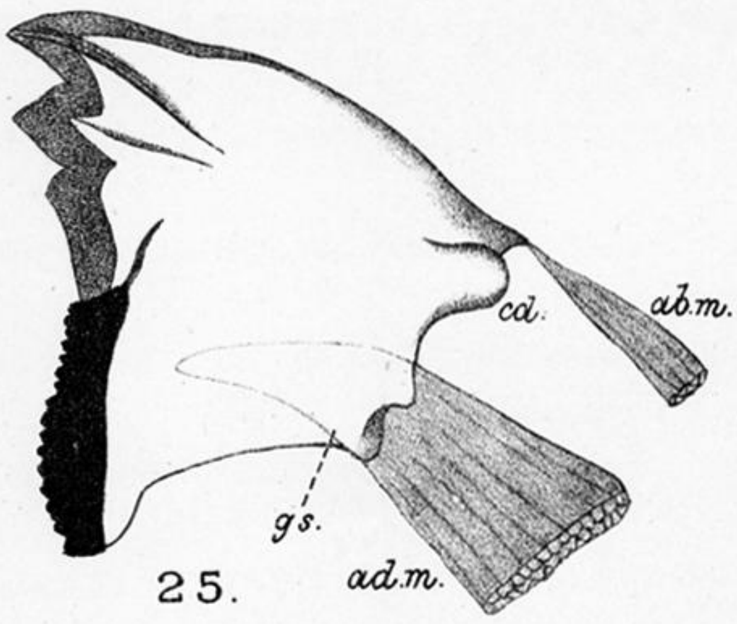

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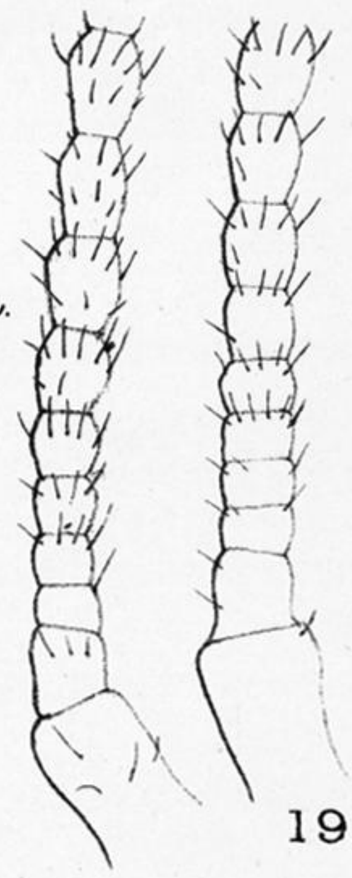

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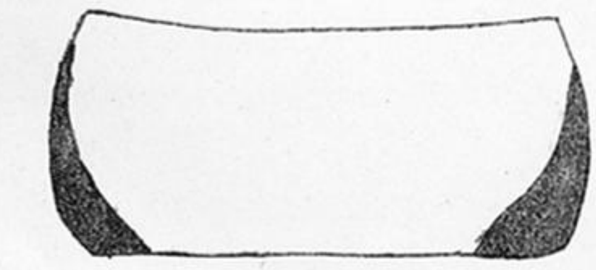

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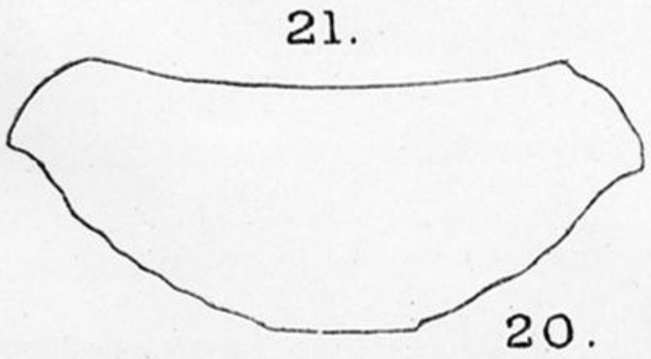

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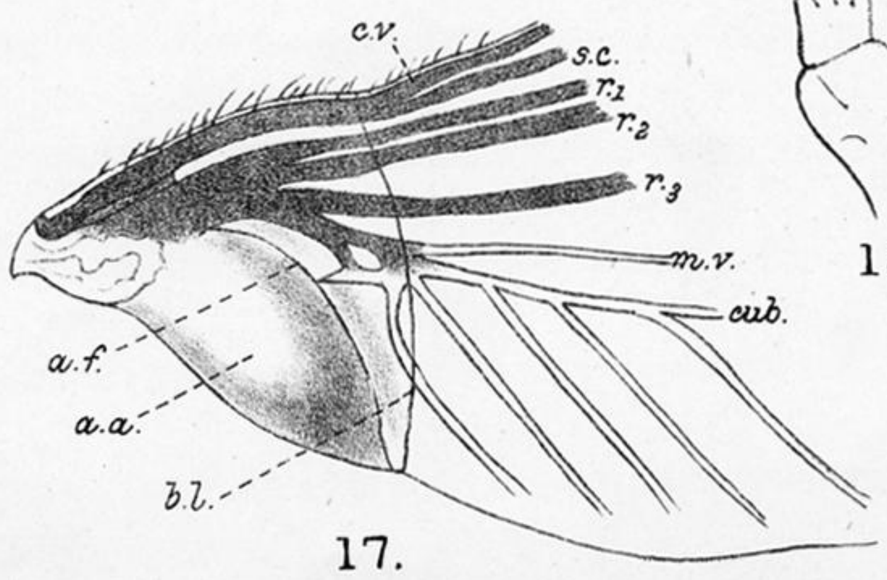

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14.

ARCHOTERMOPSIS WROUGHTONI DESN.

Plate 5.

Fig. 14.—Second maxillæ (labium) of the soldier seen from its ventral or pharyngeal aspect. × 24.

Fig. 15.—Lateral and slightly dorsal view of the hypopharynx of the soldier, together with the associated parts of the second maxilla. × *circa* 85.

Fig. 16.—Fore and hind wings of the right side (from an adult female). × 5½.

Fig. 17.—Base of the fore wing showing roots of the nervures and the vestigal anal area. × 17.

Fig. 18.—Basal joints of left antenna of a winged female. × 41.

Fig. 19.—Basal joints of left antenna of a late larval soldier. × 41.

Fig. 20.—Dorsal view of the metathorax of a young soldier larva, 8·5 mm. long. × 20.

Fig. 21.—Dorsal view of the metathorax of a larva of a sexual form, showing developing wing rudiments. × 20.

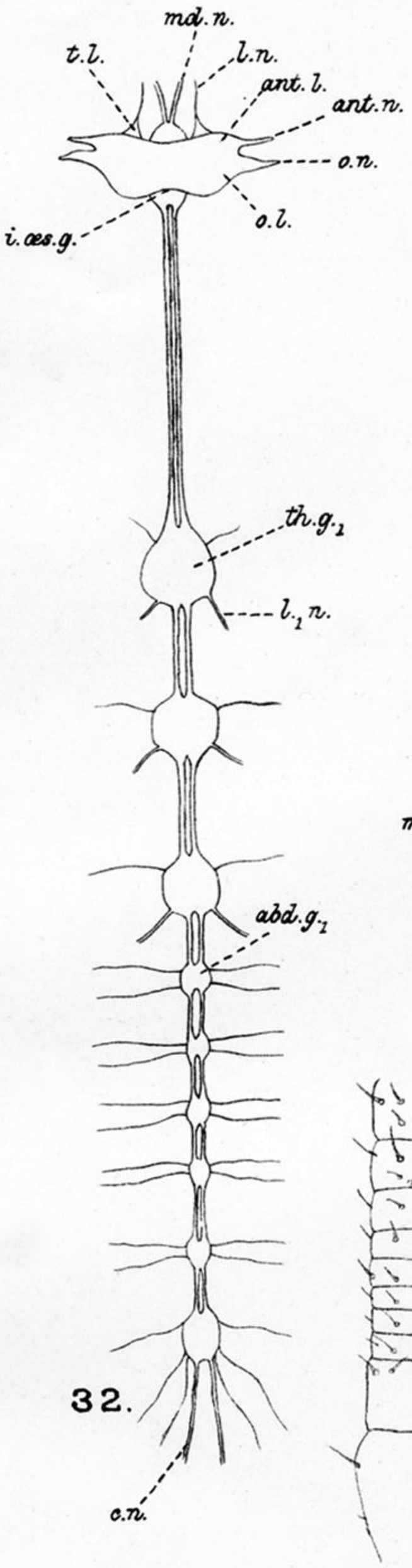
Fig. 22.—Apex of the abdomen of a winged female (ventral aspect). × 18.

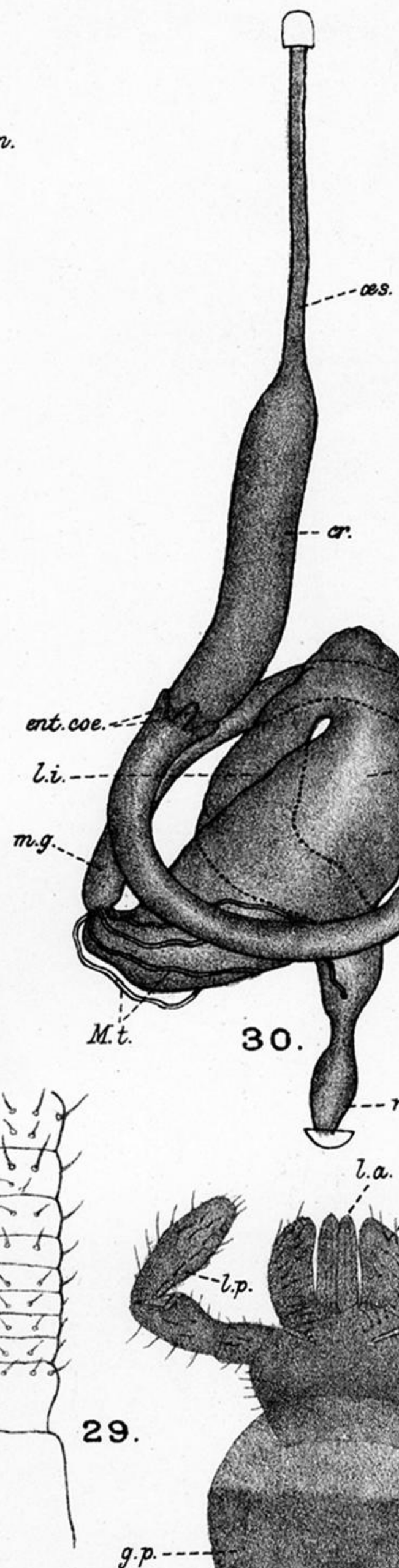
Fig. 23.—Apex of the abdomen of a winged male (ventral aspect). × 18.

Fig. 24.—Left mandible of a winged female (dorsal view). × 38.

Fig. 25.—Right ditto. × 38.

Fig. 26.—Right hind leg of a larval soldier, 3 mm. in length (inner aspect). × 95.





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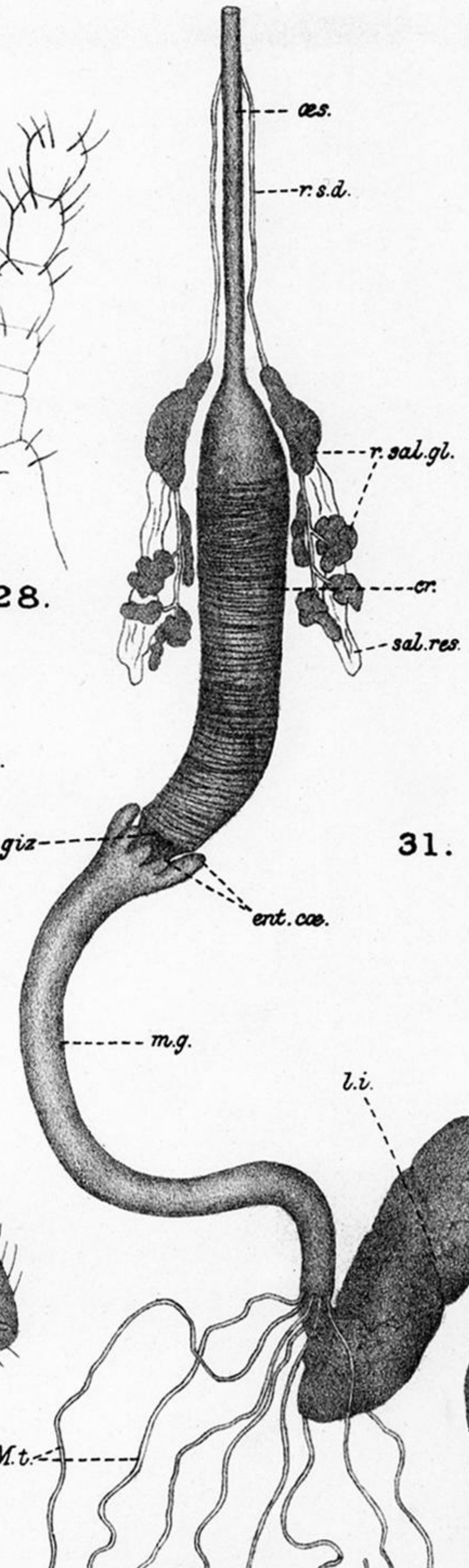

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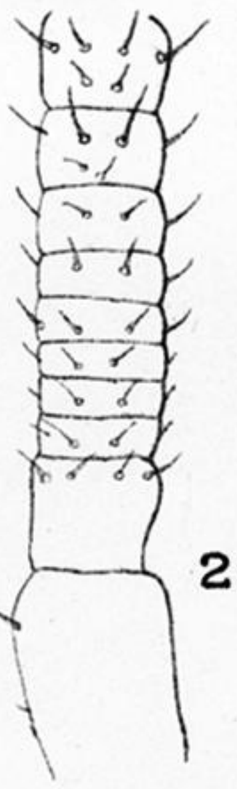

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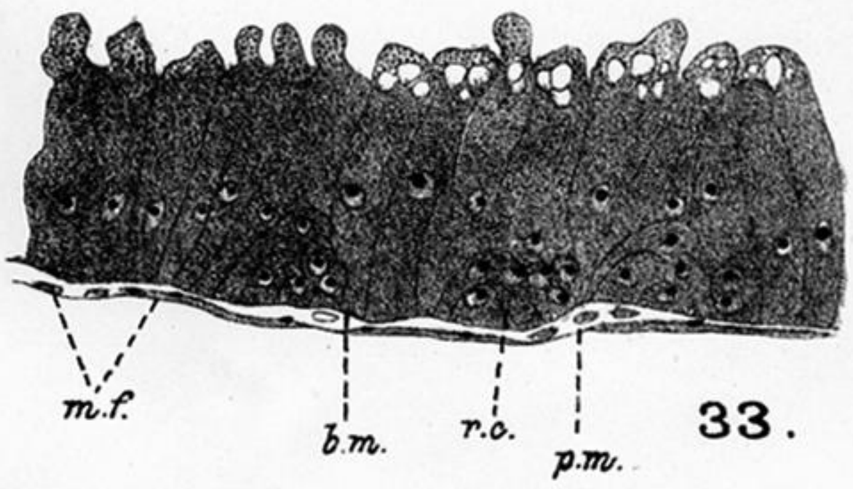

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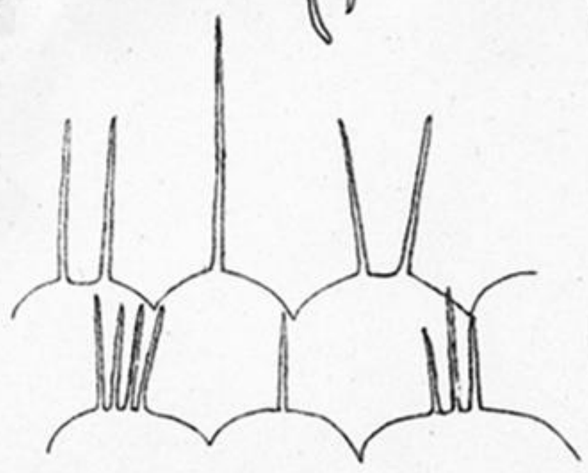

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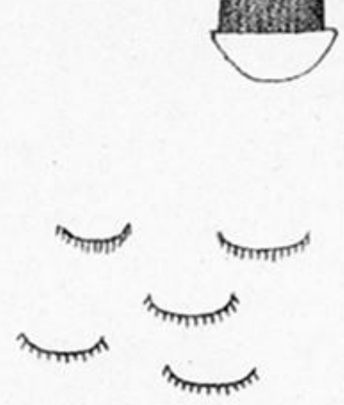


35.

ARCHOTERMOPSIS WROUGHTONI DESN.

Plate 6.

Fig. 27.—Second maxillæ (labium) of a winged female. × 35.

Fig. 28.—Basal joints of left antenna of an adult soldier. × 41.

Fig. 29.—Basal joints of left antenna of a larva 3 mm. long. × 95.

Fig. 30.—Digestive system of the soldier, showing the organs *in situ*. × *circa* 10.

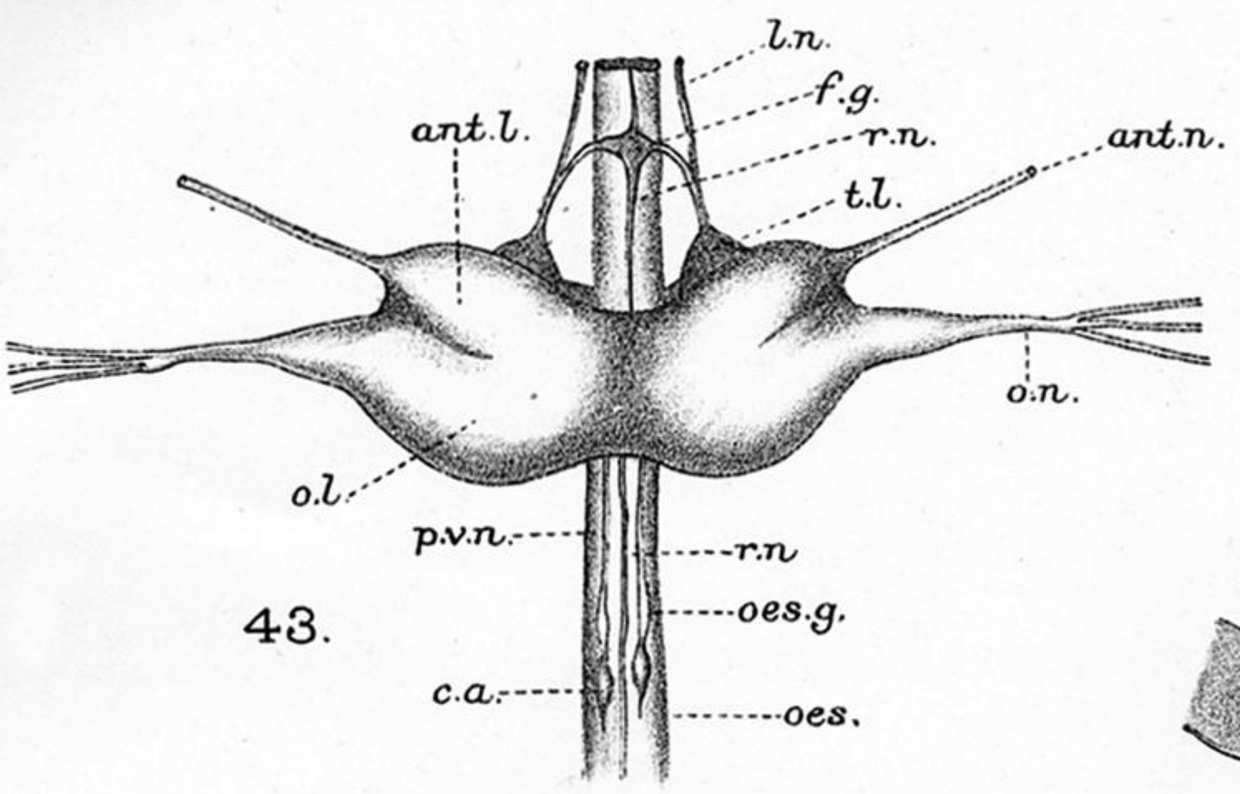
Fig. 31.—Digestive system of the soldier, showing the organs unravelled and extended. × *circa* 10.

Fig. 32.—Central nervous system of the soldier. × *circa* 10.

Fig. 33.—Longitudinal section through the wall of the mid-gut of the soldier (Ehrlich's hæmatoxylin). × 500.

Fig. 34.—Scale-like papillæ armed with spines from the circlet of cushions or pads situated immediately behind the gizzard (adult soldier). × 1800.

Fig. 35.—Semi-lunar papillæ of the inner lining of the crop immediately in front of the gizzard. × 950.



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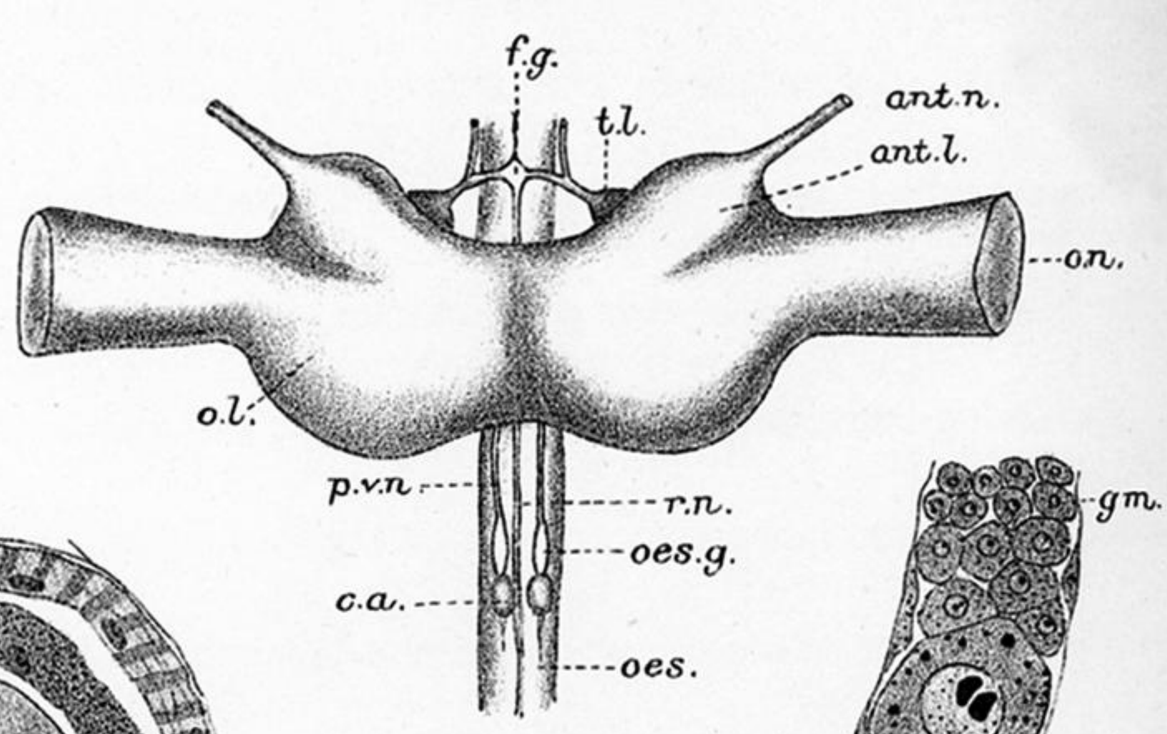

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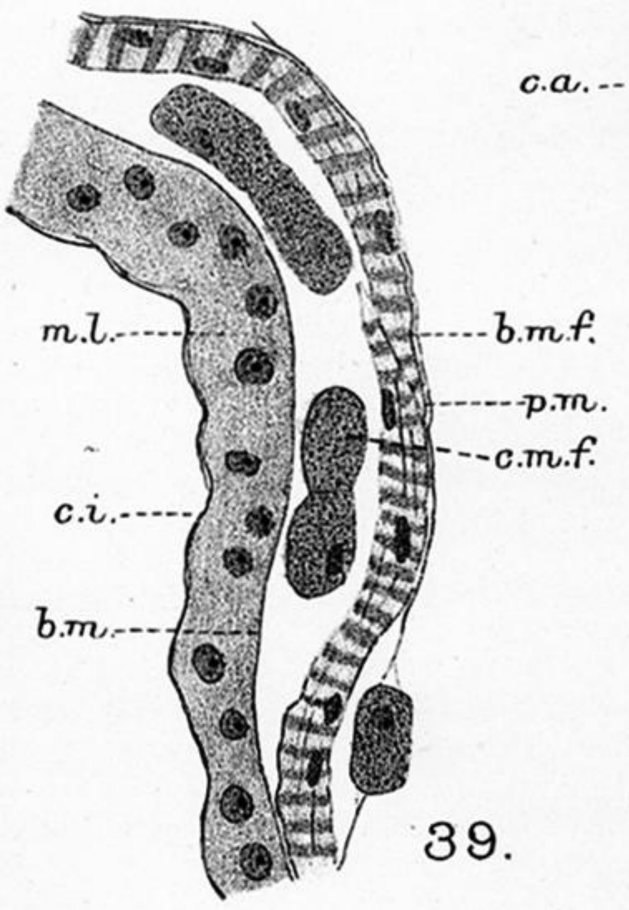

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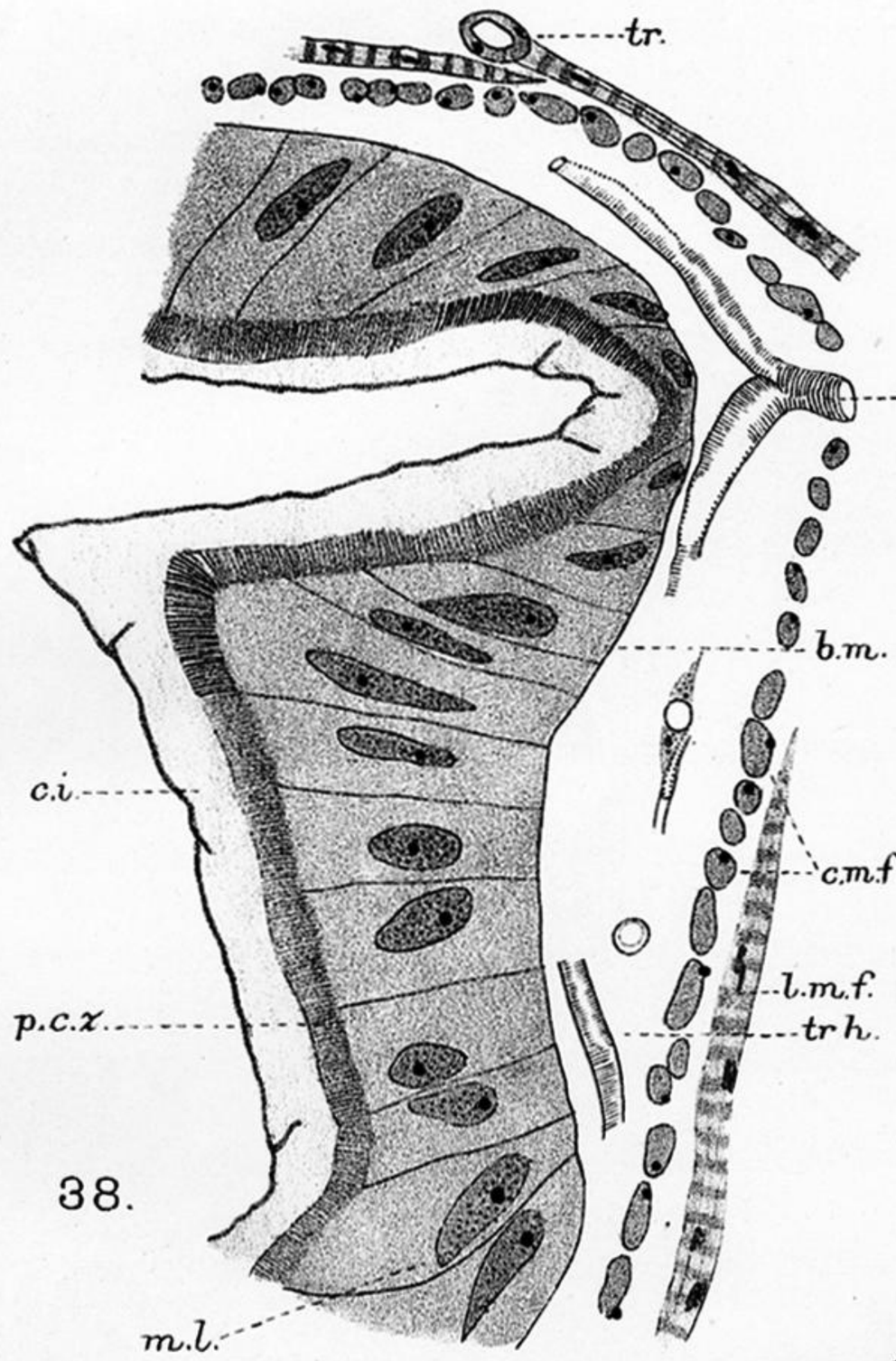

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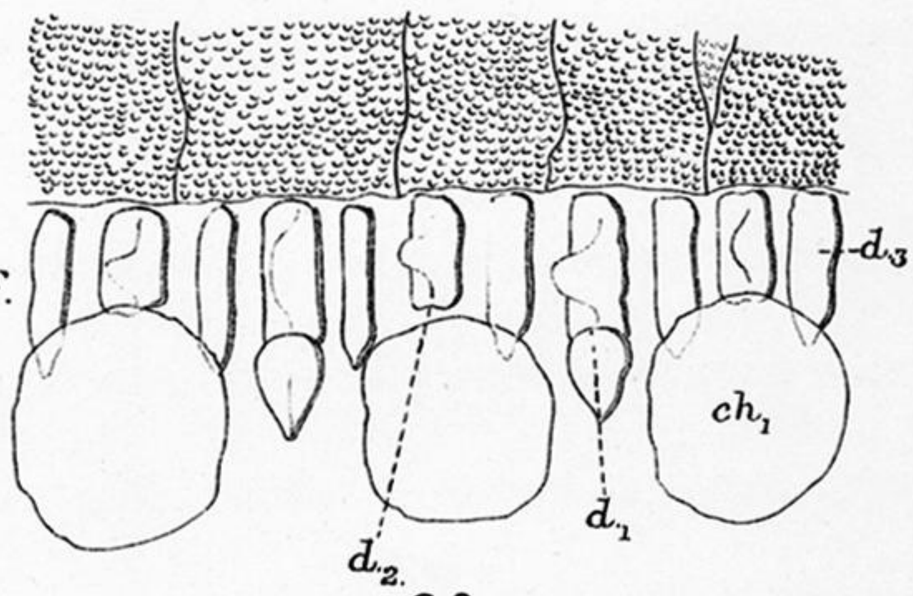

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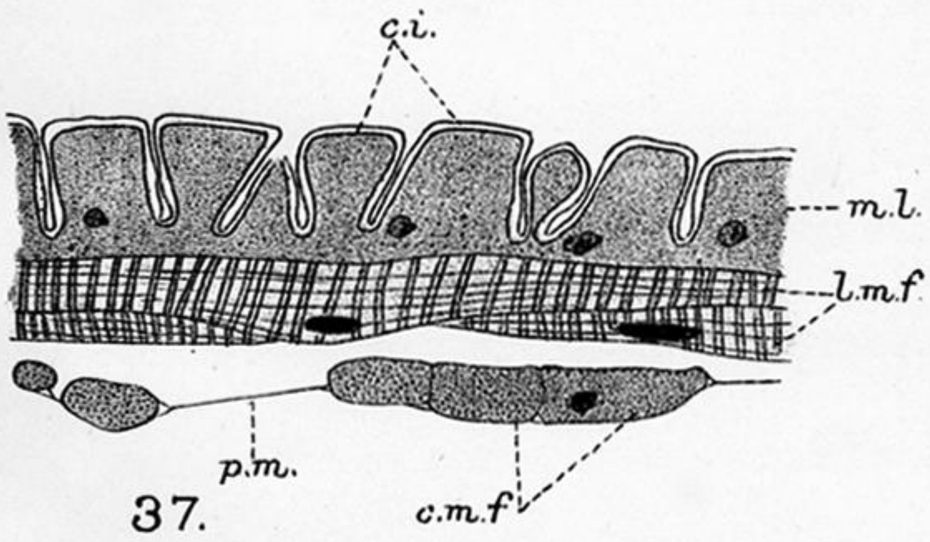

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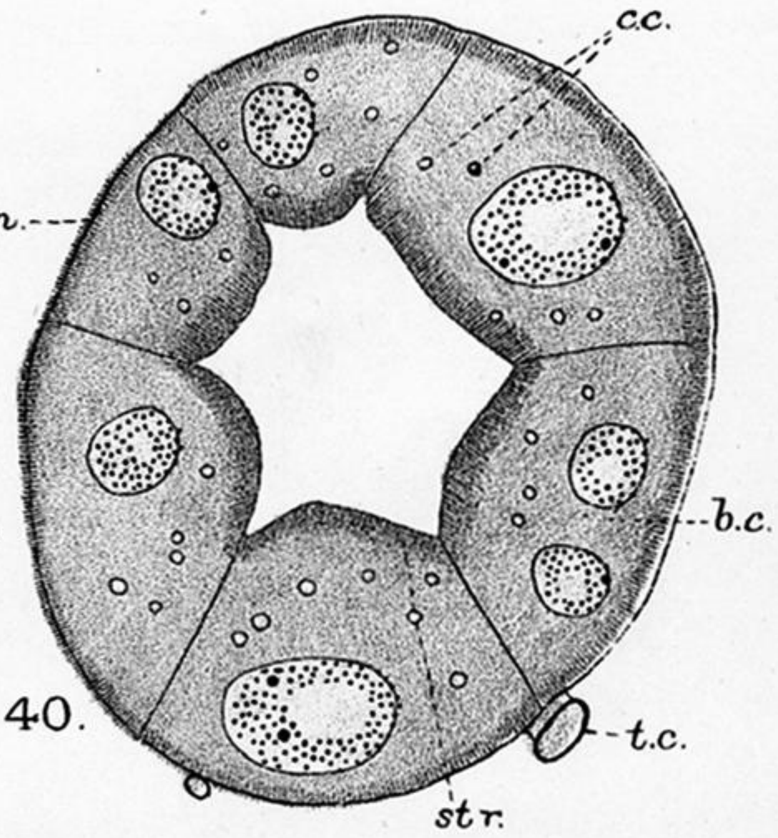

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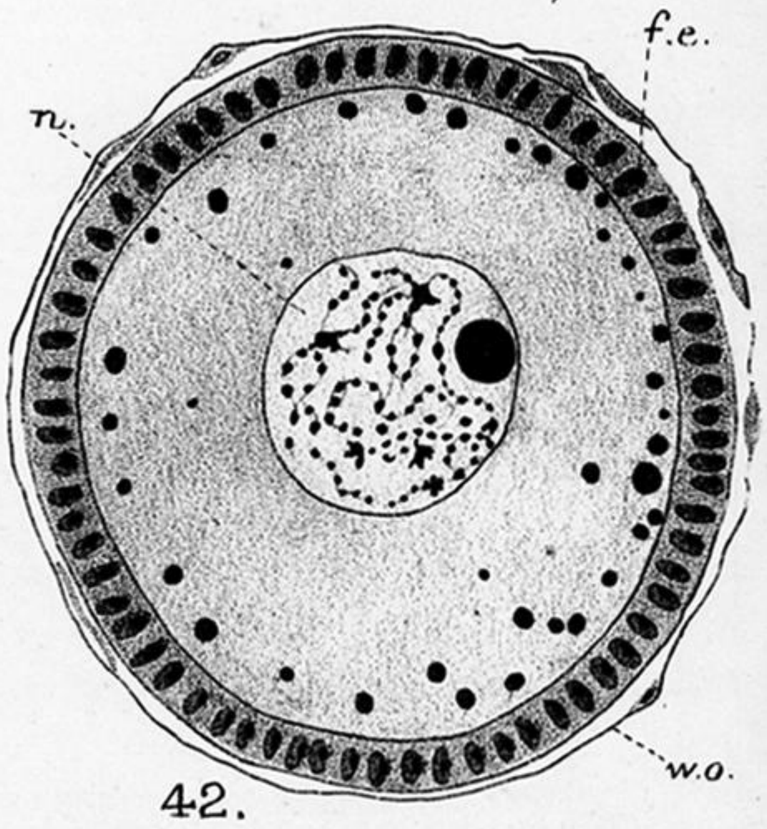


42.

ARCHOTERMOPSIS WROUGHTONI DESN.

Plate 7.

Fig. 36.—A preparation of a portion of the chitinous inner lining of the gizzard mounted in glycerine. Just in front of the gizzard teeth the wall of the crop is seen to be invested with minute semi-lunar papillæ (vide also Fig. 36).

Fig. 37.—Longitudinal section through the wall of the œsophagus of the soldier (posterior region). × 820.

Fig. 38.—Longitudinal section through the wall of the rectum of the soldier. × 500.

Fig. 39.—Longitudinal section through the wall of the large intestine of the soldier. × 920.

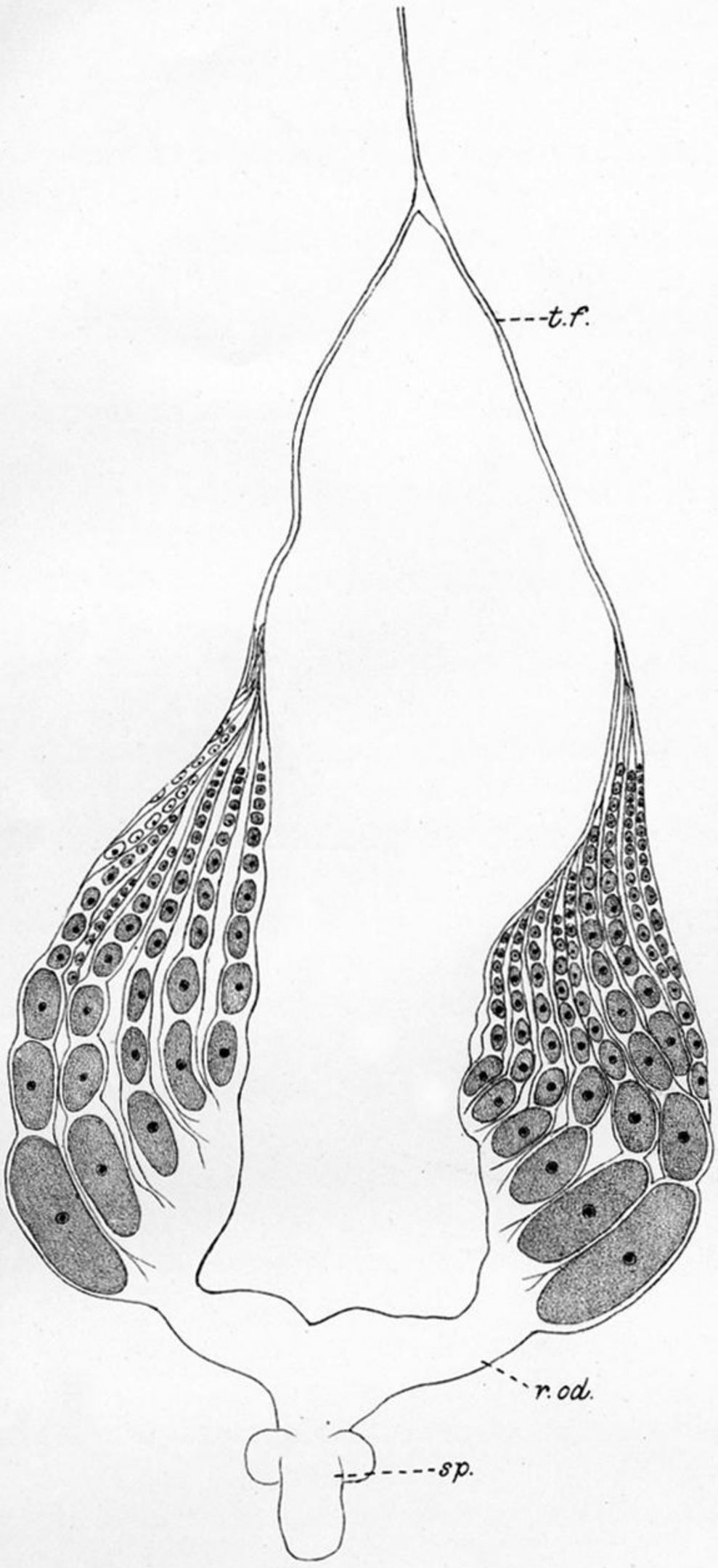
Fig. 40.—Transverse section of a Malpighian tube of the soldier. × 920.

Fig. 41.—Upper portion of an ovariole of the adult soldier stained with Mann's methyl-blue-eosin. × 550.

Fig. 42.—Transverse section through the lower portion of an ovariole and an egg follicle of the soldier. × 550.

Fig. 43.—Brain of the adult soldier, together with the sympathetic nervous system and the corpora allata. × *circa* 33.

Fig. 44.—Ditto of winged female. × *circa* 34.



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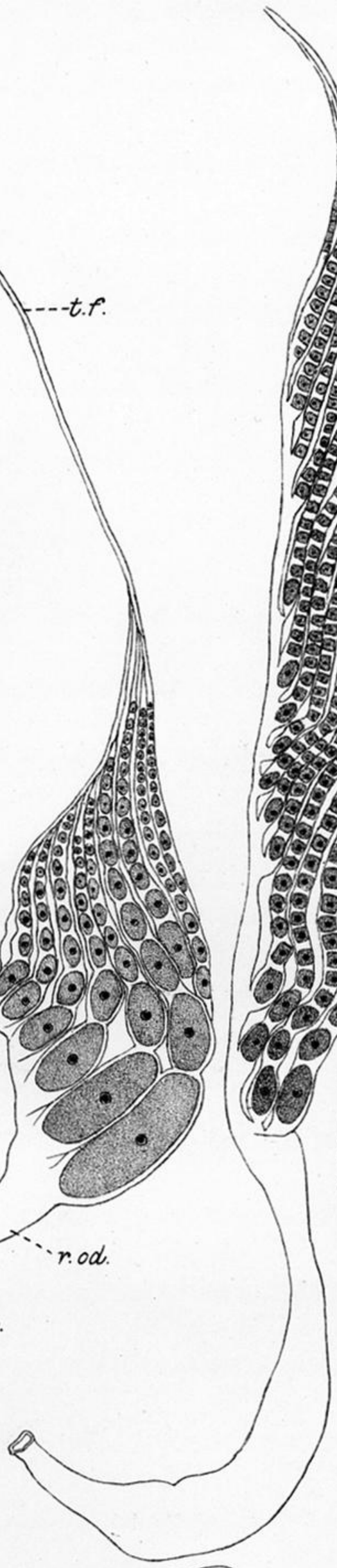

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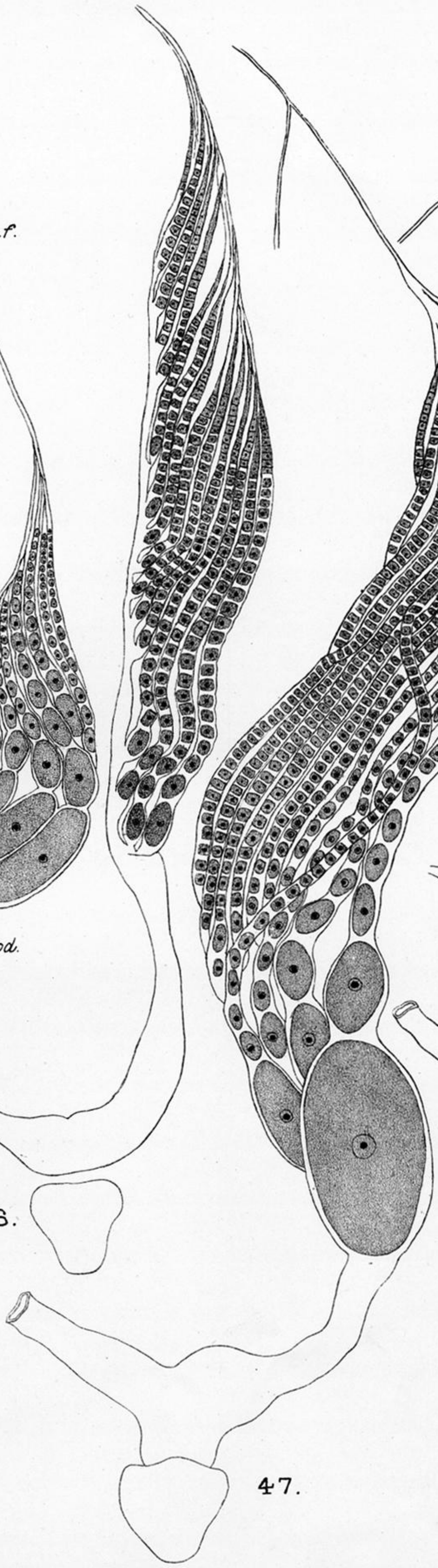

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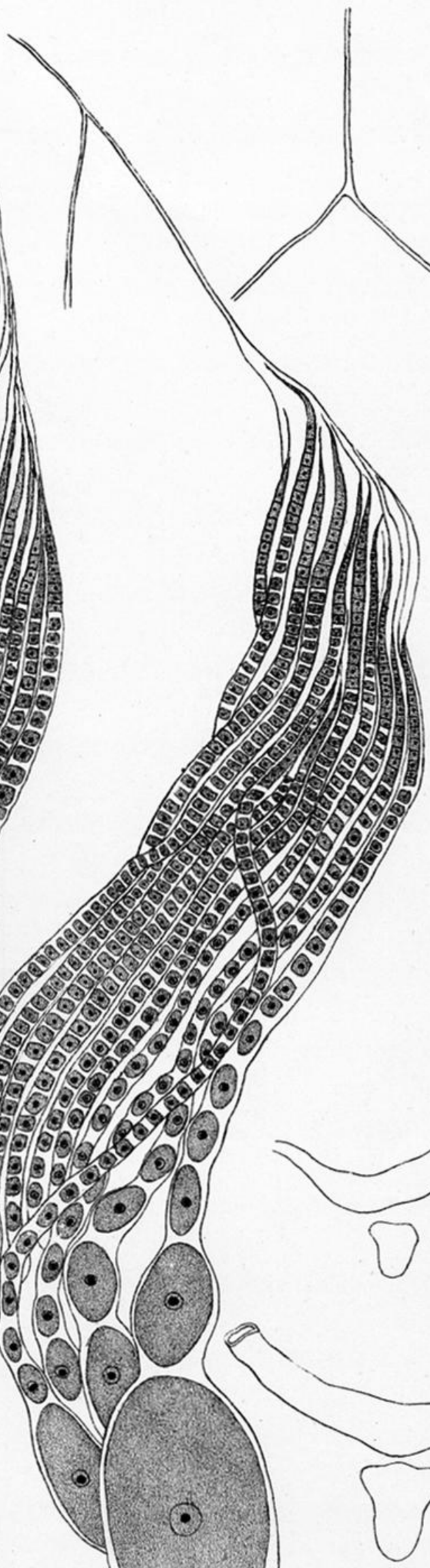

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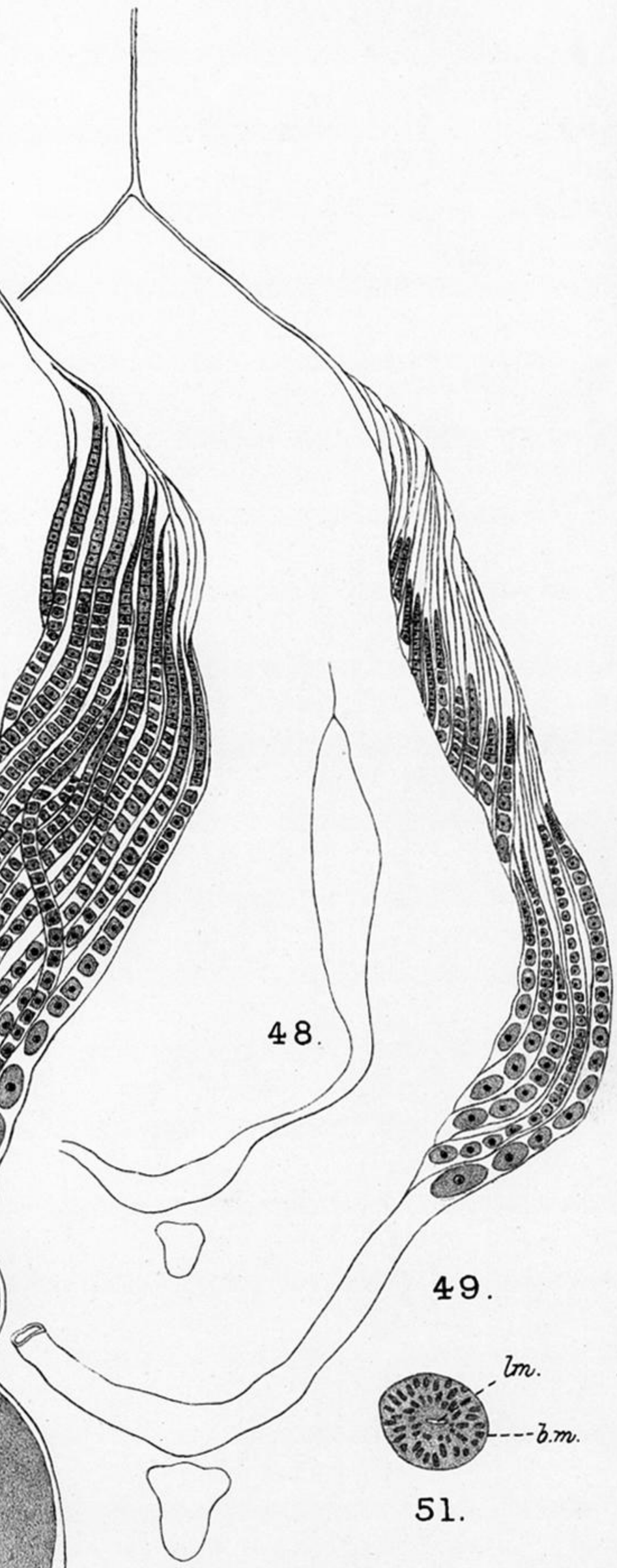

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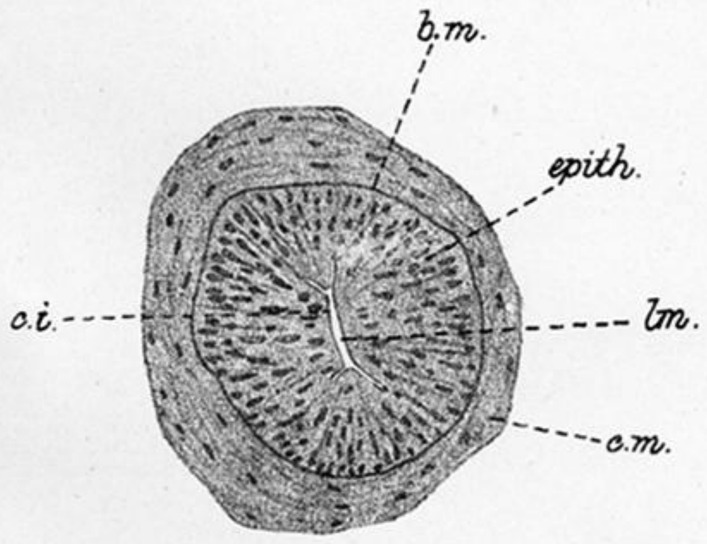

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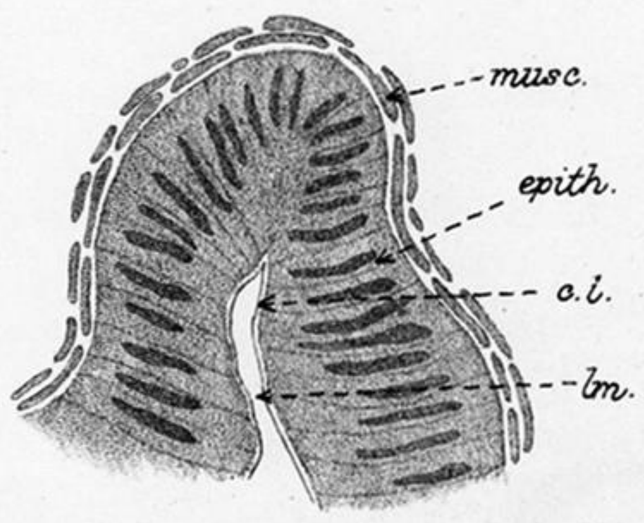
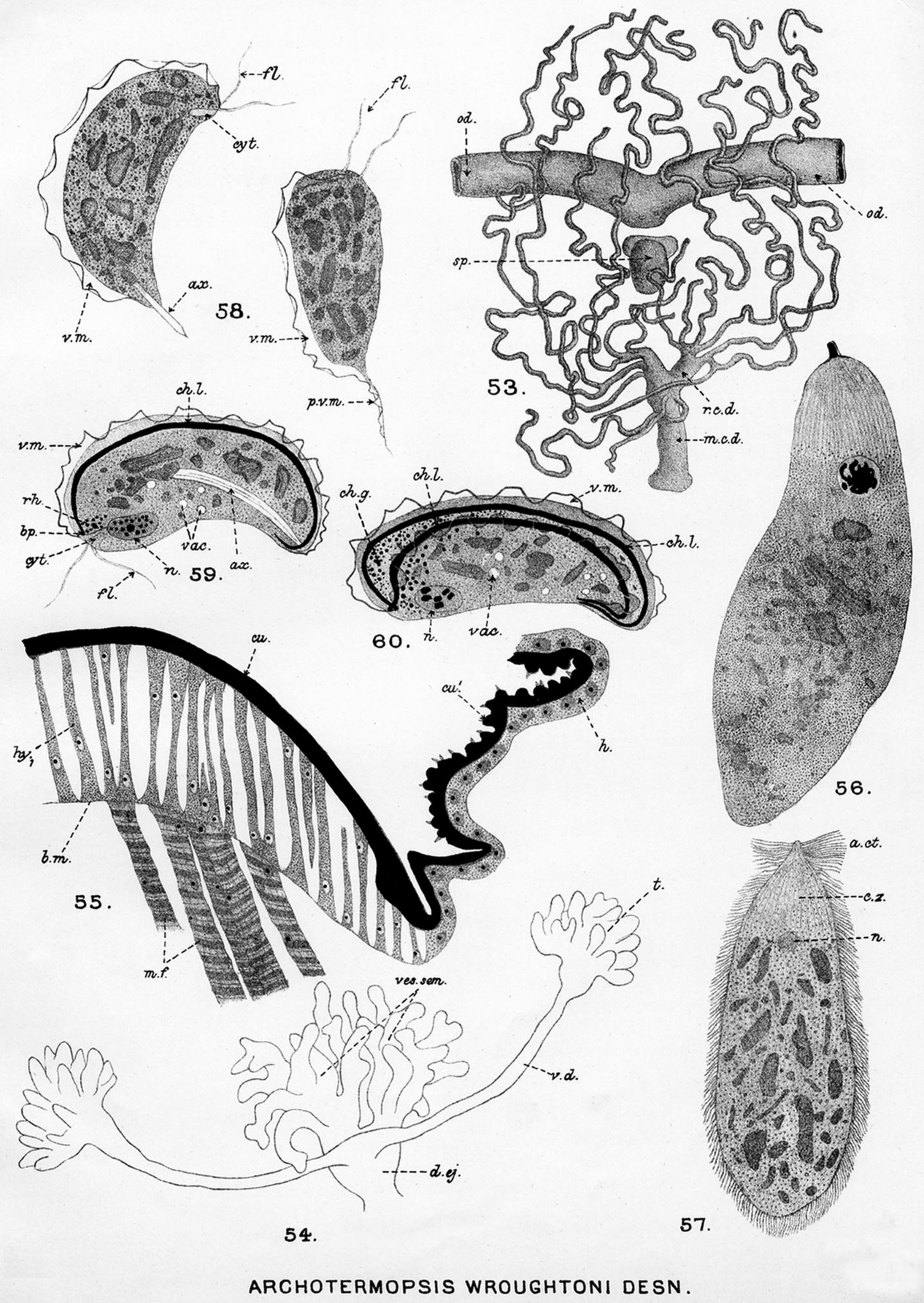


52.

ARCHOTERMOPSIS WROUGHTONI DESN.

PLATE 8.

Fig. 45.—Ovary of an unfertilised winged female, 13 mm. long. × 32.
Fig. 46.—Ditto of an adult soldier. × 32.
Fig. 47.—Ditto of a gynæcoid worker-like form. × 32.
Fig. 48.—Ditto of a young larval soldier, 8·5 mm. long. × 32.
Fig. 49.—Ditto of a first stage nymph. × 32.
Fig. 50.—Transverse section across the main common duct of the colleterial gland; stained with brazilin. × 240.
Fig. 51.—Transverse section across a tube of the colleterial glands; stained with brazilin. × 240.
Fig. 52.—Longitudinal section through a portion of the spermatheca; stained with brazilin.



ARCHOTERMOPSIS WROUGHTONI DESN.

PLATE 9.

Fig. 53.—Colleterial glands, spermatheca and proximal portions of the oviducts of an adult soldier. From a preparation stained with Mann's methyl-blue-eosin and mounted in euparal. Owing to the extension of the abdominal sterna during mounting the spermatheca appears slightly further behind the oviducts than occurs in the living insect. × 46.

Fig. 54.—Male reproductive organs of the adult soldier. × 48.

Fig. 55.—Section through the body-wall in the head of a winged male near the position indicated by *h* in Plate 10, fig. 61.

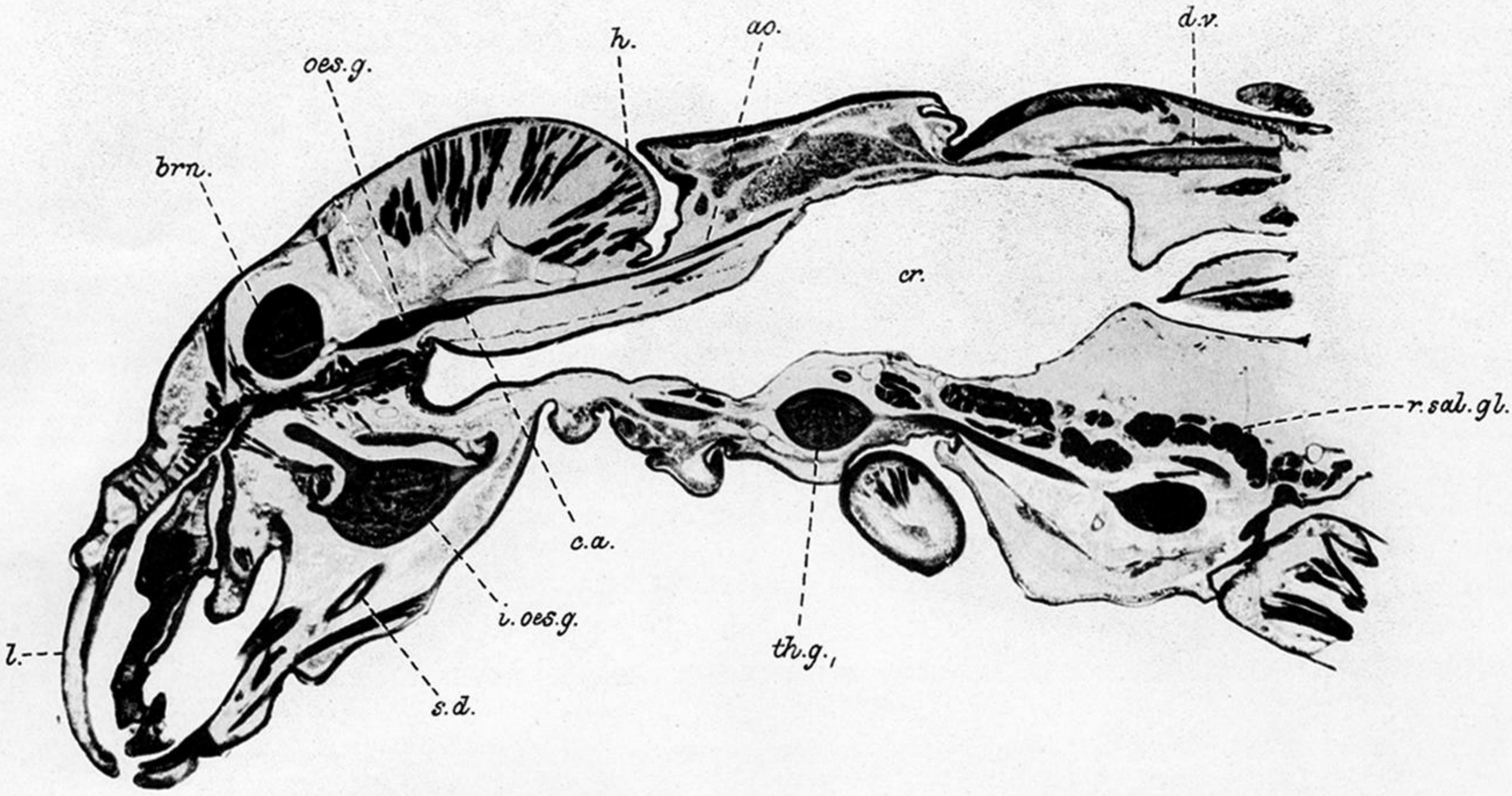
Fig. 56.—*Trichonympha pristina* Imms. sp. nov. from a specimen fixed in hot Schaudinn's fluid and stained with Heidenhain's iron-alum hæmatoxylin. × 400.

Fig. 57.—*Trichonympha pristina* Imms sp. nov. from a living specimen examined in salt solution. ×

Fig. 58.—*Trichomonas termitis* Imms sp. nov. Two living specimens examined in salt solution. ×

Fig. 59.—*Trichomonas termitis* Imms sp. nov. from a specimen fixed in hot Schaudinn's fluid and stained with Heidenhain's iron-alum hæmatoxylin. × 1000.

Fig. 60.—Ditto ditto undergoing longitudinal fission. × 1000.



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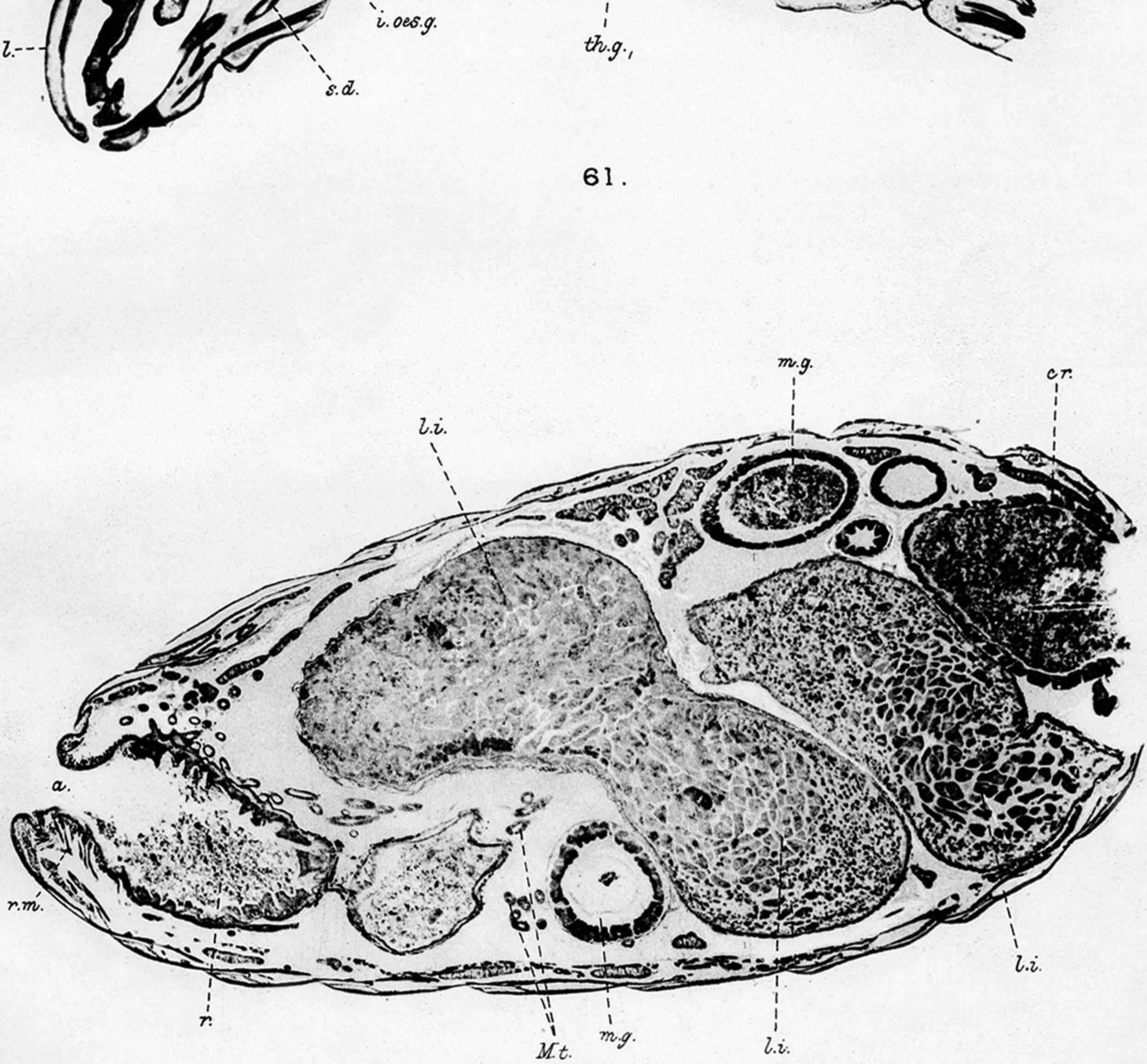

62.

PLATE 10.

Fig. 61.—Longitudinal section through the head and thorax of a winged male stained with Heidenhain's iron-alum hæmatoxylin. (Enlargement from a photograph taken by Mr. J. T. WADSWORTH.) × 30.

Fig. 62.—Longitudinal section through the abdomen of an adult soldier (female), showing the distension of the large intestine owing to the presence of great numbers of Protozoa. (Enlargement from a photograph taken by Mr. J. T. WADSWORTH.) × 26.