Liverpool Marine Biology Committee.

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY W. A. HERDMAN, D.Sc., F.R.S.

XIII.

ANURIDA

BY

A. D. IMMS, B.Sc. (Lond.),
Christ's College, Cambridge.

(With 7 Plates)

PRICE FOUR SHILLINGS

LONDON
WILLIAMS & NORGATE
OCTOBER, 1906

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XIII.

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EDITOR'S PREFACE.

The Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the Fauna and Flora of the Irish Sea.

The dredging, trawling, and other collecting expeditions organised by the Committee have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Nineteen Annual Reports of the Committee and five volumes dealing with the "Fauna and Flora" have been issued. At an early stage of the investigations it became evident that a Biological Station or Laboratory on the sea-shore nearer the usual collecting grounds than Liverpool would be a material assistance in the work. Consequently the Committee, in 1887, established the Puffin Island Biological Station on the North Coast of Anglesey, and later on, in 1892, moved to the more commodious and accessible Station at Port Erin in the centre of the rich collecting grounds of the south end of the Isle of Man. A new and larger Biological Station and Fish Hatchery, on a more convenient site, has now been erected, and was opened for work in July, 1902.

In these nineteen years' experience of a Biological Station (five years at Puffin Island and fourteen at Port Erin), where College students and young amateurs form a large proportion of the workers, the want has been frequently felt of a series of detailed descriptions of the structure of certain common typical animals and plants, chosen as representatives of their groups, and dealt with by specialists. The same want has probably been felt in other similar institutions and in many College laboratories.

The objects of the Committee and of the workers at the Biological Station were at first chiefly faunistic and speciographic. The work must necessarily be so when opening up a new district. Some of the workers have published papers on morphological points, or on embryology and observations on life-histories and habits; but the majority of the papers in the volumes on the "Fauna and Flora of Liverpool Bay" have been, as was intended from the first, occupied with the names and characteristics and distribution of the many different kinds of marine plants and animals in our district. And this faunistic work will still go on. It is far from finished, and the Committee hope in the future to add still further to the records of the Fauna and Flora. But the papers in the present series, started in 1899, are quite distinct from these previous publications in name, in treatment, and in purpose. They are called "L.M.B.C. Memoirs," each treats of one type, and they are issued separately as they are ready, and will be obtainable Memoir by Memoir as they appear, or later bound up in convenient volumes. It is hoped that such a series of special studies, written by those who are thoroughly familiar with the forms of which they treat, will be found of value by students of Biology in laboratories and in Marine Stations, and will be welcomed by many others working privately at Marine Natural History.

The forms selected are, as far as possible, common L.M.B.C. (Irish Sea) animals and plants of which no adequate account already exists in the text-books. Probably most of the specialists who have taken part in the L.M.B.C. work in the past will prepare accounts of one or more representatives of their groups. The following list shows those who have either performed or promised.

Memoirs from I. to XIII. have now been published.

No. XIV., on *Ligia*, by Mr. C. G. Hewitt, will be out in a few weeks. It is hoped that Cycloporus, Cancer, Antedon, and the Oyster will follow soon.

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Cancer, J. Pearson.
Oyster, W. A. Herdman and J. T. Jenkins.
Antedon, H. C. Chadwick.
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PECTEN, W. J. Dakin.
DIATOMS, F. E. Weiss.
FUCUS, J. B. Farmer.
BOTRYLLOIDES, W. A. Herdman.
CUTTLE-FISH (ELEDONE), W. E. Hoyle.
ACTINIA, J. A. Clubb.
HYDROID, E. T. Browne.
CALCAREOUS SPONGE, R. Hanitsch.

In addition to these, other Memoirs will be arranged for, on suitable types, such as *Sagitta*, a Cestode (by Mr. Shipley), *Pagurus*, and a Pycnogonid.

As announced in the preface to ASCIDIA, a donation from Mr. F. H. Gossage, of Woolton, met the expense of preparing the plates in illustration of the first few Memoirs, and so enabled the Committee to commence the publication of the series sooner than would otherwise have been possible. Other donations received since from Mr. Gossage, from Mrs. Holt, and from others, are regarded by the Committee as a welcome encouragement, and have been a great help in carrying on the work.

W. A. HERDMAN.

University of Liverpool,
September, 1906.

L.M.B.C. MEMOIRS.

No. XIII. ANURIDA.

BY

A. D. IMMS, M.Sc. (Birm.), B.Sc. (Lond.),

Christ's College, Cambridge.

CONTENTS.

PREFACE.

Although the Insecta have received the attention of so large an army of workers in many lands, very few have deemed it worth their while to search for these animals below the level of the high-water mark of the sea. It is very generally believed that insects are totally unfitted to endure the salinity of the sea-water and, consequently, they have been very little sought for in that habitat. The number of marine insects which are at present known is, therefore, comparatively small.

The subject of this Memoir is the Collembolan *Anurida maritima* (Guer.) and it has, perhaps, more to commend itself to the attention of the general student of Zoology than is the case with other marine insects. It has not been my intention to confine myself solely to a description of the type with which the Memoir deals, but rather to make the work of a wider interest. With this aim in view, I have included chapters on the general structure and affinities of the Collembola, together with a fairly extensive bibliography of the order, and some additional remarks relating to other marine insects.

This work was commenced at the Port Erin Biological Station, where the insects were collected and their habits studied. The greater part of the anatomical work was carried out in the Zoological Laboratory of Birmingham University, while the remaining portion has been completed in the Morphological Laboratory of the University of Cambridge. I am indebted to Prof. E. W. Wace Carlier, M.D., for helpful assistance as regards the details of histological technique which were carried out in the Physiological Laboratory at Birmingham. Dr. David Sharp has also supplied me with several valuable suggestions.

It has been necessary to consult a considerable amount of literature while preparing this Memoir, and I wish to acknowledge my indebtedness more particularly to the writings of Fernald, Folsom and Willem. They are numbered **8**, **10** and **27** respectively in the bibliography to be found at the end.

I. INTRODUCTORY REMARKS.

The general characters of the class Insecta are familiar to every student of Zoology. Among this vast assemblage of animal forms, there is an obscure group of great phylogenetic importance possessing certain definite characters which separate it from the other members of that class. Until comparatively recently, it has been customary to regard this group as constituting a single order, viz., the Aptera, and the latter was divided into the two sub-orders Collembola and Thysanura. It was in the year 1885 that Brauer recognised that the Aptera possessed characters which merited their being raised to something more than ordinal rank. He, therefore, proposed to call them Apterygogenea in contradistinction from the rest of the Insecta, which he termed Pterygogenea. The investigations of the last thirteen years all tend to establish Brauer's contention. In preference, however, to his terms, the shortened names of Apterygota and Pterygota are in more general use.

The following characters, taken collectively, separate the Apterygota from the rest of the Insecta or Pterygota:—

(1) The absence of any true process of metamorphosis.

(2) The total absence of wings.

(3) The presence of an evident pair of mouth-parts, the maxillulæ, intercalated between the mandibles and first maxillæ.

The Apterygota are the most generalized of all Insecta, and in their external form they resemble the larvæ of many of the Pterygota, or transient stages in the larval development of others. A very marked characteristic of the group is the existence of abdominal appendages, either in the form of terminal processes at the end of the body, or as processes in relation with the sterna of the abdominal segments. The mouth-parts are mandibulate, except in the few instances where they have become imperfectly suctorial.

It is true that wingless forms are by no means of infrequent occurrence among other groups of Insecta, but in them the apterous condition is a secondary acquisition, and not an ancestral character, as is the case in the Apterygota. Furthermore, maxillulæ may also be present in other insects, but in the few instances where such are known to occur they are found only in a vestigeal condition.

The Collembola and Thysanura each possess certain very marked characters, and are best regarded as two separate orders of insects.

The COLLEMBOLA are popularly known as "springtails." In them the antennæ have from four to six joints, and the abdomen consists of six segments and is never terminated by any appendages. The first abdominal segment always bears a ventral tube, and the fourth segment usually carries a springing organ. The mouthparts are always sunk within the head, the nervous system consists of a brain and four ventral ganglia, and there are no Malpighian tubes.

The THYSANURA are commonly known as "bristletails." They have many-jointed antennæ, and the abdomen consists of ten segments and is provided with a variable number of pairs of short, unmodified limbs. The last abdominal segment is terminated either by caudate or forcipate appendages. A ventral tube is never present. The mouth-parts may, or may not, be sunk within the head, the nervous system consists of a brain and ten or eleven ventral ganglia, and Malpighian tubes are generally present.

The relations of the Collembola to the rest of the Insecta are shown in the table on page 6.

The Collembolan described in the present Memoir is a convenient insect to study, as it can be obtained in plenty in various localities scattered around the coasts of the British Isles. According to Plateau it was first discovered in Denmark by Ström, who named it *Podura ambulatoria cauda carens.* It was afterwards found in Normandy by Guérin-Ménneville, who, in 1836, re-named it *Achorutes maritimus*; Nicolet, however, refers to it as *Anoura maritima.* In 1864 Laboulbène erected for its reception the genus *Anurida*, but in Lubbock's "Monograph of the Collembola and Thysanura" it is described as *Lipura maritima.* At the present day its nomenclature has become settled, and it is now universally known as *Anurida maritima.*

Those who have not the opportunity of working at the sea-side can use with advantage the common *Podura aquatica* as a substitute for *Anurida. Podura* is a very plentiful species in many parts of Britain, and is to be sought for on the surface of the water of wayside ponds and ditches.

II. BIONOMICS.

Anurida maritima is a dark blue-black insect measuring 2-3mm. in length. The individuals seen in fig. 2 show the general appearance of the species to the naked eye, and will aid in recognising it as it crawls about on the sea-shore.

A. APTERYGOTA.		
1. Collembola. Spring-tails.		Ametabola. Young forms resemble adult: no metamorphosis.
2. Thysanura. Bristle-tails.		
B. PTERYGOTA.		
3. Dermaptera. Earwigs.	Homomorpha. Young animal resembling adult in general form but distinguished by the absence of wings and external genital armature.	Metabola. A Metamorphosis, either incomplete or complete, always present.
4. Orthoptera. Cockroaches, Locusts, Crickets, etc.		
5. Platyptera. Book-lice, Termites, Stone-flies, etc.		
6. Thysanoptera. Thrips.		
7. Plectoptera. Mayflies.		
8. Odonata. Dragonflies.		
9. Hemiptera. Bugs, Cicadas, Green-fly, etc.		
10. Neuroptera. Alder-flies, Lacewing-flies, etc.	Heteromorpha. Larvæ differing very greatly from the adults and always passing into a pupal stage.	
11. Coleoptera. Beetles.		
12. Trichoptera. Caddis-flies.		
13. Lepidoptera. Butterflies and Moths.		
14. Diptera. Flies, Fleas, Sheep-ticks.		
15. Hymenoptera. Ants, Bees, Wasps, Saw-flies, &c.		

The habits of *Anurida* have been observed by the present writer principally on the shores of Port Erin Bay in the Isle of Man.* About the rock-pools in that locality, when the tide is low and the weather calm and bright, numbers of this insect are generally to be seen. It may be found both on the surface of the water and on the surrounding rocks and weed. *Anurida*, unlike the majority of the Collembola, is unable to perform any leaping movements on account of the atrophy of the springing-organ, and it is only capable of a moderately active crawling motion. Those individuals which are to be seen floating on the rock-pools are only able to walk over the surface-film while the water remains motionless. When, however, the slightest ripple arises they become drifted about from one part to another in a helpless condition until they are enabled by chance to cling to the sides of the pools and crawl out on to the surrounding rocks and weeds. Frequently numbers get blown together into little groups on the surface of the water, and the individuals composing them may be seen actively crawling over one another and apparently endeavouring to reach the shore. Sometimes these groups are of a considerable size and may consist of a hundred, or more, individuals. There is every reason to believe that their occurrence on the surface of the water is not due to the insect voluntarily resorting to that medium, but that it is merely the result of accident. Numbers of the insect frequently fall into the pools in their attempts to climb steep rock surfaces, and also very many get blown thither by gusts of wind.

When the weather is cold and stormy, or otherwise unfavourable, very few *Anurida* are to be found, and often they appear to be absent altogether. At these times

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* On the Continent the habits of the insect have been studied to some extent in France by Laboulbène (**2**) and Moniez (**4**).

they seek shelter under weeds, or ensconce themselves in crevices among the rocks or in crannies and niches between the encrusting barnacles, and specimens are then to be obtained only after a careful search.

The distribution of this insect about Port Erin Bay is confined to a tolerably definite zone of the sea-shore. The insect does not wander above the high-water mark of ordinary tides, neither does it appear to venture further seaward than about half-way between that limit and the Laminarian zone.

It is plentiful during spring and summer, but towards autumn it becomes more sluggish in its habits and decreases in its numbers. In winter it is not often seen.

As the tide rises *Anurida* retreats far into the niches in the rocks, where it is able to withstand submersion for a considerable period twice each day. Since the average tide in Port Erin Bay is about fifteen and a half feet, it would be immersed to a depth of about eight feet. The rocks round the shore of that locality are very markedly jointed, and it is in the crevices of these joints that *Anurida* seeks refuge from the incoming tide. An abundant supply of specimens can usually be obtained by following down the retreating tide and examining the rocks as they become uncovered. Since the insects work their way into the crevices often to a depth of four or five inches, it is necessary to split open the rock with the aid of a hammer and a stout steel chisel. In suitable chinks as many as several hundred *Anurida* will sometimes be found congregated together and, strewn about the crevices among them, there are usually to be seen numbers of their exuviæ, which appear like minute white flakes. The relatively large orange-yellow eggs of the species, arranged in little irregular clusters, are often to be met with at the same time.

If a specimen of the insect be examined with a hand lens, it will be seen to be covered with a coating of whitish hairs. When the animal is submerged under water, a sufficient supply of air is retained by this hairy coating to enable respiration to go on freely for a considerable period, and at the same time it renders the insect incapable of being wetted. In order to test the truth of this, it is only necessary to take a few specimens and place them in a deep glass vessel together with some sea-water. If the vessel be shaken sufficiently, the animals will become submerged below the surface of the water, and each individual will then be seen to be enveloped in a glistening coat of air. When once they are submerged they are unable to reach the surface again, and they crawl aimlessly about the bottom of the vessel. The animals thus treated remained active for four and a half days whenever the vessel was slightly shaken. On the fifth day they had used up all the air investing them, and on the sixth day scarcely any movement was noticeable among them, and they appeared to be in an asphyxiated condition. On the seventh day they seemed to all purposes to be quite dead.

In sandy localities *Anurida* resorts to burrowing for protection from the incoming tide. In the neighbourhood of Rhyl, North Wales, it occurs plentifully at low water about the sands and on the surface of the pools left by the retreating tide among the depressions and inequalities in the shore. Since there are no rocks or other means of shelter at hand, the insect has to bury itself in the wet sand as the tide rises and to remain there until the next ebb. It also appears to live under somewhat similar conditions at Tréport in Normandy, for in that locality it is mentioned as frequenting the mud at the mouth of a rivulet. About the sandy beach on the north side of

Long Island, Mass., there are found, according to Davenport, (**1**) three species of Collembola belonging to as many genera. *Anurida*, however, is the least common among them in that locality. Among other interesting observations, this author has proved that the Collembola burrow to escape from the flood tide; he remarks that, with a hand lens, he has observed them as they issue from the sand during the fall of the tide.

In regard to the nature of the food of *Anurida*. Folsom (**10**) states that it feeds on the soft tissues of the Mollusc *Littorina littorea*. Laboulbène (**2**) also stated that its food consists of the tissues of Molluscs. He remarked:—"Les *Achorutes* [*i.e.*, *Anurida*] mangent évidemment des petits Mollusques, si abondants sur les rochers submergés à la marée haute, car lorsque j'écrasais un de ces Mollusques pendant mes recherches, je voyais. au bout de cinq ou six minutes, un bon nombre d'Achorutes qui se réunissaient sur cette proie, et, par ce moyen, je pouvais en prendre jusqu'à une douzaine à la fois." In the experience of the present writer, its food is dependent upon the nature of the locality which it frequents, and, consequently, varies a good deal. In the rocky locality of Port Erin it subsists chiefly upon the dead bodies of various small marine animals, principally Mollusca and Crustacea. At times numbers of *Anurida* may be seen congregated around, and also inside, the shells of dead barnacles, actively engaged in feeding upon the remains of the latter. Vegetable matter appears also to enter into its food occasionally, for remains of Desmids and other green Algæ may be found at times among the contents of the mid-gut. In barren, sandy localities the insect has to rely for its food upon whatever dead organic matter that is obtainable.

III. GEOGRAPHICAL DISTRIBUTION.

Anurida maritima has been recorded from a number of localities scattered all around our British coasts. It appears to be abundant in the neighbourhood of Penzance and Land's End (Marquand, **75**), it also occurs at Plymouth (Parfitt, **80**), and the present writer has met with it sparingly at Torquay. On the coasts of Wales it is known from Gower, Nevin and Llandudno,* and it is also common on the broad stretches of sand in the neighbourhood of Rhyl. On the west coast of Scotland it is described as being common among seaweed-covered rocks at Peaton, Loch Long (Evans, **60**); it is also found on the shores of Ayrshire and Buteshire (Boyd, **52**). On the east coast Lubbock (Lord Avebury) mentions it from St. Andrews, and it is plentiful about the shores of East Lothian at Aberlady and North Berwick (Carpenter and Evans, **57**). In the Isle of Man it is abundant among the rocks on the north side of Port Erin Bay, and can also be met with at Poolvaish near Castletown. In Ireland it occurs on the east, south and west coasts (Carpenter and Evans), and Lubbock mentions having received it from Kinsale.

On the continent of Europe *Anurida* is plentiful in France at Tréport, Havre, Boulogne and other places, together with the Channel Isles. It has also been recorded from Holland, Belgium, Denmark, Heligoland and Scandinavia.

In North America† it is reported from the Atlantic coast from Cape Ann, Annisquam, Long Island, New

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* For these localities, the writer is indebted to Dr. D. Sharp, F.R.S., for Gower, and to Mr. F. A. Potts for Nevin and Llandudno.

† Packard (**79**) states that the American examples of *Anurida* have been examined by Lubbock and found to be identical with the European form.

Haven, Nantucket and Wood's Holl, and it extends as far south as the shores of Florida.

From the above remarks it will be noted that *Anurida maritima* is a form ranging into both the Palæarctic and Nearctic regions. This wide distribution of an animal with practically no means of self-dispersal is remarkable. Folsom (**63**) believes that marine currents have been the principal agents for its distribution. They would certainly account for its presence on the barren rocky islands off the Scandinavian coast and at Heligoland and the Isle of Man.

An allied terrestrial species, *Anurida* (*Aphoromma*) *granaria* (Nic.), has likewise a very wide geographical distribution. It has a very extensive range in Europe, being known from Great Britain, France, Scandinavia, the Tyrol and Bohemia, and it is also recorded in Arctic regions from Spitzbergen, Franz-Josef Land and North Siberia. *A. tullbergi*, Schött, which frequents the surface of ponds of fresh water, is found in northern Europe and has also been recorded from the United States. Another species, *A. clavata*, Schäff., is found in Tierra-del-Fuego; *A. amorita*, Fols , is known from Alaska and Siberia, and *A. steineni*, Schäff, is a South Georgian species.

IV.—MORPHOLOGY.

1. General Features of External Anatomy.

The general appearance of *Anurida* when viewed under the lower power of the microscope will be seen on referring to fig. 1. As in all insects, the body consists of three well defined regions, viz., the head, the thorax and the abdomen. Its exo-skeleton is but feebly chitinised, and consequently the different regions do not exhibit the complex differentiation into the various sclerites which is seen among the Pterygota.

The **head** (fig. 4) is relatively large in size and has its long axis disposed in the same plane as the rest of the body. In form it is somewhat triangular, and it is considerably flattened, as if it had been compressed in the dorso-ventral direction. In the mid-dorsal region of the head there is situated a very prominent elevation, shaped rather like an inverted isosceles triangle having each of its angles truncated. From the antero-lateral corners of this protuberance arise the antennæ, and on either side of it is a well-marked oval elevation, bearing on its surface a group of glistening black dots. These dots are the eyes of the animal (figs. 4 and 5), they are five in number on each side. A curious circular sense organ, known as the post-antennal organ (*p.a.o.* in figs 4 and 5) lies on each side just in front of the protuberance just mentioned. The labrum and clypeus (fig. 13) jut forwards in front of the head somewhat in the form of a beak; they form the roof of the pharynx and somewhat overhang the mouth. The antennæ are relatively short, being scarcely as long as the head; they each consist of four joints, the second being the largest. The articulation between the third and fourth joints is but imperfectly developed, and is only visible on the ventral aspect (fig. 3). The extremity of each antenna is abundantly clothed with hairs, and situated among the latter is a minute trilobed sense-organ (fig. 7); a short distance below this structure are several patches of modified cuticle (*s′.o′.*) which may perhaps also be of a sensory nature. The mouth is slightly ventral in position; it is bounded dorsally by the labrum, ventrally by the labium, and its sides are formed by the oral folds which are prolongations of the sides of the head. The ventral region of the head appears to be formed almost entirely by the second maxillæ or labium.

The **thorax** consists of three segments, viz., the prothorax, the mesothorax and the metathorax (figs 1 and 3), the first being the smallest division of the three. The three pairs of legs differ in no important features from one another. Each leg is six-jointed and terminates in a single claw, which, in the majority of individuals, is armed with a small tooth on its inner margin (fig. 9). Tarsi are absent in all Collembola, and, consequently, the joint with which the claw articulates corresponds with the tibia of other insects.

The **abdomen** consists of six segments, the third segment being greatly enlarged. On the ventral aspect of the first segment is situated a prominent bilobed papilla known as the ventral tube (*v.t.* in fig. 3). This organ is the most characteristic of Collembolan structures, and it varies a great deal in the degree of development to which it attains in various genera. There arises from a point in the mid-ventral line of the head a narrow furrow, which is termed the ventral groove or linea ventralis (fig. 3); this groove is traceable backwards, passing between the bases of the legs to the anterior aspect of the ventral tube, where it terminates (Plate IV., fig 36). As will be explained in a later chapter, the secretion of two pairs of glands situated in the head flows down the ventral groove and discharges over the surface of the ventral tube, which it serves to moisten. The genital aperture is situated on the ventral surface of the fifth abdominal segment near to its posterior margin, and on the sixth and last segment is situated the anus (fig. 3). The latter is surrounded by three papillæ, one of which is median and dorsal, and the other two ventro-lateral.

There is no sexual dimorphism among the Collembola, and the only difference between the sexes in *Anurida* is that the females are, as a rule, somewhat larger and more bulky than the males and, moreover, the ripe ovaries usually show through the lesser pigmented cuticle on the ventral side as a pair of yellow patches. By the latter character the females can generally be recognised with a hand lens.

2. INTEGUMENT AND COLOURATION.

The integument consists of (*a*) the chitinous cuticle, (*b*) the hypodermis or chitogenous layer, and (*c*) a basement membrane (*vide* Plate II., figs. 16 and 17).

The cuticle varies slightly in thickness in various parts of the body, being thinner on the appendages than elsewhere. It is quite colourless, and its surface is thickly studded with minute, somewhat conical tubercles, which are very evenly spaced apart (fig. 6). Over the apex of the labium these tubercles are replaced by irregular protuberances of the cuticle, but all transitions are observable between the two (fig. 12). On the labrum the tubercles are also modified, and they exhibit a tendency to be arranged in horizontal rows (fig. 13). The tubercles are absent from the inner aspect of the basal half of each of the legs, and scattered over the abdomen are numerous small areas from which they are likewise wanting; these latter areas correspond with the positions of insertion of the tergo-sternal and other muscles (Plate VI., fig. 60). The cuticle, when viewed in very thin sections, is seen to consist of two layers, the line of separation between them passing just below the bases of the tubercles. These layers are best differentiated in preparations stained with Mann's methyl-blue-eosin, when the inner stratum of the two stains a brilliant blue, while the outer one has a stronger affinity for the eosin and appears pinkish in colour (figs. 16 and 17). Interspersed among the tubercles are numerous hairs, some of which are small and pilose, while others are larger and stouter and rather of the nature of setæ. The latter kind are specially prominent about the sides of the head and on the lateral margins of the abdominal segments (figs. 1 and 3). Both kinds of hairs arise from a circular base (fig. 6), which, when viewed in section, is seen to be in reality a cup-like depression in the cuticle (fig. 17).

The hypodermis, or chitogenous layer, is everywhere of the nature of a syncytium, no cell boundaries being distinguishable. Its cellular nature is evident, however, by the presence of numerous large oval nuclei. It contains a great quantity of a very dark indigo-blue pigment (*p.* in fig. 16), and it is to this material that the colouration of the animal is due. The pigment is deposited in the form of minute granules and, except in very thin sections, it appears black, and frequently greatly obscures the nuclei. On the ventral aspect of the body, which is less exposed to the influence of light, the pigment is not quite so abundant as in other parts. When a number of freshly-caught examples of *Anurida* are placed in a small quantity of strong alcohol a little of the pigment becomes soluble in the latter and imparts to it a faint bluish-green tinge. The bulk of the pigment, however, appears to be incapable of being extracted by most of the ordinary reagents. It is not dissolved out by water, neither does ether nor strong hydrochloric acid affect it, and Fernald (**8**) remarks that when sections of the animal were treated with 45 per cent. nitric acid for ten minutes the latter failed to remove the pigment. Weak solutions of strong alkalies turn it a bright reddish colour. Distributed at intervals in the hypodermis are large, pear-shaped cells (*h. cell.* in fig. 17), which are situated not far from the bases of the hairs. They are the trichogenous or hair-forming cells; their positions are easily recognised by their very large nuclei.

The basement membrane (*b.m.* in figs. 16 and 17) is an extremely thin and apparently structureless layer; it is easily seen in preparations stained with methyl-blue-eosin, and appears bright blue.

3. The Mouth Parts.

The structure and development of the mouth-parts of *Anurida* have formed the subject of an elaborate paper by Folsom (**10**), and much of the following account is based on his memoir.

They consist of (1) the labrum or upper lip, (2) the mandibles, (3) the maxillulæ, (4) the lingua or tongue, (5) the first maxillæ, and (6) the second maxillæ or labium.

The principal mouth-parts are remarkable in that they are deeply insunk within the head-capsule and in that they are capable of being partially protruded from it when in use (Plate V., fig. 52). This deep-seated position of the mouth-parts is a secondary condition, and has been brought about in the following manner. In the embryo the sides of the facial region of the head develop from two lateral evaginations of the germ band. These evaginations eventually fuse with the developing fundaments of both the labrum and labium, and in this way form a kind of enclosing box which, by further growth, comes to surround all the remaining mouth-parts. By this means, the latter appear in the adult insect as if they were deeply pushed back into the cavity of the head. This condition of the mouth-parts is eminently characteristic of the Collembola and, with the exception of certain Thysanura, it is found nowhere else among insects.

The **labrum** (fig. 13) forms the dorsal or anterior wall of the mouth-cavity. It is seen to be somewhat rhomboidal in form, and on its dorsal surface are distributed some stiffish hairs, which are probably of a sensory nature. Situated immediately behind the labrum is the clypeus (*clyp.*), which is separated from it by means of a flexible suture. This suture functions as a hinge, and admits of a certain amount of movement for the labrum in the vertical plane. Posteriorly, the clypeus is separated from the epicranial region of the head by a shallow groove, while laterally it merges into the sides of the head (*pl.*). The posterior or pharyngeal surface of the labrum is lined with a soft membrane; the latter, however, does not exhibit any special chitinizations, either in the form of hairs or gustatory organs, etc., which would constitute an "epipharynx."

The **mandibles** (figs. 11 and 15) are elongate tubular structures, which are flattened and somewhat expanded at their apices and provided with five sharp teeth, of which the last is the largest. At the base of each mandible is situated a large opening (Plate II., fig. 15, *cav.*) through which muscles pass to be inserted on the walls of the mandibular cavity. With the exception of its basal attachment, each mandible lies free within a pocket-like evagination of the pharynx (Plate IV., fig. 35). The mandibles of *Anurida* differ from the usual Collembolan type in the absence of a masticatory surface. This feature is correlated with the soft and unresisting nature of the food in this species, which necessitates rather the use of a cutting edge than a crushing surface.

The **maxillulæ**[*] (figs. 11 and 14) are intercalated between the mandibles and the first maxillæ. They are situated immediately dorsad of the lingua, to which they are closely applied. In form the maxillulæ are broad and plate-like, but are feebly chitinised and relatively delicate structures. Along their anterior borders they are finely serrated, and they each bear a tooth-like projection at their outer angles. Unlike the first maxillæ, at no stage in their development do the maxillulæ exhibit any indications of a differentiation into a galea and lacinia, neither are there any traces of palpi.

The **lingua** or tongue is a median unpaired structure, and is moderately strongly chitinised (figs. 11 and 14). It has a paired appearance owing to being lobed anteriorly and in being grooved dorsally down the middle line. Posteriorly, the lingua rests on two strong chitinous props, which are termed the lingual stalks (*ling. st.*). The latter structures are not, *sensu stricto*, parts of the tongue; they are developed as longitudinal thicken-

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[*] Most writers on the Collembola have referred to these organs as paraglossæ. The latter name, however, is undesirable since it renders them liable to confusion with parts bearing the same name in the second maxillæ of the Pterygota. Hansen (*Zool. Anz.*, 1893) was the first to recognise that they represented a complete and separate pair of gnathites and he termed them *maxillulæ*. Seven years later the embryological work of Folsom (**10**) definitely established the truth of Hansen's conclusions. On account, however, of their intimate relations with the lingua, Folsom named them *superlinguæ*. In the generalized Collembolan *Isotoma palustris* Carpenter has recently shown (*Proc. Roy. Irish Acad.*, 1903, vol. xxiv. ser. B. p. 325) that the maxillulæ are of a very primitive nature, each being subdivided into a galea and lacinia which have become lost in *Anurida*. Among the Thysanura the maxillulæ are likewise differentiated into a galea and lacinia, and a palp is present in addition. In the Pterygota these gnathites have, as yet, been very little studied and they appear to be either greatly reduced and very intimately associated with the lingua or tongue (Orthoptera and Plectoptera) or atrophied altogether. In the earwig-like genus *Hemimerus* the maxillulæ appear to approximate to the apterygote condition very closely (Hansen, *Ent. Tidskr.*, 1894, p. 65). Folsom (**10**) regards the "hypopharynx" of the Pterygota as being a composite structure formed by a fusion of the maxillulæ with the tongue.

ings of the maxillary pockets, which acquire a secondary connection and ultimate fusion with the lingua.

The **first maxillæ** (figs. 11 and 14) each consist of an apical portion or "head," which articulates by means of a hinge joint with a long stalk-like stipes (*st.*). Each stipes in its turn articulates with a shorter piece, which is termed the cardo (*car.*), whose opposite extremity is attached to the proximal end of the lingual stalk of its side. The "head" of the maxilla consists of three parts. The uppermost of them is a thinly chitinised membranous lamella, which is finely serrated along its inner margin and appears to correspond to a greatly modified palp (*plp.*). Underneath the palp is situated the galea (*gal.*); it is the most massive piece of the three, and is armed with strong teeth. The third piece is the lacinia (*lac.*), which very closely resembles the palp in form, but is rather more deeply toothed. The existence of a palp in the adult insect seems to have been overlooked by Folsom, notwithstanding the care with which he studied the mouth-parts and the fact that it has been figured by Fernald (**8**, pl. xlviii., fig. 9). The latter author, however, made no suggestion as to its homologies. Its presence in the embryo *Anurida* is described and figured by Folsom, who adds that in the newly-hatched insect no trace of a palp can be made out, and he concludes that it must have been resorbed. The palp is frequently difficult to make out as it usually lies closely apposed to the sides of the galea, and in this position it is easily overlooked on account of its extreme transparency. Like the mandibles, each maxilla lies in a separate pharyngeal pocket, which is situated somewhat ventrad of the mandibular pocket of its side (Plate IV., fig. 35).

The **second maxillæ** or labium form practically the whole of the ventral region of the head. Although they develop from paired fundaments in the embryo (Plate VII., fig. 75), almost all traces of such an origin become obliterated in the completed structure. Its distal extremity, however, is seen to consist of two halves, which are in close contact with one another along the mid-ventral line without being fused together (fig. 12, *lb.*). Each half is to be regarded as the equivalent of an undifferentiated galea and lacinia. Labial palpi are present in the embryo, but they subsequently become resorbed. The remaining portion of the labium extends from the suture to the anterior margin of the prothorax, and would appear to be the equivalent of an undifferentiated mentum, sub-mentum, and gula.

While feeding is taking place, both the mandibles and first maxillæ are protruded from their pockets for the purpose of seizing the food, and they can be seen with the aid of a strong lens to be projecting a short distance through the mouth. By means of the retraction of these parts, aided by the movements of the labrum and labium, the food is taken into the mouth. Mastication is chiefly performed by the combined action of the mandibles and first maxillæ. The part played by the maxillulæ appears to be a more or less passive and subsidiary one, for, since they are closely applied to the lingua, they possess but little power of movement. When the food is finely comminuted, it is sucked up into the œsophagus by means of the alternate contraction and expansion of the radial and circular muscles of the pharynx.

4. The Digestive System.

The digestive system is divisible into three well-defined regions, viz., the fore-gut, the mid-gut or stomach, and the hind-gut. It passes in a perfectly straight course from the mouth to the anus, and is remarkable on account of its extremely simple structure. With the exception of a pair of salivary glands there are no accessory organs in association with it.

The **fore-gut** consists of the pharynx and the œsophagus. The pharynx is a capacious cavity and occupies about one-sixth of the total length of the fore-gut. Its dorsal or anterior wall is formed by the labrum and its ventral wall or floor by the labium or lower lip (Plate III., fig. 27). The pharynx is evaginated into four backwardly directed pockets, two on either side for the reception of the mandibles and first maxillæ (Plate IV., fig. 35). The lingua occupies a median position in the floor of the pharynx, and the maxillulæ are closely applied to the upper surface of the former.

The œsophagus is a narrow tube of a very uniform calibre throughout its length (Plate III., fig. 27). At the point where it joins the mid-gut it projects for a short distance into the cavity of the latter in the form of a papilla (Plate III., fig. 28). The lumen of the œsophagus is roughly H-shaped in transverse section, owing to four inwardly directed bulgings of its epithelial walls (fig. 29).

The walls of the fore-gut consist of three layers; the innermost is a chitinous intima, the middle one is an epithelium, and the outer one is muscular. The chitinous lining, which is secreted by the underlying epithelial layer, is continuous with the cuticle of the integument. It is very thin and, with the exception of a few scattered tooth-like projections in the region of the pharnyx and the anterior part of the œsophagus, its surface is perfectly smooth. Whether the epithelial layer is of the nature of a true epithelium or not is uncertain. It has not been possible to detect any cell-boundaries even after a prolonged treatment of sections with suitable staining reagents; it appears as a syncytium containing oval nuclei dispersed at frequent intervals, and is similar in its structure to the hypodermis, with which it is directly continuous (figs. 27 and 28). As Fernald remarks, there are slight depressions in the chitinous lining which alternate in position with the nuclei and may perhaps indicate the boundaries between adjacent cells. Externally, the epithelial layer rests on a delicate basement membrane (*b. m.* in fig. 29), and immediately outside the latter is a strongly developed layer of circular muscle fibres (figs. 27, 28 and 29). The structure of these fibres is remarkable; they are all cross striated, and each fibre is in the form of a ring completely encircling the gut, with its two ends meeting in the mid-dorsal line. The sarcoplasm of each fibre lies wholly external to the contractile substance, and in it is situated the nucleus of the fibre (fig. 29). The nuclei of the fibres are all situated in the dorsal line, and they form a continuous row, stretching right along the fore-gut. Each muscle fibre is invested externally by an extremely delicate sarcolemma (*slmma* in fig. 29).

In relation with the pharynx and a small tract of the adjacent portion of the œsophagus a remarkable system of radial muscles is developed and, furthermore, the circular fibres are more strongly developed in this region than elsewhere. These muscles fall into two groups, viz., a dorsal or anterior series and a ventral or posterior series (Plate III., fig. 27). The muscles forming these two groups take their origin in the cuticle of the body wall. Those of the dorsal series cross the cavity of the head in an oblique direction and, passing between the circular fibres, attach themselves to the chitinous intima of the gut. In the case of the ventral series, they cross the head cavity in the horizontal plane, and converge to become inserted into the tentorium. A similar system of radial muscles occurs in *Tomocerus*, *Orchesella* and other Collembola; they are termed the *dilatores pharyngii*, and act in conjunction with the circular fibres and convert the pharynx into a kind of pumping organ.

The **mid-gut** commences in the posterior end of the prothorax, and extends backwards into the fourth abdominal segment, where it is joined by the hind-gut (Plate IV., fig. 35). The lumen of the mid-gut is practically circular in section, but its diameter narrows considerably in the posterior fourth of its course. In regard to its structure, it is very uniform throughout its length, and its walls consist of a layer of large epithelial cells resting externally on a relatively stout *tunica propria*, and on the outside of the latter is a system of circular and longitudinal muscle fibres, both of which are markedly striated (Plate V., fig. 49, and Plate VI., fig. 61). The epithelial layer consists of a row of very regular cubical cells, which have a tendency to become somewhat columnar. The boundaries between adjacent cells are best seen towards the posterior region of the gut; over the rest of the area they vary greatly in their degree of definition, and for the most part are hard to distinguish, but their distinctness depends a good deal upon the particular phase of physiological activity the cells happen to be in at the time of killing and fixation. Each cell contains a large oval or rounded nucleus situated near to its centre; the chromatin granules of the nucleus are congregated together into several large masses (figs. 30 and 49). Towards the base of each cell there is, as a rule, a deeply-staining granule of chromatic material (*ch. b* in fig. 30); the significance of this body is unknown. The free margins of the mid-gut cells have a finely striated appearance, which forms a "striated hem" or "Härchensaum" (*hs.* in fig. 30).

Fernald has described a process of regeneration which takes place in the mid-gut cells, but it has not been possible to confirm his observations with any degree of certainty. He remarks that "The nuclei of the epithelium divide, and one of the two that are thus formed in each cell passes towards the free face of the cell, while the other passes towards its base. The cells' walls now become indistinct and delamination occurs, the outer half of each cell being thrown off. These moulted cells collect in the lumen of the gut, and remain there until the chitin of the remainder of the body is thrown off, when this is also removed from the body. The outer edges of the cells remaining form a new 'Härchensaum,' and resume their normal condition" (**8**. p. 455). A somewhat similar process of moulting or regeneration of the mid-gut cells has been described by Sommer in *Tomocerus* (*Macrotoma*) (**23**), and by Prowazek in *Isotoma* (**21**).

The musculature of the mid-gut consists of two layers, an outer longitudinal and an inner circular set (Plate V., fig. 49, and Plate VI., fig. 61). The circular fibres each consist of a single greatly elongated cell, the opposite ends of which meet in the mid-dorsal line. Previous to uniting, the two ends of each fibre break up into their component fibrillæ or sarcostyles, and also receive contributions from adjacent fibres (Plate VI., fig. 61). The longitudinal fibres consist of greatly elongated cells placed end to end. The nuclei of both the circular and longitudinal fibres are hard to detect; they are very minute, and those of the circular muscles are principally dorsal in position. A fine membrane of connective tissue closely invests the outer surface of the muscle fibres, and also lines the rectangular spaces enclosed between them (fig. 30). Where the mid-gut joins the hind-gut its epithelium becomes greatly thickened, and forms a ring-like bulging which reduces the lumen of the gut at that point to less than one-third of its usual diameter (fig. 49). Surrounding the adjacent portion of the hind-gut is a strongly developed pyloric or intestinal valve, which is formed by the circular muscles at that point becoming enormously thickened (*valve c. m.*).

The **hind-gut** extends from the posterior border of the fourth abdominal segment to the anus. It is lined by a perfectly smooth chitinous cuticle, directly continuous with that of the integument (*cut.* in fig. 49), and underlying it is a cellular layer (*h. g. epith.*), which rests externally on a basement membrane (*t. p.*). In the anterior third of the hind-gut its epithelial layer is greatly thickened, the nuclei are larger and cell-boundaries are discernible; over the rest of its course this layer is relatively thin and of the nature of a syncytium. Circular muscle fibres of the striped variety are well developed in relation with the anterior half of the gut, but they dwindle away as they proceed further backwards. The cuticular and epithelial lining of the gut is thrown into numerous folds and bulgings, but the circular muscles do not follow their course and large spaces are consequently left. (Plate III., fig. 31). These spaces are in free communication with the general body cavity between the muscles, and usually contain blood corpuscles. In addition to circular muscles, there is also a system of radial muscles in relation with the hind-gut; they fall into two groups, the *dilatores recti* and the *dilatores ani* (fig. 49, *dil. rect. m.* and *dil. an. m.*). The dilatores recti chiefly arise from the middle section of the gut, where it is considerably enlarged and forms a kind of rectal chamber. They cross the cavity of the fifth abdominal segment in dorsal, ventral, and lateral directions, and are inserted into the cuticle of the body-wall. The dilatores ani are a similar series of muscles, situated immediately around the anus.

The anus is situated on the last segment of the body, and is surrounded by three papillæ, the largest of which is median and dorsal and the other two ventro-lateral in position (Plate I., fig. 3, *an.*).

5. THE MUSCULAR SYSTEM.

In order to explain the muscular system at all adequately a very lengthy description would be necessary, and such an account is beyond the scope of this Memoir; only its general features, therefore, will be referred to.

The musculature of the abdomen may be broadly divided into three systems. Firstly, a series of longitudinal tergal muscles, which are arranged in the form of an outer and an inner set on either side of the dorsal vessel in each segment (*l. t. m.* in figs. 50 and 51). Secondly, and corresponding with these on the ventral side, a system of longitudinal sternal muscles (*l. s. m.*); and thirdly, a system of tergo-sternal muscles, some of which pass vertically and others obliquely from the tergum to the sternum in each segment (*t. s. musc.*).

In the thorax this general arrangement is adhered to, but it has undergone modification in conformity with the requirements of the mobility of the legs.

In the head the musculature is very complex; it is principally concerned with the movements of the various mouth-parts. In addition to the usual muscles in connection with those organs, there are special muscles for drawing the mandibles and first maxillæ forwards, and partially protruding them through the mouth, and there is also an antagonistic set for retracting these organs back again into the cavity of the head. In *Anurida* more than twenty pairs of muscles can be made out in connection with the mandibles and the first and second maxillæ; the jaw muscles have been described in detail by Folsom for the Collembolan *Orchesella*, and the reader is referred to his paper (**9**).

Excepting the circular muscle bands of the walls of the heart, the fibres of both the somatic and splanchnic muscles of *Anurida* belong to the striated variety throughout. The principal muscles of the body consist of a large number of very small fibres, and the latter do not exhibit any tendency to be grouped together into bundles. When viewed in transverse sections (Plate IV., fig. 45) the central portion of each muscle is seen to be composed of a large number of fibres, which appear as deeply staining angular fields separated from one another by interstitial protoplasm. The periphery of the muscle is formed of a thick layer of protoplasm, in which are situated one or more relatively large, oval nuclei. The whole muscle is invested externally by a limiting membrane or perimysium. In preparations treated with Heidenheim's iron-alum-haematoxylin the minute structure of the muscles can be made out with great clearness, and in this respect the Collembola are very favourite subjects for the study of the histology of this tissue. The typical light and dark transverse stripes are seen with extreme clearness; the dark bands or "sarcous elements" are subdivided longitudinally into extremely fine lines, which are the interspaces between the fibrils or sarcostyles of the muscle (Plate VI., fig. 60). Each light stripe is seen to be bisected by an irregular transverse line (*k. m.*) which indicates the position of the transverse or Krause's membrane; the segment of a sarcostyle contained between two transverse membranes constitutes a sarcomere or "muscle segment." By careful focussing by means of a high power a transverse line can also be made out bisecting each of the dark bands, and is known as Hensen's line.

At the points where the muscles are attached to the cuticle the hypodermis undergoes some modification, and, moreover, the pigment is absent from those positions. In many instances the points of attachment of the muscles to the cuticle is indicated externally, for over such areas the characteristic tubercles are frequently not developed (fig. 60).

The muscles of the walls of the alimentary canal consist of single fibres, and their structure is referred to in the account of the digestive system.

In the head and thorax there are developed endoskeletal structures for the purpose of giving a firm attachment to certain of the muscles. The endoskeleton of the head is known as the tentorium (Plate III., fig. 27), and consists of a chitinous plate lying parallel with the frontal plane, from which diverge two pairs of chitinous arms extending respectively to the dorsal and ventral integument of the head. Between the dorsal arms lie the œsophagus and supra-œsophageal ganglion above it, and the ventral arms embrace the infra-œsophageal ganglion (Folsom **10**). To the tentorium are attached a great number of muscles, including the posterior or ventral group of the dilatores pharyngii, and many of the muscles moving the mouth-parts. In the thorax the endoskeleton consists of three apodemes, one to each segment, and which are termed respectively the antefurca, the medifurca and the postfurca. These give attachment to many of the muscles of the legs, as well as lending support to the nervous system, and take the form of chitinous pillars, which project upwards from the sterna and bifurcate into a pair of forks or arms (Plate IV., fig. 37). The medifurca and post-furca are better developed than the corresponding part in the prothorax.

6. THE VENTRAL TUBE OR ABDOMINAL VESICLE.

The ventral tube is a large papilla-like organ situated on the middle of the ventral aspect of the first abdominal segment (fig. 3). It presents a considerable range of variation, both in form and in degree of development among various Collembola, but in *Anurida* it is relatively simple in structure and remains in a rudimentary condition.

As is demonstrated by its development, the ventral tube is formed by the fusion together of the pair of abdominal appendages belonging to its segment (*vide* text-fig. 1). It consists of a short basal column, which is divided distally by a median longitudinal cleft into two lobes or vesicles, and these latter are the only indication in the adult of the paired origin of this organ (Plate IV., fig. 36). It is invested by the general cuticle of the body-wall, but where the latter is prolonged over the two terminal vesicles it becomes extremely thin and flexible, its tubercles are wanting and it is quite smooth (Plate II., fig. 21). In the structure of its walls it closely resembles the general integument of the body: they consist of a well-developed layer of hypodermis, but contain very little pigment and there is no basement membrane. Where the hypodermis lines the lobes or vesicles of the organ, it alters very considerably in character; certain of its cells being very large, elongated in a vertical direction, and tapering into a point (*h.c.* in fig. 21). Each of these cells contains a large nucleus with abundant chromatin granules.

Arising from the terminal lobes of the organ are several muscles; they pass down its central cavity and converge towards one another to be inserted into the body-wall on either side (*ret. musc.* in figs. 21, 23 and 36). By means of the contraction of these muscles the distal lobes are capable of being withdrawn into the basal column when the organ is not in use.

The cavity of the ventral tube is in direct communication with the general body-cavity of the animal, and contains numerous blood corpuscles (*b.c.* in fig. 21), and it is by means of the pressure exerted by the blood that the protrusion of the vesicles is effected. When the organ is in a retracted state its cavity is shut off from that of the body of the animal by the contraction of the longitudinal sternal muscles, which are disposed in two bundles situated slightly to the outside of the organ on either side (*l. s. m.* in fig. 38). The effect of the contraction of the muscles is to approximate its anterior and posterior walls. When the full expansion of the organ is desired both its retractor muscles and the longitudinal sternal muscles are relaxed. The slackening of the latter set of muscles results in a sudden flow of blood into its cavity, and in virtue of the turgidity thus acquired its terminal vesicles are protruded to their fullest extent.

With regard to the function of the ventral tube, there has been, and is still, a great diversity of opinion. Almost all investigators who have given any attention to the structure of the Collembola have made suggestions concerning it, and some of the views which have been put forward appear to rest on a very slender basis. By Kolenati (**67**) and Latreille* the ventral tube was believed to be the external generative organ, and Claypole (**31**) suggests the possibility of it being the relic of a former outlet of the reproductive organs. Burmeister†

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* *Nouv. Ann. d'Hist. Nat.*, t. 1, 1832.

† *Handbuch der Entomologie*, 1838.

believed it to be an apparatus for affording additional support to the body. By Bourlet‡ it was thought to serve to moisten the springing organ as well as serving as an adhesive organ on which the creature might alight after springing, thus lessening the effect of the shock of that movement. Reuter (**22**) looked upon it as being a kind of hydrostatic organ. He believed that the claws of the feet collected moisture from the hairs of the general surface of the body and conveyed it to the ventral tube, which served to absorb it into the system. Sommer (**23**) believed it to be an adhesive organ, and suggested that it also performed the same service for the integument as does the preen gland for the feathers in Birds. Schött (**93**) maintained a somewhat similar opinion.

The view which has received the widest support is the one which regards the ventral tube as being an adhesive organ enabling the insects to walk over smooth or steep surfaces. This opinion is upheld by Bourlet (in part), de Olfers (**19**) and Tullberg (**96**), who believed that its power of adhesion was brought about by means of suction. De Geer*, Nicolet† and Lubbock, however, thought that the adhesive function was effected by means of a special secretion of the tube itself. Lubbock, who studied the action of the organ in *Sminthurus*, where it attains its greatest development, remarks that if one of these animals be laid on its back, and a piece of glass be brought within its reach, it will endeavour to seize it with the feet, but at the same time it will protrude one or both of the vesicles, emitting as it does so a minute drop of fluid, which, no doubt, enables it to obtain a better hold.

‡ *Mem. Soc. d'Agric. du départment du Nord*, 1841.

* *Abhandlungen zur Geschichte der Insekten*, Bd. vii., 1783.

† *Recherches pour servir à l'histoire naturelle des Podurelles*, 1841.

The view that the ventral tube is an adhesive organ which produces a glandular secretion is also upheld by Haase‡, Uzel (**38**) and Prowazek (**21**), but these writers regard it as being only a secondary function of the organ, and assert that its principal significance is as an organ of respiration. The thinness of its investing cuticle, and the fact that it always contains a large amount of blood, adapt it for aerating the latter and, therefore, lend support to this contention.

The two most recent investigators, viz., Willem (**27**) and Hoffmann (**12**) both agree in their opinion that though it may fulfil the secondary function of being an organ of respiration, its main function is to serve as an organ of adhesion to aid the animal in climbing. These writers believe that the secretion which moistens the surface of the ventral tube is supplied by a pair of glands situated in the head. The ducts of these glands were first shown by Fernald to open by means of a small pore into the commencement of the ventral groove. Willem and Hoffmann believe that the secretion flows down the ventral groove and reaches the ventral tube and bathes the surface of the latter. The observations of these writers are confirmed in the case of *Anurida* in the succeeding chapter in this Memoir. By keeping various Collembola in a damp chamber, and observing them climb steep and smooth surfaces, it can be made out that the primary function, at any rate, of the ventral tube is that of an organ of adhesion. The present writer believes that it also plays an important part as a respiratory organ. Both Willem and Hoffmann regard the modified hypodermis cells lining the ventral tube (*h.c.* in fig. 21) as being simply ordinary hypodermis cells which have assumed an unusual form; while on account of their large

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‡ Die Abdominal-anhänge der Insekten, *Morph. Jahrb.*, 1889.

size and the prominence of their nuclei they have been regarded by previous writers as being the glands which provide the secretion which moistens that organ.

7. The Cephalic Glands and Ventral Groove.

In *Anurida* three pairs of cephalic glands are present, two of which discharge their secretion into the ventral groove, and the third pair open into the buccal cavity and are to be regarded as salivary glands. Three pairs of cephalic glands have also been made out by Willem and Sabbe in *Sminthurus* (**28**), by Willem in *Orchesella* (**26**), and by Hoffmann in *Tomocerus* (**12**).

The **salivary glands** of *Anurida* are lodged in the hinder region of the head, one on either side (Plate VI., figs. 63 and 65). They are composed of groups of acini, and each acinus consists of a group of eight or nine very large cells, which are disposed in a radial fashion around a central ductule (*dtl.* in fig. 63). The cells of these glands have very large nuclei, rich in chromatin, and a considerable portion of the inner half of each cell is filled with a dense and compact mass of secretory granules (*s. g.*). The ductules are of very small calibre and are intra-cellular at their commencement; a little lower down they converge and unite with those from neighbouring cells to form a fine canal, which becomes inter-cellular in structure. The canals from adjacent acini in their turn unite with one another to form the main duct of the gland. This duct (fig. 67) is composed of flattened cells, containing small elongate nuclei; both it and all other parts of the glands are invested internally and externally by a delicate membrane. The course of the duct is difficult to make out among the numerous other structures of the head, but it appears to converge with its fellow, from the opposite side, towards the median line and to approach the lingua; it has not been possible, however, to detect the point where they open into the buccal cavity. Willem, who has specially studied these glands, states that in *Sminthurus* their ducts open on to the lingua on either side. He remarks as follows:—"Le conduit en question se rapproche de la ligne médiane de la tête en passant contre le pivot de la mandibule, puis côtoie obliquement la commissure perioesophagienne: sa dernière portion, à paroi chitineuse plus épaisse, est logeé dans une rigole de la base de l'hypopharynx; elle aboutit dans la cavité buccale sur le côté de cet organe, un peu au-dessus de la région occupée par le bord superieur de la plaque molaire de la mandibule" (**26,** p. 655). According to him a similar arrangement prevails in *Orchesella*.

The salivary glands are regarded by Willem as being a pair of metameric glands pertaining to the first maxillæ, and he bases this conclusion on the embryological researches of Uzel (**38**). He remarks that "Morphologiquement, on doit les considérer comme des glandes métamériques appartenant au segment de la première maxille: la partie de l'hypopharynx où aboutissent leurs conduits excréteurs se forme, en effet, au se dépens d'une protubérance médiane qui apparâit chez l'embryon sur le premier segment maxillaire." If this observation of Uzel be confirmed, the important generalization that the salivary glands of the Collembola are homologous with the shell glands of the Crustacea would be evident. The Crustacean shell glands open on the second maxillary segment, and it will be seen on referring to the table given on page 74 that the second maxillæ of the Crustacea are homodynamous with the first maxillæ of insects.

Of the two pairs of glands which open into the ventral groove, the most important pair are known as the tubular glands and the other as the globular or acinose glands.

The **tubular glands** (Plate VI., figs. 63 and 65) are situated very near to the salivary glands in the hinder region of the head. Both the secretory and conducting portions of these glands are tubular in structure, and are inter-cellular throughout their course. The distinction between the two portions is very slight; in the glandular part the cells and their nuclei are rather larger than those of the duct. The ducts of opposite sides pass downwards and forwards close under the hypodermis of the ventral region of the head and, approximating towards one another, eventually open into a common chamber (fig. 64). From the latter a short duct passes downwards in an oblique direction, and opens on to the exterior on the ventral surface of the head at the commencement of the ventral groove. The walls of the common chamber are invested with a layer of circular muscle fibres, which evidently have the power of controlling the flow of the secretion into the ventral groove. These fibres resemble in their structure those of the fore-gut, and consist (fig. 64) of a layer of sarcoplasm on the outside with the muscle substance lying wholly internal to it.

The **globular or acinose glands** (figs. 65 and 66) are situated in the anterior region of the head, and close to the hypodermis on either side. They each consist of a group of cells, which are similar in structure to those of the salivary glands, and from them a fine duct passes forward and opens into the common canal or chamber in front of the ducts of the tubular glands.

The **ventral groove** (Plate I., fig. 3, *v.g.*) arises close behind the suture (*sut.* in fig. 12) of the labium, and passes backwards in the median ventral line until it reaches the anterior aspect of the ventral tube, where it terminates

(Plate IV., fig. 36). At its commencement it is in the form of a closed canal (Plate II., fig. 26), which appears to have been developed by the union with one another of a pair of parallel ridges of the cuticle; traced further backwards, in the prothorax, the canal is incomplete, the ridges not having fused with one another; in the metathorax each ridge has been folded on itself, and the two together form a pair of tubes with a groove or channel between them (figs. 24 and 26*c*), and in this condition it continues the remainder of its course on to the ventral tube.

The secretions of the tubular and acinose glands flow down the groove to reach the surface of the ventral tube, which they serve to moisten. The fact that the ventral tube receives the secretion of cephalic glands was first ascertained by Fernald, and, although doubted by other investigators, it has been recently confirmed by both Willem and Hoffmann. Fernald, however, appears to have regarded what are here described as salivary glands as being the glands which furnish the secretion, and what he has regarded as their ducts opening into the ventral groove, appear to be really the ducts of the tubular glands.

8. The Nervous System.

The nervous system consists of a chain of five ganglia united together by means of a double series of nerve cords or connectives (Plate IV., fig. 48). The first of these is the supra-œsophageal ganglion or brain; it is situated in the head immediately above the œsophagus (fig. 35). The remainder of the system forms the ventral nerve cord and lies beneath the digestive canal. It comprises a large sub- or infra-œsophageal ganglion, which is followed by three ganglia, lodged respectively in the prothorax, the mesothorax and the metathorax (fig. 35). The sub-œsophageal ganglion is joined to the brain by means of a pair of para-œsophageal connectives, which pass around and encircle the gullet, one on either side (*conn.*).

The brain of *Anurida* arises in a similar manner to that which has been found to obtain in other insects. It is formed in the embryo by the fusion of the first three pairs of primitive ganglia, which are termed the protocerebrum, the deutocerebrum and the tritocerebrum respectively (Plate VII., fig. 74). The completed organ of the adult Insect is divisible into three main regions, which correspond with these primitive ganglia. They are as follows:—

(*a*) The protocerebrum, which is the largest division of the brain, comprises the optic and protocerebral lobes (fig. 48). The optic lobe on either side gives origin to the main optic nerve (*op. n.*), and the latter sub-divides into five branches, each branch supplying one of the eyes. The protocerebral lobes form the greater part of the brain when viewed from above.

(*b*) The deutocerebrum, which is composed of the two antennary lobes. From each lobe a stout nerve (*at. n.*) passes to the antenna of its side, and on nearing the apex of that appendage it divides into a number of fine branches, supplying the sense organs (Plate II., fig. 22).

(*c*) The tritocerebrum, which consists of the two œsophageal lobes (*trc.* in fig. 48). From the latter arise the para-œsophageal connectives and the nerves which supply the labrum.

The sub-œsophageal ganglion or, more properly, the sub-œsophageal ganglionic mass, is formed by the fusion of four pairs of primitive ganglia. From it arise paired nerves, which supply respectively the mandibles, the maxillulæ and the first and second maxillæ, together with an unpaired nerve which passes to the lingua.

The prothoracic and mesothoracic ganglia each give off a pair of principal nerves on either side, which supply the various muscles of their respective segments. The ganglion situated in the metathorax (*th. g.* 3) is in reality a ganglionic complex formed by the fusion of the pair of primitive metathoracic ganglia with those of the abdomen. Several pairs of nerves arise from this ganglion, and they appear to supply the musculature of the metathoracic and first abdominal segments.

Directed backwards into the abdomen is a pair of stout parallel nerve cords (*nv.*). These are, perhaps, to be regarded as the remaining connectives of the abdominal nerve chain, the nerve ganglia of which have migrated forwards during embryonic development and become fused with the metathoracic ganglion. Along their course these nerves give off branches (*l.n.*) which can be traced to the generative organs and to the musculature.

Histologically, the nervous system is constructed upon an exceedingly simple plan. The brain is composed on the outside of a layer of unipolar and bipolar ganglion cells provided with very small but deeply-staining nuclei. Internally it consists of a mass of extremely fine nerve fibres, which are arranged for the most part in transverse and longitudinal directions. It presents none of the complex arrangement of nerve cells and fibres which is exhibited in the brain of most Pterygote Insects. The succeeding ganglia also each consist of an outer layer of nerve cells enclosing a central core of nerve fibres (figs. 46 and 47). Nerve cells are wanting from the thoracic connectives, but a few are distributed along the course of the abdominal cords. All the ganglia and connectives are invested by a neurilemma (*neur.* in figs. 46 and 47) of dense connective tissue; it takes a bluish colouration in preparations treated with Mann's methyl-blue-eosin.

Lying immediately dorsad of the ventral nerve chain there exists what may be regarded as a median accessory nerve cord (*m.n.* in figs. 46 and 48). It is confined to the region of the thorax, and is present between and above each pair of connectives joining the thoracic ganglia. It does not appear as a continuous cord, but is seen to arise from the sub-œsophageal ganglion, and from there to pass backwards to the anterior border of the prothoracic ganglion, where it appears to terminate. It then, however, takes fresh origin from the hinder margin of the latter ganglion, and is continued backwards to the mesothoracic ganglion. After repeating itself again, it finally terminates in the ganglion in the metathorax. This system is very delicate, and is difficult to make out; it is probable that its fibres pass as a continuous strand through each of the ganglia, and so connect together each section of the cord. Three pairs of transverse nerves belong to this accessory nerve cord (*m.n. br.* in fig. 48), and in one or two fortunate preparations they were seen to pass to certain parts of the ventral musculature.

A similar accessory system to the above has been described by Oudemans in the Thysanuran *Machilis.* It is there found in relation with each pair of ventral ganglia throughout the whole length of the body, and is said to supply the tracheal trunks and the occlusor muscles of the spiracles. There appear to be no grounds for regarding this system, either in *Anurida* or *Machilis* as being of a sympathetic nature.* In *Anurida* its

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* In the Collembola a true sympathetic (stomatogastric) system has been described and figured by Willem in *Podura aquatica.* It is, however, only very feebly developed. No certain indications of such a system have been met with in *Anurida.* Claypole states that in the embryo of the latter a cord-like proliferation of ectoderm cells arises from the hinder end of the stomatodœum, and regards it as a remnant of a sympathetic system; it disappears, however, before hatching.

function is quite obscure; in *Machilis* it might possibly be analogous with the vagus system of Vertebrata. A somewhat similar system of nerves occurs among various Pterygota, notably in the caterpillars of *Cossus ligniperda* (Lyonnet) and *Sphinx ligustri* (Newport), and in the larva of *Chironomus* (Miall and Hammond).

9. THE SENSORY ORGANS.

The sensory organs of *Anurida* consist of the eyes, the post-antennal organ, the apical sense organ of the antennæ and sensory hairs.

The **eyes** form a group of five glistening black dots on either side of the head. Each group is situated on a very marked oval protuberance a short distance behind the base of the antenna of its side (Plate I., figs. 1 and 4).

Each eye, when viewed from above, is seen to be oval in form and somewhat convex, it is invested by the general cuticle of the body-wall, which forms a perfectly smooth and transparent corneal lens. When viewed in vertical section each eye is seen to be shaped very much like an inverted cone (Plate III., fig. 34). Situated immediately beneath the lens are four small cells, which belong to the hypodermis and are directly continuous with it; they contain no pigment and are full of clear protoplasm. Two of these cells are visible in the figure, and as they secrete the lens they may be termed the lentigen cells. Situated internally to the latter are four very large, deeply pigmented cells, which together form the retina. The inner ends of these cells pass into and are directly continuous with a branch of the optic nerve. They are invested with a mass of pigmented hypodermis which also fills the interstices between adjacent eyes.

It will be noted that the eyes of *Anurida* are structures formed on an extremely simple plan. The researches of Willem go to prove that in the greater number of Collembola (*i.e.*, in the Sminthuridæ, the Entomobryidæ and in some of the Achorutidæ) the eyes are constructed on the eucone principle, and he regards them as being incipient compound eyes. In several genera of the Achorutidæ (including *Anurida*) he points out that there is no layer for the secretion of a crystalline cone, and hence he looks upon the eyes of such forms as being ocelli or stemmata. He remarks (**27** p. 90):—"La considération que les ocelles s'observent parmi les Podurides, chez des formes animals où les organes visuels sont manifestement régression, incite à admettre que ces stemmates sont productions dérivées de l'ommatidie eucône par la disparition du système lentigène, conclusion qui accords avec des faits observés par Patten dans le developpement des ocelles de *Vespa* et de larve d'*Acilius*, et qui autorisent à admettre que les stemmates à deux couches cellulaires de ces Insectes dérivent d'un oeil à trois couches (comme l'ommatidie eucône) par l'atrophie ou le developpement incomplet de la strate moyenne."

If the extreme simplicity of the structure of the eyes of *Anurida* is due to retrogression, and is not a primitive character, it lends support to a belief maintained by certain students of the Collembola, viz., that *Anurida* is, in some respects, a degenerate type.

The **post-antennal organ** (Plate I., figs. 4, 5 and 10, Plate III., fig. 34) is a curious cuticular structure, circular in form and situated one on each side of the head immediately in front of each protuberance which bears the ocelli. It consists of a variable number of somewhat triangular bodies, which are in close contact with one another, with their apices directed towards its centre. The number of these bodies varies in different individuals, but there are most usually nine of them. Out of eight individuals which were specially examined with reference to this organ, four of them had nine triangular bodies, two had ten, and the remaining two possessed seven and eight respectively. Both Laboulbène and Fernald have observed specimens which had seven to the organ on one side of the head, and eight to the organ on the other side.

The elements (triangular bodies) of which the organ is composed appear to be nothing more than greatly enlarged tubercles of the cuticle which have become hollowed out and mounted on short pedicles and arranged in a circular manner around a common centre (fig. 34). The cavity of each of the elements is filled with protoplasm containing a small amount of pigment, but it has not been possible to detect any nuclei.

Each post-antennal organ is supplied by a small nerve (*p.o.n.* in fig. 34).

It is clear that this structure is a sensory organ from the fact of its having a special nerve supply, and the extreme thinness of its cuticular investment shows that it is adapted to receive impressions of external stimuli. What function it is likely to perform is wholly a matter of conjecture; possibly it is an olfactory organ, as is suggested by Willem.

The **apical sense organ** is situated somewhat towards the inner side of the apex of each antenna (Plate I., fig. 7). It is a hollow tri-lobed structure (fig. 8), and its lobes are in free communication with one another at their bases. It is innervated by a branch from the antennal nerve (Plate II., fig. 22), which enters the organ through a small oval foramen situated at its base (fig. 8).

The function of the organ is uncertain; Fernald remarks that "the three lobes are so placed relatively to each other that they might easily give the animal some idea of the form of any object, corresponding, as they do, to the three dimensions in space." It seems more likely, however, that it functions as an olfactory organ, if it be safe to reason from analogy with what is known concerning the antennal sense organs of the Pterygota.

The **sensory hairs** are found principally at the apices of the antennæ, and on the upper and lower lips, but possibly some of the hairs scattered over the general surface of the body may be of a sensory nature also.

10. THE CIRCULATORY SYSTEM.

The circulatory system of *Anurida* consists of the heart and the general body-cavity.

The **heart** is a narrow tube situated just beneath the integument in the median dorsal line of the body above the digestive canal (Plate IV., fig. 35). It is divided by means of segmentally arranged constrictions into a series of six consecutive chambers, which are in free communication with one another. Anteriorly, the heart extends as far as the anterior border of the mesothoracic segment, and from that point it is prolonged forwards as the aorta (*a.*). Posteriorly, it increases in calibre, and terminates rather abruptly in an enlarged and somewhat bulb-like chamber in the fourth abdominal segment (*a. blb.*). Situated on either side of the heart at each of the constrictions is an oval oriface or ostium (*ost.* in fig. 41), and in association with the heart at these same points is a pair of alary muscles (*al. m.*).

The walls of the heart consist of an external investment of connective tissue (*w.* in fig. 40), a middle coat of obliquely disposed muscle fibres (*c.m.b.* in fig. 39 and *m.w.* in fig. 40), and an inner lining or endocardium. The muscle layer consists of bands of non-striped muscle fibres, and is the only part of the body where such are found; they are much more strongly developed in the walls of the last two chambers than elsewhere. The endocardium is an excessively thin membrane; in certain places it can be made out with the aid of an oil-immersion lens ($\frac{1}{12}$ in.), but only with considerable difficulty.

The alary muscles are attached to the dorsal integument between the two groups of longitudinal tergal muscles on either side of the body. Each muscle is composed of a small bundle of striated fibres (*al. m.* in fig. 41), and these latter are prolonged with a tendonous strand of connective tissue (*al. t.*). As each tendon approaches the heart it broadens out and splits into two fan-shaped sheets or layers, one of which spreads out over the dorsal surface of the heart and the other over its ventral aspect (fig. 43). In the space between these two layers is situated an ostium or lateral perforation of the wall of the heart, and altogether there are six pairs of ostia and alary muscles.

The **aorta** (*a.* in fig. 35) may be said to commence immediately in front of the first ostium, and directly above the junction of the œsophagus with the mid-gut. At its commencement it is triangular in transverse section (fig. 42) but, traced further forwards, it becomes more flattened, and is closely applied to the dorsal wall of the œsophagus (fig. 51). By examining a series of consecutive transverse sections, it will be seen that the aorta gradually comes to wrap itself round the fore-gut, and eventually completely surrounds it (fig. 35). Just beneath the supra-œsophageal ganglion the aorta is seen to terminate in a slightly expanded funnel-shaped mouth (fig. 27), which enables the blood to flow directly from the heart into the hæmocœlic cavity of the head. The walls of the aorta are entirely membranous, and contain no muscle fibres.

The **body-cavity** of *Anurida,* as in all the Insecta, is the blood-containing space in which are situated the various organs of the body. It extends throughout the whole length of the animal, and sends prolongations into the antennæ, the legs and the ventral tube. It is much intersected by the fat body which occupies a large proportion of its cavity in many parts of the body. The body-cavity is filled with the blood of the animal, and the corpuscles of the latter are noticeable everywhere throughout its extent; they are specially abundant in the head, where the vascular and hæmocœlic systems are in open communication with one another.

The **blood** consists of (*a*) the corpuscles and (*b*) the plasma. The corpuscles are circular in outline, but at times they become amœboid and give out pseudopodia (Plate III., fig. 33). They are practically colourless, and each contains a sharply defined circular nucleus. Frequently small granules are scattered through the cytoplasm of the corpuscle; they are probably of an excretory nature. Claypole remarks that in newly hatched individuals the blood corpuscles contain a large amount of food yolk.

11. Excretory System.

Unlike other insects none of the Collembola possess Malpighian tubes.* The excretory function is performed entirely by the fat-body, or "Exkretionsorgane," as it is termed by Sommer.

In *Anurida* the fat-body takes the form of irregular masses of tissue distributed in various parts of the body and occupying a large portion of the cavity. In the region

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* In the Thysanura Malpighian tubes are absent in *Japyx*, and in *Campodea* they are only represented by papillae (Oudemans). Among the Pterygota they are also wanting in Aphides (Witlaczil).

of the abdomen it is largely developed, and in places it closely embraces the gut and also attaches itself at many points to the hypodermis. In the thorax it is much broken up by the various muscles; two principal masses occur in close contact with the fore-gut, one on either side, and come in contact with each other in the mid-dorsal line just above the heart. Prolongations of the fat-body pass from the thorax into the head and partially surround the cephalic glands (fig. 63); they do not extend forwards in front of the brain. The organ is also present in many parts in the form of a thin layer of tissue situated in close apposition with the hypodermis and separating the latter from the body-cavity. In this form it is principally developed along the ventral side of the body, especially in the thorax.

The fat-body is limited exteriorly by a layer of connective tissue and, where it is in contact with the hypodermis, this investment is directly continuous with the basement membrane of the body-wall (fig. 16). It is wanting, however, from that surface of the fat-body which is in close contact with the hypodermis and other parts of the body.

In a newly hatched *Anurida*, before any active process of excretion has taken place, the fat-body is seen to be composed of masses of large cells with very irregular boundaries (fig. 18). These cells are composed of a somewhat granular protoplasm, and each contains a relatively small nucleus. The first indication of excretion taking place is seen in the fact that many of the cells undergo liquefaction at their centres, and eventually become vacuolated (figs. 18 and 19). These vacuoles frequently become confluent with one another, and the remaining protoplasm, together with the nuclei, becomes restricted to the periphery of the cells. At a later stage, there appear in the fluid contents of the vacuoles, numerous fine granules of excretory material (fig. 19); these granules increase in size, some much more rapidly than others, and they ultimately take the form of rounded or oval concretions. After excretion has been going on for some time, the fat-body takes the form of an irregular protoplasmic meshwork, in which cell boundaries are not discernable, and nuclei are distributed at various intervals, and the spaces enclosed within the meshes are filled with fluid which contains the excretory granules held in suspension. The process of excretion is generally most active in the central portions of the larger masses of fat-body, and the cells of the latter ultimately break down and completely liquefy, with the exception of those situated around the periphery (fig. 20).

The excretory concretions are unaffected by the action of water, alcohol, ether or toluol, but are readily soluble in acids, and are consequently absent from preparations of animals fixed by acid-containing reagents. They are best seen in animals which have been killed and fixed in strong alcohol. They are of a crystalloidal nature, faintly yellowish in colour and very eosinophilous. Their chemical composition is uncertain, and they do not exhibit any indications of lamination or other structure.

Sommer (**23**) has given some attention to the concretions found in the fatty body of *Tomocerus plumbeus*. In this species they are often of large size and are easier to study than those of *Anurida*. They are dirty white in colour when viewed with reflected light, and pale green and shining with transmitted light. In their structure they are laminated like starch-grains, and sometimes exhibit radial lines in addition. They are unaffected by water or alcohol, but dissolve in acetic, hydrochloric or nitric acids, accompanied by an evolution of gas. Each concretion is made up of a covering coat investing a central crystalline (?) mass. This is seen when nitric acid is made to act very slowly, when the central contents dissolve first and subsequently the coat vanishes also. Sommer believes that they are composed of calcium carbonate, together with an organic basis.

Willem has also studied these excretory concretions, and he used for the purpose *Sminthurus fuscus.* He remarks (**27**) that they have a concentric structure, and that they are insoluble in water, alcohol, ether, or chloroform, but are dissolved by acids. By means of appropriate tests, he came to the conclusion that they are formed of a neutral urate of sodium. It is probable that those of *Tomocerus* are of a similar composition, rather than of calcium carbonate, and Sommer mentions that he did not apply any uric acid tests.

A remarkable feature regarding the excretory function in Collembola is the absence of any ducts by means of which the products can be eliminated. The concretions consequently increase in size according to the age of the animal, and render it impossible for the lives of these insects to be prolonged for any lengthy period. An analogous case is met with in the Ascidians among the Chordata. The "renal vesicles" of these animals similarly have no means of getting rid of the excretory material stored up within them, and which increases greatly in quantity as the individuals progress in age.

It cannot be decided, in the light of existing knowledge, whether the fat-body of the Collembola is homologous with that of other insects. In the case of the latter, authorities are far from being in agreement as to its mode of development, and nothing is known of the development of the fat-body in the Collembola. Both Sommer and Willem claim that among the latter the fat-body, on account of its intimate relations with the hyperdermis, is an ectodermal product. This evidence, however, does not seem sufficient to justify that conclusion.

12. THE REPRODUCTIVE SYSTEM.

The Male Organs.—The testes consist of a pair of organs disposed along the ventro-lateral region of the body, and lying for a considerable portion of their length in close apposition to the mid-gut. Each testis is an elongated chamber, which tapers anteriorly into a delicate filamentous prolongation (Plate VI., fig. 54), and the extremity of the latter is attached to the excretory tissue lying in the mesothoracic segment. Posteriorly, in the region of the second and third abdominal segments, the calibre of the testis increases very considerably, and the mature organ occupies a large portion of the body-cavity in those segments. The hinder fourth of each testis lies completely ventral to the alimentary canal, but as each gland passes anteriorly it gradually comes to lie ventro-laterally in relation to the latter, and finally in its terminal fourth it is completely lateral. In the fifth abdominal segment each testis gives off a short efferent duct which, uniting with its fellow to form a common canal, opens to the exterior on a small papilla situated in the median line near to the posterior margin of the segment (fig. 54).

Each testis is in the form of a tube, and its walls consist of a cellular layer containing scattered oval nuclei, but without any cell-boundaries. Externally it is invested by a coat of connective tissue (fig. 59). The vasa deferentia are similar in their structure to the testis wall, and appear to be tubular evaginations of the latter. The median canal, or ductus ejaculatorius (Plate III., fig. 32), is formed by the union of the two vasa deferentia; it is roughly diamond-shaped when viewed in transverse section, and is lined internally by a chitinous cuticle which rests on an epithelial layer containing numerous nuclei. The ductus is covered externally by a coat of connective tissue. Dilator muscles arise from its chitinous lining and, passing in an oblique direction outwards, are inserted into the body wall (*musc.*).

The lumen of the testes is filled with a dense mass of nucleated tissue, which consists of different stages in the development of the spermatozoa. At the apex of the gland the testis-wall becomes drawn out into the terminal filament (fig. 58). The filament is tubular in structure, and numerous nuclei can be seen in its walls. Near to its apex the cellular wall dwindles away, and the filament becomes reduced to merely a thread-like prolongation of the connective tissue coat of the testis. It is purely ligamentous in function, and serves to maintain the testis in position in the body-cavity.

If the structure of the testes be examined from the apex of the organ and be followed downwards near to where the efferent duct is given off, the successive stages in the development of the spermatozoa can be readily traced. The germinal tissue is in the form of a mass or ridge, situated at about the middle of the length of the testis. It consists of a mass of cells (fig. 59a), which are seen in places to be roughly polygonal in shape; each cell contains a large, very deeply staining nucleus. The germinal nuclei divide, and the direct products of the division fill almost the whole of the anterior third of each testis (*d. s.* in figs. 58 and 59a). The nuclei are seen to principally arrange themselves in groups, which are more or less ovoid or circular in form, and contain an area of clear protoplasm in their centres. Traced further backwards (d^1, s^1 in fig. 59) these nuclei divide and fragment and form tiny masses of irregularly-shaped chromatic bodies embedded in a dense matrix of protoplasm. In the hinder third of the testis the cellular layer of its wall gives off numerous branched intra-testicular prolongations (*i. p.* in fig. 59). These prolongations divide up the substance of the testis into a number of separate masses by means of their branches, which freely anastomose with one another. In this way the cavity of the testis becomes sub-divided into a number of irregular chambers, each of which is filled with a mass of developing spermatozoa. The next stage in the development of the sex cells is seen where the chromatin bodies retreat towards the periphery of the masses of protoplasm in which they are distributed (d^2, s^2), and eventually become congregated together over a very limited area of the latter. Traced a little further back, the chromatin bodies gradually elongate to form the heads of the spermatozoa, and from them are seen to extend delicate filaments, and each mass becomes easily recognisable as being a bunch of spermatozoa (*s. p.*). During the last stage in development the intra-testicular prolongations, which have served to nourish the developing sperms, are seen to break down and ultimately liquefy, and the posterior end of the testis becomes filled with spermatozoa floating in a thickish fluid.

The process of spermatogenesis has also been studied in *Anurida* by Fernald, but the above account differs very considerably from the description detailed by that author. According to his observations, it would seem that the process is a much more lengthy one than that just described. What are in the present account interpreted as bundles of fully-developed spermatozoa, correspond with his stage where there are a number of elongate granules with fine threads passing from them forming bundles lying in various directions. According to him, this is not the final condition, but is merely a prelude to a further series of changes. He states that this structure soon changes, and the entire substance begins to undergo degeneration, and an entirely homogeneous mass results containing many deeply-staining granules. Fat globules appear in small numbers, and a columnar epithelium becomes formed near to the external connective tissue of the testis wall. A similar epithelium becomes developed in the granular mass nearer to the testis. Traced further back the fat globules increase in number, and among them are multitudes of spermatozoa which have been formed from the epithelial cells.

These later changes described by Fernald are very remarkable, and there can be little doubt that they do not represent the normal state of affairs, and most probably they are of a pathological nature. The observations of the present writer confirm in all essentials the brief account of the spermatogenesis given by Lécaillon (**16**). In many examples of *Anurida* the writer has found Nematode worms,* and their developmental stages in the testes (Plate VII., figs. 79 and 80). In several instances, these parasites were found to be so numerous as to destroy the whole internal structure of the testes, leaving behind little more than the bare walls. In other cases the worms were less numerous, and the structure of the organs was only partially destroyed, while many oil globules were present. It is the belief of the present writer that the cycle of later changes described by Fernald are not stages in the process of spermatogenesis, but are of a pathological nature, probably due to the presence of Nematode worms in the testes of the animals which he studied. Unless the presence of these worms is

* These parasites were also occasionally met with in the ovaries.

suspected, sections of the testes containing them present a deceptive and puzzling appearance.

The Female Organs.—The female organs (Plate VI., fig. 53) are extremely simple, and in their external form they very closely resemble those of the male. They consist of a pair of ovaries, which have similar relations to the alimentary canal as the testes (Plate IV., fig. 35). Each ovary is in the form of a simple tube, tapering anteriorly into a delicate terminal filament (*t. f.*). This filament, as in the male, functions as a suspensory ligament which serves to retain the ovary in position, and is attached to the fat-body near to the median dorsal line in the mesothoracic segment. The ovaries increase in calibre as they are followed posteriorly, and in the fourth abdominal segment each gives off a short oviduct (fig. 35). The two oviducts quickly unite with one another and form a median canal, which may be termed the vagina (*vag.*). The vagina opens to the exterior by a median aperture situated near to the posterior margin of the fifth abdominal segment. From the ventral wall of the vagina there arises a forwardly-directed flattened diverticulum (*div.*). The homology of this structure is very doubtful, and Fernald has suggested that it may be a receptaculum seminis, but in no instance has it been possible to detect any traces of spermatozoa in its cavity.

The wall of the ovary consists of a thin cellular layer containing scattered flattened nuclei, but does not show any cell boundaries (fig. 55). On the outside the ovarian wall is limited by a coat of connective tissue (*t. p.*). At the apex of the gland the wall becomes prolonged forwards as the terminal filament, which becomes reduced near its extremity to only a strand of connective tissue.

The oviducts are outward prolongations of the ovarian walls, and have the same essential structure as the latter.

The walls of the vagina consist of a layer of columnar epithelium, resting externally on a basement membrane and lined internally by a layer of chitin (Plate III., fig. 31). The median diverticulum from the vagina has a closely similar structure, except that its nuclei are larger and no cell boundaries are distinguishable in its epithelial layer. Its lumen, on account of the flattening of the organ, is extremely narrow and is in the form of a transverse slit.

A few muscle fibres are attached to the walls of the vagina, and pass outwards in an oblique direction to be inserted into the neighbouring body-wall. They probably aid in the extrusion of the ova by bringing about the alternate expansion and contraction of the cavity of the vagina.

The germinal tissue is situated in each ovary as a protruding ridge lying in the region of the third and fourth abdominal segments. The ridge is dorsally placed in each ovary, and is inclined somewhat towards the outside of the body (Plate VI., fig. 57). It consists of a mass of irregularly-arranged cells, each cell with an oval nucleus with the chromosomes regularly disposed around its periphery. By means of rapid mitotic divisions the germinal ridge buds off a mass of cells, which lie free in the ovarian cavity. At an early stage two kinds of cells become distinguishable, viz., vitellogenous or nutritive cells, which have rounded nuclei rich in chromatin material, and the egg cells or ova, which are much less numerous and are scantily supplied with chromatin, which is arranged in eight small granules disposed around the periphery of each nucleus (fig. 55).

There is no arrangement of the ova into follicles, but a number of vitellogenous cells become grouped around each ovum. As development goes on the ova accumulate food yolk within them, and increase greatly in size (fig. 56). When the eggs are fully developed the vitellogenous cells, which have served to nourish them, having nothing further to do, rapidly degenerate and eventually disappear. According to Lécaillon (**14**), in some Collembola (*e.g.*, *Papirius*) intra ovarian prolongations of the wall of the ovary are developed, and serve to assist the vitellogenous cells in the elaboration of food material for absorption by the eggs. In *Anurida*, according to that writer, these prolongations are only very slightly developed. For the details of the process of oogenesis the student is referred to the works of Lécaillon and of Claypole (**31**).

V.—EMBRYOLOGY.

The eggs of *Anurida* when freshly laid are pale yellow in colour, with a smooth, glistening surface. As development proceeds they darken, and eventually become dark orange. They are spherical in form, and each measures on an average about ·30 mm. in diameter. They are deposited by the female in little groups, which are usually to be found in plenty about the shores of Port Erin Bay. They occur in the furthermost recesses of the fissures in the rocks, and may be obtained by splitting open the latter in the manner already mentioned (p. 8). These groups consist of from seven or eight up to twenty or thirty eggs, which are laid together in an irregular fashion (Plate VII., fig. 69). The individual females appear to take no pains to keep their own eggs separate and distinct from those of their fellows, and through this cause large confluent masses, often consisting upwards of a hundred eggs, may be met with.

The relatively large size of the eggs of *Anurida* renders them favourable objects for the study of Apterygote embryology. What is known of the development of this insect is due to the researches of Ryder (**37**), Wheeler,* Miss Claypole (**31**) and Folsom (**32**). The following account is mainly derived from the observations of the two latter writers.

The egg is invested by two clearly distinguishable membranes. Firstly, an outer shell-like coat (*ch'.* in fig. 71), which is very brittle and can be easily dissected off with the aid of a pair of fine needles and, underlying this, is a thin crenated membrane (*memb.*) These coats may, perhaps, be homologous with the chorion and vitelline membrane respectively of other Insecta. During the early stages of development, a third and very delicate membrane closely envelopes the embryo, except where it is interrupted by the dorsal or pre-cephalic organ. In addition to these coats, Claypole distinguishes two other egg membranes, and the authoress maintains that all five membranes arise from the egg or the blastoderm.

The unsegmented ovum (fig. 70) is formed of a large central mass of protoplasm, which gives off outwardly directed strands. These strands ramify as they approach the periphery of the egg, and enclose numerous yolk bodies within their meshes. The germinal vesicle early becomes invisible, and does not again appear until after the extrusion of the polar bodies. The latter do not completely separate from the egg, and are eventually resorbed into it.

The segmentation is especially noteworthy, it being holoblastic but slightly unequal, and results in a solid morula. After the morula has been formed, a breaking down of the cell-boundaries takes place, and many of the nuclei begin to migrate to the periphery of the egg,

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* A contribution to Insect Embryology. *Journ. Morph.*, viii, 1893.

leaving the yolk bodies in the central protoplasmic mass. The nuclei undergo division as they pass to the exterior, and they eventually arrange themselves to form a two-layered blastoderm—the future ectoderm and mesoderm. Of the cells which are left behind in the yolk, some are scattered singly through its substance, and have large and deeply-staining nuclei; the rest have a tendency to remain congregated together in little clusters. The former are the yolk cells or vitellophags, which serve to transform the yolk for the nutrition of the embryo; the latter, at a subsequent stage in development, form the rudiments of the future endoderm (*y.c.* and *c.n.* in fig. 76).

About the time of the completion of the blastoderm a modification of its cells takes place at the upper pole of the egg, forming the precephalic or dorsal organ. At this point the cells become markedly columnar, and when viewed in section they form a lens-shaped mass of cells (fig. 76, *pc. o.*). This remarkable structure is apparently a vestigeal organ; it soon commences to degenerate, and eventually disappears altogether. Wheeler* homologises this organ with the " dorsal organ " of certain Crustacea with the indusium of the Orthopteron *Xiphidium*. There are no traces at any stage in the development of structures corresponding with the amnion and serosa of other Insecta.

The ventral plate or germ band first appears as a narrow area of mesoderm. It is formed by the cells of the latter migrating from their original position and becoming restricted to a band-like zone. This zone, with the exception of where it is interrupted by the dorsal organ, forms a girdle completely encircling the egg. As the result of this migration of the mesoderm, the greater

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* *Loc. cit.* p. 55, Vide also Willey. *Quart. Journ. Mic. Sci.*, xii, 1899.

part of the egg is left only covered by the ectoderm (fig. 78, *mes.*).

The various appendages appear for the most part in a regular succession from before backwards (fig. 71). The antennæ are the first pair to develop, and they are followed by the medium unpaired rudiment of the labrum and clypeus. Behind the former there arise in rapid succession the mandibles, the first and second maxillæ, the three pairs of thoracic feet, and a pair of appendages to each of the first four abdominal segments. Between the antennæ and mandibles there are developed a pair of transient tritocerebral or intercalary appendages (fig. 73). They were first discovered in this insect by Wheeler, and both Claypole and Folsom have since confirmed their existence. A little later there arise between the mandibles and first maxillæ the rudiments of another pair of mouth-parts (*mxul.* in fig. 75). These have been recently discovered by Folsom, and were named by him the super-linguæ, but, as already stated (footnote p. 19), the term maxillulæ is preferable for them. About this time the rudiments of the stomatodæal and proctodæal invaginations become visible, and the dorsal organ commences to degenerate. A very marked flexure of the embryo now takes place, and when it is complete the latter becomes more or less folded on itself (fig. 72). The result is that whereas the anterior end of the embryo retains its relations with the precephalic organ, the anal portion becomes retracted away from the latter, and the embryo itself becomes restricted to less than one-half of the whole circumference of the egg, instead of completely encircling it, as happened in the earlier stages. Furthermore, the mouth-parts become crowded together to form a definite head. The last mouth-part to appear is the lingua, which does not become visible until after the flexure of the embryo has commenced. It arises as a median unpaired rudiment, situated between the fundaments of the first maxillæ (*ling.* in figs. 7 and 75).

Mention has already been made of the origin of the endoderm from certain of the cells which are left over in the yolk during the formation of the blastoderm. At a stage a little subsequent to the condition of the embryo represented in fig. 72, these cells commence to separate. They increase in size, and, engulphing yolk, they so arrange themselves as to form a definite mesenteron. It is remarkable that none of the yolk is enclosed in the mesenteron during the process of formation of the latter; much of it remains in the body-cavity, while the rest becomes included in the reproductive organs. Whether the yolk cells have anything to do with the endoderm is not clear; although they take no part in the formation of the mesenteron, Claypole suggests that they may, perhaps, be endoderm cells which have acquired their digestive powers at a very early stage.

The nervous system arises as a proliferation of ectoderm cells in localised positions in the various segments. The masses of cells so formed give rise to the primitive ganglia, and they subsequently join up with one another to form the brain and ventral nerve chain. The brain is formed from the first three primitive ganglia, which are termed respectively the proto-, deuto-, and trito-cerebrum (fig. 74). There follows then in succession ganglia pertaining to the segments of the mandibles, maxillulæ, and first and second maxillæ, together with three thoracic ganglia and a ganglion for each of the six abdominal segments. The subsequent changes result in the union of the three cerebral ganglia to form the completed brain, while the remaining cephalic ganglia consolidate into a single ganglionic mass to form the sub-œsophageal ganglion, and ultimately the abdominal ganglia become involved in the meta-thoracic ganglion.

The germ cells appear at a comparatively late period in development; they arise a short time previous to the commencement of the formation of the mesenteron. They take their origin from the splanchnic mesoderm in the second and third abdominal segments, and according to Claypole their method of development is as follows:—Those germ cells which ultimately give rise to the male gonads arise from the inner side of the mesoderm, and come to lie free among the yolk (fig. 77). In the case of the female they are budded off from the outer side of the splanchnic mesoderm, and form a group of cells lying free in the mesoblastic somites of those segments. In the case of the male the cœlomic spaces are not formed. In the female the splanchnic mesoderm forms one side of a spacious cavity, which evidently results from a fusion of the contiguous cavities of the mesoblastic somites. The inner wall of this cavity eventually breaks through, and the cœlom becomes confluent with the general hæmocœlic body-cavity, and at the same time the germ cells come in contact with the yolk. The further development of the germ cells has not been followed in any detail but, in both sexes, as they develop they incorporate among themselves a large amount of the food yolk distributed in the body-cavity. In newly-hatched individuals much of the yolk is still present in the gonads, and it conduces greatly towards the rapid maturition of the generative elements.

Of the abdominal appendages, the first pair fuse together and persist in the adult as the ventral tube. The remaining pairs become resorbed, and ultimately completely disappear.

The eyes and post-antennal organs first become clearly indicated about the stage represented in fig. 72. At the time of its first appearance, the post-antennal organ consists of an irregular group of cuticular elevations. In the newly-hatched animal the latter have decreased in number and arranged themselves in a circular form, and before the permanent form is attained the organ undergoes further changes and development [*vide* Laboulbène (**2**)].

The recently-hatched insect is perfectly white, except for the eyes, which are enveloped in a patch of dark pigment on either side.* Except in size and colouration, the young animal does not differ from the adult. The pigmentation of the integument is acquired after exposure to daylight, but it is some time before it is developed to its fullest intensity. After several moults the full growth of the animal is attained.

VI.—GENERAL REMARKS ON THE COLLEMBOLA.

The general characteristics of the Collembola have already been noticed (Introduction, p. 4). About four hundred species have been described up to the present, most of which are very small in size, and but few forms attain a length greater than 5 mm. The Collembola are divided into three families, and these are classified by Borner (**48**) under two sub-orders, as follows:—

Sub-Order I.—Arthropleona.

Body linear and sub-cylindrical, the limits between each of the segments of the abdomen distinctly indicated. Vesicles of the ventral tube short and sac-like.

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* Folsom remarks that if the eggs be exposed to sunlight the embryos become blackish blue before hatching.

Fam. I., Entomobryidæ.—Scales present or absent. Springing organ well developed. *Isotoma*, *Entomobrya*, *Orchesella*, *Lepidocyrtus*, *Actaletes*, *Beckia*, &c.

Fam. II., Achorutidæ.—Scales never present. Springing organ greatly reduced or absent. *Podura*, *Achorutes*, *Anurida*, *Xenylla*, *Aphorura*, *Neanura*, &c.

SUB-ORDER II.—SYMPHYPLEONA.

Body sub-globular, the abdominal segments more or less fused together. Vesicles of the ventral tube long and tubular or short and sac-like.

Fam. III., Sminthuridæ.—With the characters of the sub-order. *Sminthurus*, *Sminthurides*, *Papirius*, *Neelus* (*Megalothorax*).

These insects are found in a great variety of situations; they occur among dead and decaying vegetable matter of all kinds, they may be found among moss, under the bark of trees, and can be obtained from roadside herbage of almost every description. They are plentiful on the borders of ponds and streams, and are also to be met with on the surface of the water itself; some few species inhabit the sea-shore and others are to be found on the surface of the snow and glaciers. The only condition which seems essential for their welfare is that considerable amount of moisture is present, for they seem incapable of surviving in very dry situations.

The order is practically world-wide in its distribution, and it is remarkable also on account of the extremely wide distribution enjoyed by many of its individual genera and species. The genus *Isotoma*, for instance, seems almost cosmopolitan, it being known from both Arctic and Antarctic regions, and is distributed throughout Europe and many parts of North America. It has been recorded from Argentina, Sumatra, the Sandwich Isles, and the Bismarck Archipelago, and also from the Azores. Among species, *Achorutes armatus* is found throughout the greater part of the Holarctic region, as well as in South America, New Zealand and Sumatra; and *Sminthurus hortensis* has a wide distribution in northern and central Europe, and is also known from North America, Tierra del Fuego, and Japan.

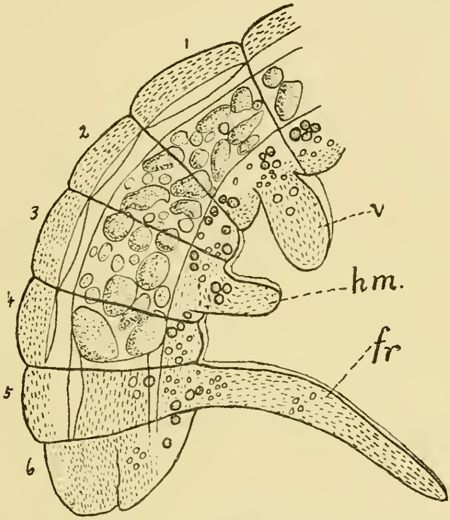
In colouration a wide range is exhibited among the various species. Many forms are of a uniform dull blue-black, as in *Anurida*; others are green or yellowish, with irregular patches of a darker colouring; a few species are banded or ringed; some are all white; and metallic forms are not infrequent.

In the greater number of Collembola the body is clothed with hairs, but in some genera, such as *Tomocerus* and *Lepidocyrtus*, it is scaled, although hairs are not altogether wanting. The hairs (text-fig. 4) may be simple and tapering, clavate, or flattened and partially resembling scales, or compound as in the Entomobryidæ. The scales bear a close resemblance to those of the Lepidoptera but, acording to Sommer (**23**), they differ from them in that they have no connection with the underlying hypodermis. They are familiar to microscopists on account of their being favourable test objects for the capabilities of high power objectives.

The head varies considerably in the three families. In the Sminthuridæ it looks almost vertically downwards, among the Entomobryidæ it is also pointed downwards, but in rather an oblique direction, while in the Achorutidæ it is directed straight forwards in a line with the rest of the body. The antennæ have from four to six joints; they may be short and stout, as in the Achorutidæ, or long and slender, as in *Orchesella* and

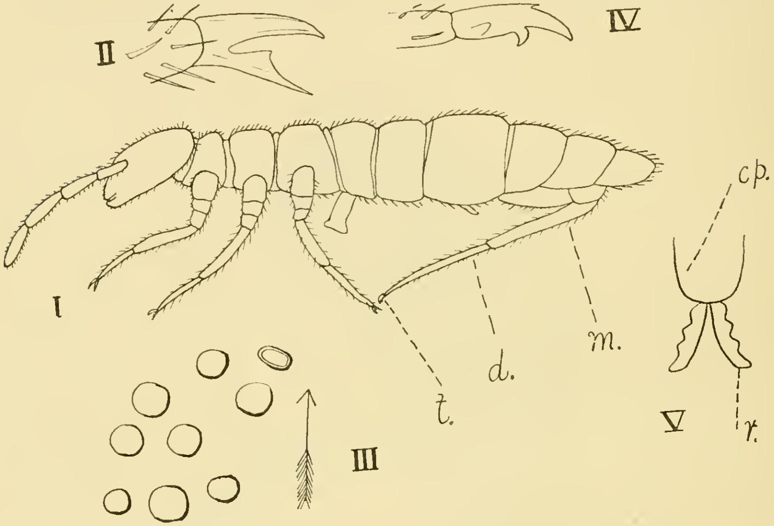
Tomocerus. In the latter genus and some species of the Sminthuridæ the terminal joint is much longer than the rest and is annulated. With the exception of *Neelus,* the Sminthuridæ usually have elbowed antennæ.

The thoracic segments are usually sharply defined; the prothorax is generally the smallest division of the three. In the Sminthuridæ the thorax is greatly compressed between the relatively large head and abdomen and, furthermore, the metathorax becomes partially fused with the first abdominal segment. *Neelus* (*Megalothorax*), however, is remarkable on account of the enormous development of the thorax, which greatly exceeds the abdomen in length and bulk.



Text-Fig. 1.—Abdomen of an embryo *Isotoma*, showing appendages (after Prowazek, enlarged). *v*, ventral tube; *hm*, hamula or 'catch'; *fr*, furcula or 'spring.'

The legs have no true tarsal segments, and they terminate usually in two claws, an upper and a lower, which are inserted on the end of the tibia (text-figs. 2, 3 and 4). In frequent instances the lower claw is greatly reduced, or it may be wanting altogether, as is the case in *Anurida.* There are frequently found in relation with the claws several (usually three) stiff hairs or setæ, which are swollen at their extremities.* These structures are inserted into the distal end of the tibia, and are known as tenent hairs (text-fig. 4). They appear to be modified glandular setæ, and exude from their extremities a small drop of a sticky semi-gelatinous fluid. These hairs are adhesive in their function, and they aid the insect in climbing smooth or steep surfaces.



TEXT-FIG. 2.—I., *Isotoma palustris: m*, manubrium; *d*, dens; *t*, mucro. II., Extremity of fore foot. III., Eyes and post-antennal organ (the arrow is directing forwards.) IV., Mucro. V., 'Catch': *cp*, corpus or basal portion; *r*, ramus.

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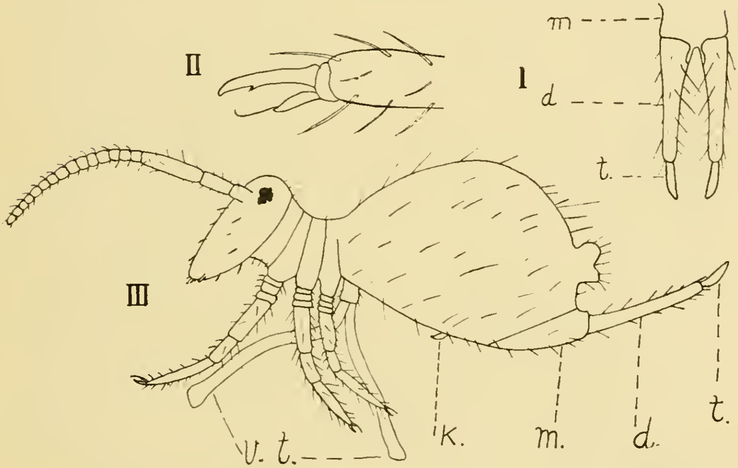
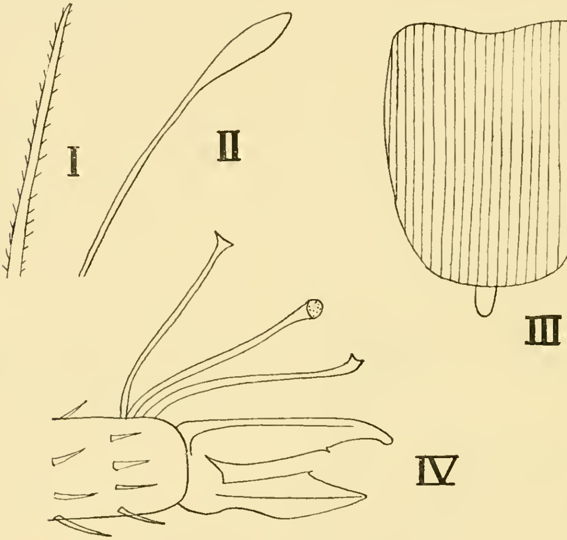
* These hairs are not peculiar to the Collembola, but are found in many larvæ as well as in those adult insects in which the adhesive pads or pulvilli are wanting.

The abdomen never consists of more than six segments; the first segment always bears the ventral tube, which represents a pair of fused appendages. Appendages may also be present on the third (the " catch ") and fourth (the springing organ) segments respectively (text-fig. 1). The ventral tube is the most constant of all Collembolan structures. It attains its highest degree of development in the Sminthuridæ, where it can emit a pair of long, tubular vesicles (text-fig. 3). These may exceed in length the whole animal, and they are frequently studded with small papillæ. Almost every transition can be found between this greatly developed condition to where the ventral tube exists only in the form of a bilobed tubercle and capable of only a very limited amount of protrusion.



TEXT-FIG. 3.—*Sminthurus viridis.* I., Springing organ: *m*, manubrium; *d*, dens; *t*, mucro. II., Extremity of fore foot. III., Animal viewed from the side: *vt*, ventral tube; *k*, 'catch'; *m*, manubrium; *d*, dens; *t*, mucro.

By far the majority of Collembola possess a pair of partially fused appendages in relation with the fourth abdominal segment and which function as a springing organ to enable the Insect to take sudden leaps when alarmed or otherwise disturbed. The force necessary to generate the leap is obtained partly by the action of special muscles and partly in virtue of the elasticity of the organ itself. In form the springing organ is fork-like (text-fig. 3), and is composed of an unpaired basal piece or manubrium (*m*), carrying at its distal end a pair of arms, which are termed the dentes (*d*). Each dens terminates in a small claw-like process—the mucro (*t.*); the mucro varies greatly in form among different species, and affords a useful character for the recognition of the latter. In the Achorutidæ the springing organ is either greatly reduced in size, as in *Podura*, *Achorutes*, and



Text-Fig. 4.—I., Compound hair of an *Entomobrya*. II., Clavate hair of a *Tomocerus*. III., Scale of *Tomocerus vulgaris*. IV., Extremity of middle foot of *Isotoma sensibilis*, showing three tenent hairs.

Neanura, or is wanting altogether, as in *Anurida*, and *Anurophorus*.

Many species also retain a pair of appendages on the third segment of the abdomen. These resemble the springing organ in their general form, but are very much smaller in size. Similar to the spring, they consist of a basal piece, which carries two arms; the former is termed by Tullberg the corpus (*cp.* in text-fig. 2), and the two latter the rami (*r.*). This organ is usually known as the "catch," or hamula, and it is believed to serve to retain the spring in position when the latter is stowed away under the abdomen while not in use. The manubrium of the springing organ is retained between the two rami of the "catch."

A variable number of eyes are generaly present on either side of the head behind the antennæ; their number may vary even among different species of the same genus. In *Templetonia* there is but a single eye on each side; in *Anura muscorum* there are three; in *Xenylla* and *Anurida maritima* there are five; in *Tomocerus* and *Orchesella* six; while in *Achorutes* they reach the maximum number, viz., eight. In some Collembola they are absent, as in *Lipura*, *Beckia* and *Anurida granaria*.

The post-antennal organ assumes a great variety of forms among various genera. In *Isotoma* and *Anurophorus* it is simple and ring-like, but in *Lipura* and *Anura* it attains considerable complexity of structure. In some few forms (*i.e.*, *Lipura*) there may be present curious structures, known as pseud-ocelli or puncta ocelliformia. They are situated in front of the post-antennal organ, and between it and the antenna; they appear to have nothing to do with eyes, and their function is unknown. In certain species of *Aphorura* they have a much wider distribution over the body.

Sensory organs of varied form are usually present on the ultimate and penultimate segments of the antennæ. An account of these structures is given by Absolon (**6**) and also by Börner (**7**).

The mouth-parts in all Collembola appear deeply insunk within the head capsule; this condition is a secondary one, having been brought about through their becoming overgrown and partially surrounded by the side folds of the head. Those of *Anura* are greatly specialised and differ from the mouth-parts of other Collembola in being purely suctorial. In this genus the labrum and labium together form a conical tube, in which the rest of the mouth-parts are contained, the latter being modified into stylets and used for piercing purposes.

The digestive canal is a simple tube passing from the mouth to the anus without presenting any convolutions, and this condition appears to be constant in all the genera yet studied. The mid-gut of *Neelus* is remarkable on account of its being sub-divided into a series of four successive chambers. With the exception of salivary glands, no accessory structures are associated with the alimentary canal.

The nervous system appears to exhibit very little degree of variation throughout the order.

Special respiratory organs are wanting, except in species of *Sminthurus*, *Sminthurides*, and in *Actaletes neptuni* Giard; in these forms tracheæ are present. Trachæ are well known to be found in *Sminthurus*, and it is in that genus that they are best developed. According to Willem, on either side of the body, between the head and the prothorax, there is placed a simple stigmatic crypt, from which bunches of tracheæ arise and are distributed to the head, the legs and the abdomen; * no anastomoses

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* The exact position of the spiracles appears to require further study. Lubbock and Tullberg maintain they are situated on the head, while Haase states that they are placed on the prothorax.

take place between the tracheæ of opposite sides of the body. In *Sminthurides* and *Actaletes* Willem states that the tracheal branches are entirely confined to the head, while in *Papirius* he has discovered two invaginations which correspond in their position with the stigmata of *Sminthurus*, and regards them as being the last remnants of a tracheal system.

The heart in the Arthropleona is similar to that of *Anurida*; in the Symphypleona it is much contracted, not extending further backwards than about one-third of the length of the abdomen. Willem states that in this sub-order it is only furnished with two pairs of ostia.

The reproductive system presents very little range of variation; a median ventral diverticulum of the genital canal may occur in the male (*Sminthurus*) as well as in the female (*Anurida*).

VII.—THE AFFINITIES OF THE COLLEMBOLA.

The most marked characteristic of the Collembola is the fact that the abdomen consists of only six segments, and at no stage in the development are there known to be more than that number present. Among all other insects, including the Thysanura, wherever the embryology has been studied, the abdomen has been found to consist of not less than ten segments, together with a telson. The significance of this feature of the Collembola has not been emphasised by morphologists, although it is one of the most fundamental characteristics of the order. It is reasonable to believe that this character has been acquired from the primitive ancestors of the Insecta, whose metamerization had not yet become fixed and limited to a definite number of segments. In this respect, therefore, the Collembola are very much isolated from the rest of the Insecta, and the question arises as to where their affinities lie. The sum total of the characters of the order indicate that they are more closely allied to the Thysanura than to any other order of Insecta, but that they also possess certain generalised features in common with the lower Arthropoda.

The Collembola are allied to the Thysanura in that they are the only two orders of Insecta which possess an evident pair of mouth-parts—the maxillulæ, which are intercalated between the mandibles and first maxillæ. They further resemble the Thysanura in the absence of any traces of wings, and in the fact that they undergo no metamorphoses. It is with the genus *Campodea* that their affinities come closest, and they resemble that genus in their mouth-parts being withdrawn into the head capsule, in the ovaries consisting of a single tube on either side, there being no ovarioles, and in the absence of an amnion and serosa in the embryo.

The Thysanura have been divided by Grassi into two divisions, viz., the Entotrophi, including the genera *Campodea* and *Japyx*, and the Ectotrophi, which comprise *Machilis* and *Lepisma*. The Entotrophi, as their name implies, have their mouth-parts retracted within the head, and it is true that they are more closely related to the Collembola than is the case with the Ectotrophi. The relationship, however, is not sufficiently close to warrant the Collembola being included as a sub-division of the Entotrophi, as has been suggested by Stummer-Traunfels (**24**). The difference in the number of segments to the abdomen in the two groups presents a serious difficulty to any such system of classification. It is by no means certain that the entognathous condition of the Collembola and Entotrophi is anything more than a parallelism in evolution and, if that be so, it would be of little value as a character implying a close relationship between those two groups.

The presence of maxillulæ in the Collembola is a primitive feature which is shared with the Symphyla and Diplopoda; these mouth-parts are the representatives of the Crustacean first maxillæ (*vide* Table on p. 74). Furthermore, the occurrence of embryonic tritocerebral appendages—the homologues of the Crustacean second antennæ, is also a primitive character which they only share with the Thysanura.

In the general structure of the ovary, and the absence of follicles, the Collembola, as Claypole has pointed out, resemble the Myriapoda more closely than the Thysanura, and come nearer to *Scolopendrella* than any other type. An additional Myriapod feature is perhaps seen in the post-antennal organs, which are peculiar to the Collembola among Insecta. They are regarded by Willem as being homologous with Tomosovary's organs in Myriapods, and the recent researches of Hennings* and Haller† support that conclusion.

In addition to the above mentioned characters, there are a number of generalised features which suggest that the Collembola are primitive animals. The most important are:—(1) The extremely simple condition of the spiracles where they are present: as Willem has pointed out, they are nothing more than mere stigmatic crypts, and are to all appearances similar to those of *Peripatus*. (2) The nature of the digestive system, which is a perfectly straight canal passing from the mouth to the anus without presenting any convolutions. (3) The absence of any external genital armature. (4) The relatively simple nature of the eyes, each of which may be compared to a single ommatidium of a compound eye.

Side by side with these generalised characters,

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* *Zeitschr. f. wiss. Zool.*, 76, 1904, p. 26.

† *Arch. f. mik. Anat.*, 65, 1905, p. 181.

TABLE OF HOMOLOGIES OF THE APPENDAGES OF THE FIRST ELEVEN SOMITES OF CRUSTACEA, INSECTA, AND MYRIAPODA (SYMPHYLA AND DIPLOPODA).

SEGMENT.	CRUSTACEA.	INSECTA.			MYRIAPODA.	
	MALACOSTRACA.	APTERYGOTA.		PTERYGOTA.	SYMPHYLA.	DIPLOPODA.
		COLLEMBOLA.	THYSANURA.			
1	Stalked Eyes.	?	?	?	?	?
2	Antennules.	Antennæ	Antennæ.	Antennæ.	Antennæ.	Antennæ.
3	Antennæ.	Embryonic tritocerebral appendages (Wheeler,* Claypole,† Folsom‡).	Embryonic tritocerebral appendages which are retained in adult as a pair of tubercles (Uzel§).	—	—	—
4	Mandibles.	Mandibles.	Mandibles.	Mandibles.	Mandibles.	Mandibles.
5	1st Maxillæ. (Maxillulæ of Hansen‖).	Maxillulæ. (Hansen,‖ Folsom,‡ Carpenter**).	Maxillulæ. (Hansen,‖ Carpenter.**)	Vestiges only.	Maxillulæ. (Hansen,†† Carpenter**).	Maxillulæ. (Carpenter‡‡).
6	2nd Maxillæ.	1st Maxillæ.	1st Maxillæ.	1st Maxillæ.	1st Maxillæ.	1st Maxillæ.
7	1st Maxillipedes.	2nd Maxillæ (labium).	2nd Maxillæ (Labium).	2nd Maxillæ (labium).	2nd Maxillæ (labium). (Hansen††).	2nd Maxillæ (labium). (Carpenter‡‡).
8	2nd Maxillipedes.	1st Pair of Legs.	1st Pair of Legs.	1st Pair of Legs.	1st Pair of Legs.	1st Pair of Legs.
9	3rd Maxillipedes.	2nd Pair of Legs.	2nd Pair of Legs.	2nd Pair of Legs.	2nd Pair of Legs.	2nd Pair of Legs.
10	Chelæ	3rd Pair of Legs.	3rd Pair of Legs.	3rd Pair of Legs.	3rd Pair of Legs.	3rd Pair of Legs.
11	1st Pair of Ambulatory Limbs.	Ventral Tube.	1st Pair of abdominal appendages of *Japyx*; and *Campodea*.	Embryonic appendages.	4th Pair of Legs.	4th Pair of Legs.

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* *Journ. Morph.*, VIII, 1893. † Bibliography, No. 31. ‡ Do., No. 10. § *Zool. Anz.*, XX., 1897. ‖ *Ann. Mag. Nat. Hist.*, XII., 1894.
** *Proc. Roy. Irish Acad.*, XXIV., Sect. B, 1903. †† *Quart. Journ. Mic. Sci.*, XLVII., 1903. ‡‡ Do., XLIX., 1905.

indications of very considerable specialization are exhibited in the concentration of the nervous system, in the mouth-parts being insunk within the head capsule, in the structure of the springing organ and the ventral tube, and in the reduction of the number of abdominal segments to six.

Summing up, it may be said that the Collembola show certain features in which they resemble the Thysanura on the one hand and the lower Arthropoda on the other while, at the same time, they have undergone very considerable specialization along lines of their own. There do not appear to be any grounds for regarding them as being degenerate animals. If the results of future and more extended investigations definitely establish that none of the Collembola have more than six abdominal segments present in the embryo, their relationships with the Thysanura and the rest of the Insecta will probably prove to be much more distant than is implied by the above remarks. It would assuredly be a sufficiently fundamental character to separate them as a group from all other Insects.

VIII.—MARINE INSECTS.*

Contrary to what is usually believed among naturalists, a considerable variety of insects are known to inhabit the sea-shore below high-water mark, and to undergo daily submersion during one or more periods in their life-history. Very little attention, however, has been devoted to them at present, and most probably a

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* The term "marine" is only strictly applicable to insects in a very limited number of instances. Although many of the species included in the above account undergo frequent submersion by the tide during one or more periods in their life-histories, others do not, and are more strictly speaking to be regarded as "littoral" insects.

much larger number are awaiting discovery. With very few exceptions, marine insects are small in size, seldom exceeding more than a few millimetres in length, and perhaps the only one which attracts the attention of the casual observer is the fly *Coelopa frigida*. This insect at certain seasons of the year may be seen flying in immense swarms over the surface of decaying Fuci and other Algæ cast up on the shore by the tides.

Plateau has drawn up a list of 40 genera, and embracing 80 species of Tracheate Arthropods, which are known to inhabit the sea-shore and to be subjected to submersion by the water. In the greater number of these, he remarks, the power of living under such conditions is not due to their possessing any special mechanisms to enable them to do so, but to the general property these animals have of being able to resist asphyxiation for prolonged periods. His list includes Insects, Myriapods, Pseudoscorpions, and Acari.

Most of what is known concerning marine insects is comprised in the following works:—

A. S. Packard.—On Insects inhabiting Salt Water. *Am. Journ. Sci.*, 1871; also *Proc. Essex Inst.*, 1868, and *Ann. Mag. Nat. Hist.*, ser. 4, vol. viii.

F. Plateau.—Les Myriapodes Marins. *Journ. de l'Anat. et Phys.*, xxvi., 1890.

L. C. Miall.—The Natural History of Aquatic Insects. London, 8vo.

G. H. Carpenter.—The Insects of the Sea. *Knowledge*, 1901.

The following list includes most of the marine Insects inhabiting the British coasts, and has been principally compiled from the writings of Plateau and Carpenter.

Collembola.

Among the Collembola a marine habitat has been independently acquired by species belonging to both the Entomobryidæ and Achorutidæ but, up to the present, none of the Sminthuridæ are known to frequent the confines of the sea-shore.

In addition to *Anurida maritima*, the following species of marine Collembola occur in the British Isles. Those species indicated with an asterisk are not exclusively marine, but are also found far inland.

Isotoma littoralis, Mon.
**I. palustris* (Müll.)
I. Schötti, Dalla Torre.
I. Beselsii, Pack.
**I. maritima*, Tullb.
**I. sexoculata*, Tullb.
**Xenylla humicola*, Tullb.
**X. maritima*, Tullb.
Actaletes neptuni, Giard.
(= *Isotoma crassicauda*, Tullb.)
**Achorutes viaticus*, Tullb.

Thysanura.

Machilis maritima (Leach).

Coleoptera.

The greater number of marine representatives of this order consist of wingless forms, and many of them have their bodies very much flattened, which enables them to ensconce themselves in small crannies and fissures among the rocks during the time they are submerged by the sea. Their bodies are frequently covered with a coating of hairs, which prevents them from being wetted, and also encloses a certain amount of air, which is utilised during respiration under water. Marine beetles hide themselves by burrowing in the sand, or lurking under stones or decaying seaweed; at low tide they may be often seen running over the rocks or sands.

Cercyon littoralis, Gyll.
C. depressus, Steph.
Heterocerus marginatus, Bosc.
Lymnaeum nigropiceum, Marsh.
Cillenus lateralis Sam.
Trechina lapidosus, Daws.
Bembedium concinnum, Putz.
B. ephippium, Marsh.
Aepus marinus, Stroem.
A. Robinii, Lab.
Micralymma brevipenne, Gyll.
Trogophloeus anglicanus, Sharp.
Myrmecopora (Xenusa) uvida, Er.
M. sulcata, Kies.
Cafius cicatricosus, Er.
C. xantholoma, Grav.
C. sericeus, Holme.
C. fucicola, Curtis.
Actocharis Readingii, Sharp.
Phytosus spinifer Curtis.
P. balticus, Kraatz,
P. nigriventris, Chev.
Diglossa mersa, Hal.
D. silmaticollis, Rey

DIPTERA.

A marked feature among marine flies is the reduction or total atrophy of the wings. The first stage in the reduction is seen in *Chersodromia arenaria*, where the wings are much shortened so as to be of very little service in flight. This is carried a step further in a Southern France species, *Psamathiomya pectinata*, Derby, in which the wings have become greatly narrowed and strap-like, and the nervures atrophied; a similar condition is seen in a Californian marine fly, *Eretmoptera Browni*, Kellogg. An extreme case occurs in the females of the genus *Clunio*, where the wings have disappeared completely, although in the males they are tolerably well developed.

This reduction of the wings has been explained as being an advantageous condition, since it prevents the insects from being blown out to sea. A similar explanation has been made to account for the frequent occurrence of wingless insects on oceanic islands. Among the few insects, for instance, known from Kerguelen Land there are three species of flies whose wings are atrophied, in one instance they have gone altogther, and in the other two cases they are reduced to mere scale-like appendages.

Marine Diptera are principally met with flying over the masses of *Fuci* cast up by the tide on the shore: some few, however, may be seen skimming lightly over the surface of the water in the tide-pools. Most of the larvæ of these flies feed on thrown-up Fucus and are covered at each tide, but those of the Chironomidæ are submerged during the whole course of their life, and subsist on *Cladophora* and other green Algæ growing in the pools left among the rocks by the receding tide and, furthermore, they have also been dredged up from a depth of over ten fathoms.

The following British Diptera are all marine:—

Fucellia fucorum (Fall).
Coelopa frigida, Meig.
Orgyma luctosa, Meig.
Actora aestuum, Meig.
Glenanthe ripicola, Halid.
Chersodromia arenaria, Halid.
Aphrosylus raptor, Halid.
A. ferox, Halid.
Thalassomyia Frauenfeldii, Schiner.
Chironomus sp. ?
Clunio marinus, Halid.
Clunio bicolor, Kieff.

Hemiptera.

Aepophilus Bonnairei, Sign.

The species of *Halobates* and *Halobatoides* are exclusively marine and inhabit the tropical waters of the oceans. They have not been found further northward than Spain.

IX.—LITERATURE.

In the following catalogue the more important papers relating to the Collembola are enumerated, but it is not intended as a complete bibliography of the order. The earlier literature of the subject has been purposely omitted as references to practically all papers prior to 1870 will be found in Lubbock's "Monograph" and Tullberg's "Sveriges Podurider."

The only general treatise is Lubbock's "Monograph of the Collembola and Thysanura," published by the Ray Society in 1873.

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3. Lécaillon, A. Notes sur l'habitat et les moeurs de quelques Collemboles; *Bull. Soc. Philom. Paris,* 9e Sér., T. III., 1900-01, p. 67.

4. Moniez, R. Acariens et Insectes marins du Côtes du Boulonnais; *Rev. Biol. Nord. Fr.*, T. II., 1889-90, p. 347.

5. Willem, V. L'influence de la Lumière sur la Pigmentation de *Isotoma tenebricola*; *Ann. Soc. Entom. Belg.*, T. XLV., 1901, p. 193.

B.—**Morphology and Physiology.**

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8. Fernald, H. T. The Relationships of Arthropods; *Studies Biol. Lab. John's Hopkins Univ.*, Vol. IV., No. 7, 1890, p. 431.

9. Folsom, J. W. The Anatomy and Physiology of the Mouth-parts of the Collembolan *Orchesella cincta,* L; *Bull. Mus. Comp. Zool. Harvard,* Vol. XXXV., No. 2, 1899, p. 7.

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12. Hoffmann, R. W. Über den Ventraltubus von *Tomocerus plumbeus* L. und seine Beziehungen zu den gropen unteren Kopfdrüsen. Ein Beitrag zur Kenntnis der Collembolen; *Zool. Anz.* XXVIII., Bd. Nr. 3, 1904, p. 87.

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14. Lécaillon, A. Recherches sur l'ovaire des Collemboles; *Arch. d'Anat. micros.*, T. IV., 1901, p. 471.

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X.—APPENDIX.

The Parasites of Collembola.

Minchin (Lankester's Treatise on Zoology, Part I., 2nd Fascicule) enumerates two species of Sporozoa as being parasitic in Collembola, viz.:—*Gregarina poduræ* (Léger) from the gut of *Orchesella villosa* and *Glugea thysanuræ* (L. Pfr.) from the gonads of *Podura aquatica*. The occurrence of Sporozoa in Collembola has also been referred to by Lubbock and Sommer.

The presence of Nematodes in the gonads of *Anurida* is recorded in this Memoir, and Sommer states that he has met with them in *Tomocerus* (*Macrotoma*).

The present writer has recorded (*Ann. Mag. Nat. Hist.*, ser. 7, Vol. XV., 1905) the habits of a marine Pseudoscorpion, *Obisium maritimum*, Leach, which probably preys upon *Anurida*.

Note on *Anurida crassicornis*, Reut.

L. and O. M. Reuter (**86**) describe this species from the river Tay, near Perth, and state that it is very like and allied to *A. maritima*, but differs in its much shorter and thicker antennæ, in the structure of the head (the inter-antennal lobe being pentagonal, with almost straight sides and well separated from the rest of the head) and in the more robust body. The description is unaccompanied by any figures, and, according to Carpenter and Evans (**54**), the types are unfortunately lost.

The Economic Aspect of Collembola.

Springtails have not up to the present attracted much attention from economic biologists, though occasionally instances are known where they have done injury to cultivated plants (*vide* Carpenter, *Proc. Ass. Econ. Biol.*, Vol. I., Pt. I., July, 1905). Dr. Traquair (*Report to the Plans and Works Committee of the Edinburgh Town Council*, March, 1906; and *The Scotsman*, March 2nd, 1906) has recently dealt with the occurrence of Collembola in hydrant boxes and water cisterns in Edinburgh. Although the presence of these insects in such situations is in itself harmless, the abundance in which they were found is evidence that they find an ample food supply there, and herein lies the danger, for it points to the water being contaminated.

NOTE ON HISTOLOGICAL TECHNIQUE, &c.

Specimens of *Anurida* are best collected from off the rocks and weed by means of a camel-hair brush, and transferred into a phial containing 70 per cent. spirit; if it be desired to obtain them in large numbers, they can frequently be scooped up in quantities from off the surface of the tide-pools, using for the purpose a metal spoon or some similar instrument.

The mouth-parts and sense organs can be easily studied by treating the head with a weak solution of potassic hydrate, which, by dissolving the soft parts, renders it gradually transparent. This should be performed on a slide, under the lower power of the microscope, and the action of the alkali checked, as soon as the mouth-parts assume a pinkish-violet, by running in alcohol under the cover-glass.

If it be necessary to preserve the animals for histological purposes, they are best brought away alive in a vessel containing sea water, and then transferred with a camel-hair brush into hot 70 per cent. alcohol, and afterwards passed into that of 90 per cent. strength. Hot corrosive sublimate or picro-sulphuric acid can also be used with advantage for killing and fixation. Whichever reagents are used, the specimens should be afterwards placed in 90 per cent. alcohol, to which have been added about five drops of potassium hypochlorite (concentrated solution) to each fluid ounce of the alcohol. After remaining in this for about half an hour, they should be washed in fresh alcohol of similar strength and then passed into absolute alcohol. The potassium hypochlorite serves to remove the pigment, and also softens the chitinous parts and aids in section cutting.

The process of embedding is best performed in watch-glasses, using paraffin of a low-melting point, which is afterwards replaced by hard paraffin for cutting. For staining, the best results were obtained by using Mann's methyl-blue-eosin and Heidenhain's iron-alum hæmatoxylin. All staining was done on the slide by prolonged treatment, and afterwards washed out to the required degree of colouration.

The eggs were killed and fixed in both hot water and hot 70 per cent. alcohol, and afterwards kept in 90 per cent. alcohol for five weeks for hardening purposes. After this treatment, the egg membranes can be dissected away from the embryos with the aid of a pair of fine needles under a low-power microscope. The embryos can then be stained with borax carmine, and mounted whole in glycerine for examination. For instructions as to sectioning the eggs, *vide* Folsom (**10**).

XI.—EXPLANATION OF PLATES.

Reference Lettering.

a, b = Direction of the section in fig. 52.

ab. app. $^{1-4}$ = Abdominal appendages.

abd., $^{1,\ 3,\ \text{and}\ 6}$ = Abdominal segments.

a. blb. = Last chamber of heart.

a. gl. = Acinose gland of ventral tube.

al. m. = Alary muscle.

al. t. = Tendon of alary muscle.

an. = Antenna.

an′ = Anus.

at. n. = Antennal nerve.

b.c. = Blood corpuscles.

b. cav. = Body cavity.

b.m. = Basement membrane.

c. = Inner layer of cuticle.

c.′ = Outer layer of cuticle.

car. = Cardo.

cav. = Foramen leading into cavity of mandible.

ch. = Chromatin.

ch.′ = Outer membrane of egg.

chb. = Common Chamber.

ch. b. = Chromatin body.

ch. e. = Torn edge of outer egg membrane.

circ. m. = Circular muscle fibres of oesophagus.

clm. = Clypeo-labral rudiment.

clyp. = Clypeus.

c. m. = Circular muscle fibres of mid gut.

c. m. b. = Circular muscle bands.

c. m. j. = Union of circular muscle fibres.

conn. = Para-oesophagea connective.

conn. $^{1,\ 2,\ 3}$ = Connectives of ventral nerve cord.

c.p. = Central mass of protoplasm.

c. t.
c′. t′. m′. = Connective tissue membrane.

c. t. m. = Connective tissue coat of mid gut.

cut. = Cuticle.

d. b. = Dark transverse band.

dep. = Cup-like depression.

deu′ ceb. = Deutocerebron.

dil. an. m. = Dilator muscles of anus.

dil. rect. m. = Dilator muscles of rectum.

div. = Median diverticulum of vagina.

drc. = Deutocerebrum.

d. s.
d.′ s.′
d.^{2} *s.*^{2} = Successive stages in development of spermatozoa.

d. t. = Duct of the acinose gland.

dtl. = Ductule of salivary gland.

ec. = Ectoderm.

em. nem. = Nematode embryo.

en. = Future endoderm cells.

ep. = Epithelium.

epcr. = Epicranium.

epith. = Fore-gut epithelium.

epith. th. = Epithelial thickening.

ex. g. = Excretory granules.

exc. or. = Fatty body.

gal. = Galea.

g.c. = Ganglion cells.

g ′ c.′ = Germ cells.

gl. = Tubular gland.
gl. ap. = Aperture of tubular glands.
gl. dt. = Ducts of tubular glands.
gl.' dt.'
gon. = Gonad.
g. p. = Lateral pouch of mid-gut.
g. t. = Germinal tissue.
h. = Hair.
h. c. = Modified hypodermis cell.
h. cell. = Trichogenous cell.
hd. = Hypodermis.
h.' d.' = Ventral surface of head (2nd maxillæ).
h. g. = Hind gut.
h. g. epith. = Hind gut epithelium.
h. g. m. = Circular muscles of hind gut.
hs. = Striated hem or "härchensaum."
ht. = Heart.
inf. oes. g. = Infra-oesophageal ganglion.
inf. oes. m. = Posterior series of dilatores pharyngii muscles.
i. p. = Intra-testicular prolongations.
k. m. = Krause's membrane.
l. = Lumen.
lac. = Lacinia.
lb. = Labium (2nd maxillæ).
l. c. = Lentigen cell.
ling. = Lingua, or tongue.
ling. st. = Lingual stalk.
l. m. = Longitudinal muscle fibres.
ln. = Lens.
l. n. = Lateral nerve.
lr. = Labrum.
l. s. m. = Longitudinal sternal muscles.
l. t. m. = Longitudinal tergal muscles.
m. = Muscles.
m.'
md. = Mandible.
md. g. = Mandibular ganglion.
md. p. = Pharyngeal pocket of left mandible.
med. f. = Medifurca.
memb. = Inner egg membrane.
mes. = Mesoderm.
m. f. = Muscle fibres.
m. g. = Mid-gut.
m. g. epith. = Mid-gut epithelium.
m. n. = Median nerve.
m.' n.' = Mandibular nerve.
m. n. br. = Lateral branch of median nerve.
m. nuc. = Nucleus of muscle fibre.
mo. = Mouth.
m. pr. = Male pro-nucleus.
m. s. = Line of apposition of distal portions of 2nd maxillæ.
musc. = Dilator muscles.
m. w. = Muscular wall of heart.
mx. hd. = Head of 1st maxilla
mx.' g. = Ganglion of 1st maxilla.
mx.^{2} *g.* = Ganglion of 2nd maxilla.
mx.' n. = Nerve to 1st maxilla.
mx.^{2} *n.* = Nerve to 2nd maxilla.
mx. p. = Pharyngeal pocket of left maxilla.
mxul. = Maxillula.
mxul. g. = Ganglion of maxillula.
mxul. n. = Nerve to maxillula.
n. = Nucleus.
nuc.
nem. = Nematode worm.
nem.' = Transverse section of Nematode worm.
neur. = Neurilemma.
n. f. = Nerve fibres.
n. v. = Abdominal nerve (or nerves).
n.' v.'

o. = Ovum.
o.′ = Ovules.
oc. = Eyes.
od. = Oviduct.
oes. = Oesophagus.
o.n. = Branches of optic nerve.
op. n. = Optic nerve.
ost. = Ostium.
ov. = Ovary.
o. w. = Ovarian wall.
p. = Pigment.
p. a. o. = Post-antennal organ.
pc. o. = Precephalic organ.
per. oes. a. = Peri-oesophageal aorta.
ph. = Pharynx.
p.i. = Protoplasmic island in which female pro-nucleus is present.
pl. = Side fold of head.
p. l. = Peripheral layer of protoplasm.
plm. = Coagulated blood plasma.
plp. = Maxillary palp.
p. o. n. = Nerve to post-antennal organ.
prc. = Protocerebrum.
pr′ ceb. = Protocerebron.
ps. = Pseudopodium.
r. = Protoplasmic strands.
r. nuc. = Nucleus of fat body.
rep. ap. = Reproductive aperture.
ret. = Retinal cell.
ret. l. = Layer of fat body bordering on hypodermis.
ret. musc. = Retractor muscles of ventral tube.
s = Blood containing space.
scrp. = Sarcoplasm.
sec. = Secretion of gland.
s.g. = Secretory granules
s. gl. = Salivary gland.
slmma. = Sarcolemma.
s. o. = Sense organ.
s.′ o.′ = Possible rudimentary sense organs.
sp. = Cavity formed by breaking down of central cells of fat body.
spr. = Bunches of spermatozoa.
st. = Stipes.
str. p. = Striated portion of muscle fibre.
sup. oes. g. = Brain.
sup. oes. m. = Anterior series of dilatores pharyngii muscles.
sut. = Suture.
t.$^{1, 3, 6}$ = Abdominal sterna.
tent. = Tentorium.
t. f. = Terminal filament.
th. = Thorax.
th.$^{1-3}$ = Pro- meso- and metathorax.
th. app.$^{1-3}$ = Thoracic appendages.
th. g.$^{1-3}$ = Pro- meso- and metathoracic ganglia.
t. p. = Tunica propria.
tr. app. = Tritocerebral appendage.
trc. = Tritocerebrum.
tr′ ceb. = Tritocerebron.
t. s. = Substance of testis.
t. s. musc. = Tergo-sternal muscles.
t. w. = Wall of testis.
vacs. = Vacuoles.
vag. = Vagina.
valve c. m. = Pyloric valve.
v. c. = Nutritive cells.
v. e. = Epithelial layer of vagina.
v. g. = Ventral groove.
v. m. = Transverse muscle.
vs. = Terminal vesicles of ventral tube.
v. t. = Ventral tube.
w. = Connective tissue coat of heart.
x = Organ of unknown function.
y. = Yolk.
y. c. = Yolk cells.

Plate I.

Fig. 1. *Anurida maritima*, adult male viewed dorsally. × 35.

Fig. 2. A group of *Anurida* showing their general appearance when alive. *Nat. size.*

Fig. 3. Ventral aspect of adult female (shading omitted). The ventral groove is seen as a slightly sinuous line arising from a point in the middle line of the head and passing midway between the bases of the legs to terminate on the anterior border of the ventral tube. × 35.

Fig. 4. Outline figure of the dorsal side of the head showing the position of the sense organs. × *circa* 50.

Fig. 5. Right lateral oval protuberance of the head, together with the five eyes of its side. The post-antennal organ is seen immediately in front. × 230.

Fig. 6. A piece of the chitinous cuticle from the abdomen showing the tubercles and some of the large seta-like hairs. × 200.

Fig. 7. Terminal joint of left antenna viewed from its inner aspect. It shows the trilobed apical sense organ together with patches of modified cuticle, which are probably of a sensory nature. × 180.

Fig. 8. The apical sense-organ of the left antenna. × 600.

Fig. 9. Claw of left fore foot. × 420.

Fig. 10. Right post-antennal organ. × 1,200.

Fig. 11. Diagram for the purpose of showing the relative positions of the mouth-parts to one another when viewed from the ventral surface. × *circa* 100.

Fig. 12. Ventral aspect of the apex of the 2nd maxillæ (labium). This figure and the succeeding one are from preparations which have been depigmented to show the sculpturings of the cuticle. × 160.

Fig. 13. Dorsal aspect of labrum and clypeus. × 160.

PLATE II.

Fig. 14. Dorsal aspect of the maxillulæ, the lingua and the left first maxilla—soft parts removed. × 360.

Fig. 15. Dorsal aspect of right mandible. × 360.

Fig. 16. Vertical section of the integument, together with a parietal extension of the fat-body. From the ventral region of the meso-thorax. × 800.

Fig. 17. Vertical section of the integument passing through the base of a hair and a trichogenous cell. × 800.

Fig. 18. Mass of fat-body from the thorax: excretion scarcely yet commenced. × 400.

Fig. 19. Mass of fat-body from the abdomen: excretion actively taking place. × 400.

Fig. 20. Mass of fat-body from the abdomen: excretion far advanced. × 320.

Fig. 21. Longitudinal and vertical section of the ventral tube. × 200.

Fig. 22. Apex of antenna showing fine branches of antennal nerve passing to sensory organ and hairs. × 180.

Fig. 23. Horizontal section taken across the vesicles of the ventral tube. × 200.

Fig. 24. Portion of the ventral groove: region of the meta-thorax. × 200.

Fig. 25. Organ of unknown function situated on the floor of the fourth abdominal segment. × 320.

Fig. 26. Three successive transverse sections through the ventral groove; (*a*) in the head region; (*b*) in the prothorax; (*c*) in the meta-thorax. × 800.

Plate III.

Fig. 27. Reconstruction of sections taken through the head close to the middle plane. × 360.

Fig. 28. Section passing through the junction of the fore-gut with the mid-gut. × 360.

Fig. 29. Transverse section across the œsophagus. × 600.

Fig. 30. Section of wall of mid-gut. × 1,200.

Fig. 31. Transverse section taken across the rectum together with the vagina and its median diverticulum. × 550.

Fig. 32. Transverse section of the ductus ejaculatorius. × 550.

Fig. 33. Blood corpuscles from a living animal. × 1,200.

Fig. 34. Vertical section through the post-antennal organ and two of the eyes (partly after Willem). × 1,000.

Plate IV.

Fig. 35. Diagrammatic figure of *Anurida* showing the relations of the principal internal organs to one another. × *circa* 40.

Fig. 36. Figure showing the termination of the ventral

groove on the anterior aspect of the ventral tube. × 45.

Fig. 37. Section of the mid-ventral region of the mesothorax showing the relations of the nervous system, medifurca and the ventral groove. × 200.

Fig. 38. Vertical and transverse section of the ventral tube. × 180.

Fig. 39. Portion of the heart showing the non-striated circular muscle bands. × 550.

Fig. 40. Vertical and longitudinal section of a chamber of the heart. × 550.

Fig. 41. Portion of the heart showing alary muscles. × 550.

Fig. 42. Transverse section of the heart in the posterior region of the œsophagus. × 420.

Fig. 43. Transverse section of the heart, together with the alary muscles; third abdominal segment. × 420.

Fig. 44. Transverse section of the heart; fifth abdominal segment. × 420.

Fig. 45. Transverse section across three of the longitudinal tergal muscles. × 400.

Fig. 46. Longitudinal section through the first and second thoracic ganglia, taken slightly to the left side to show the median accessory nerve. × 150.

Fig. 47. Longitudinal section through the metathoracico–abdominal ganglion. × 320.

Fig. 48. Semi-diagrammatic reconstruction of the nervous system of *Anurida*. × *circa* 100.

PLATE V.

Fig. 49. Longitudinal section through the posterior half of the alimentary canal. × 550.

Fig. 50. Transverse section across the fourth abdominal segment. × 200.

Fig. 51. Transverse section across the posterior region of the prothorax. × 200.

Fig. 52. Transverse section across the head. × 200. The section is taken along the line *a*, *b* in fig. 27.

PLATE VI.

Fig. 53. Diagrammatic figure showing the position of the ovaries (mature). × *circa* 10.

Fig. 54. Diagrammatic figure showing the position of the testes. × *circa* 15.

Fig. 55. Apex of ovary and base of terminal filament. × 400.

Fig. 56. Longitudinal section through the ovary showing developing eggs. × 180.

Fig. 57. Transverse section across the ovary through the germinal tissue. × 350.

Fig. 58. Apex of testis and base of terminal filament. × 400.

Fig. 59. Longitudinal section through the hinder third of the testis. × 400.

Fig. 59*a*. Transverse section across the testis, passing through the germinal tissue. × 400.

Fig. 60. Longitudinal section of a tergo-sternal muscle at its point of insertion. × 400.

Fig. 61. Portion of musculature of mid-gut, showing junction of the circular fibres in the median dorsal line. × 400.

Fig. 62. Ditto of hind-gut. × 550.

Fig. 63. Salivary and tubular glands of *Anurida*. × 450.

Fig. 64. Common chamber receiving the ducts of the tubular glands (partly diagrammatic). × 400.

Fig. 65. Diagram of head showing relations of the cephalic glands. × *circa* 65.

Fig. 66. Acinose gland of ventral tube in longitudinal section. × 450.

Fig. 67. Aperture of the glands of the ventral tube; section taken parallel with the long axis of the body. × 400.

Fig. 68. Portion of duct of salivary gland. × 500.

PLATE VII.

Fig. 69. Group of eggs of *Anurida*. × 10.

Fig. 70. Section through unsegmented egg (after Claypole, reduced).

Fig. 71. Egg of *Anurida*, showing precephalic organ and developing appendages. The outer egg-membrane (*ch.*^{1}) has been dissected away from the lower half of the egg. × 85.

Fig. 72. Embryo *Anurida*; flexure almost complete. The precephalic organ is seen to be degenerating (after Claypole, reduced).

Fig. 73. Embryo *Anurida* at the time of development of the tritocerebral appendages (after Wheeler).

Fig. 74. Paramedian section to show primitive cephalic ganglia about the stage in fig. 72 (after Folsom, reduced.)

Fig. 75. Ventral aspect of cephalic region, about the stage in fig. 72 (after Folsom, reduced).

Fig. 76. Blastoderm with precephalic organ (after Claypole, reduced).

Fig. 77. Transverse section through second abdominal segment on one side of the body of the male, at the stage prior to that seen in fig. 72 (after Claypole, reduced).

Fig. 78. Transverse section showing early mesoderm formation (after Claypole, reduced).

Fig. 79. Diagrammatic figure showing Nematodes in the testis. × *circa* 100.

Fig. 80. *a*, Embryo of Nematode; *b*, the same in transverse section. × 200.

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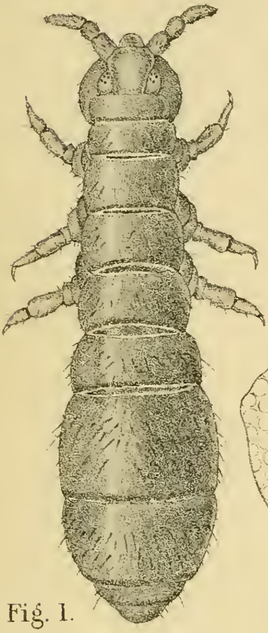
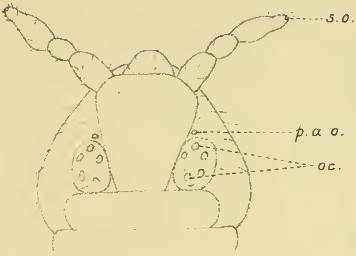


Fig. 1.



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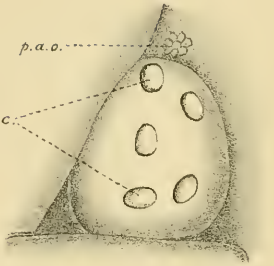

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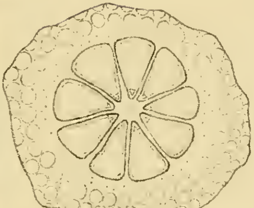

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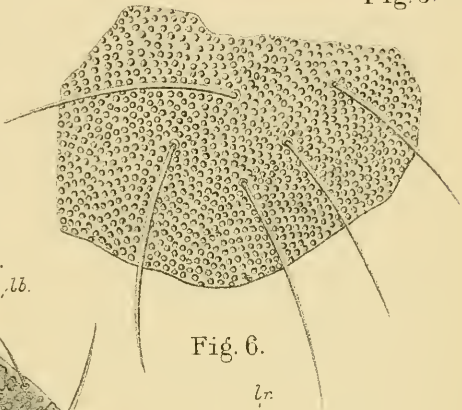
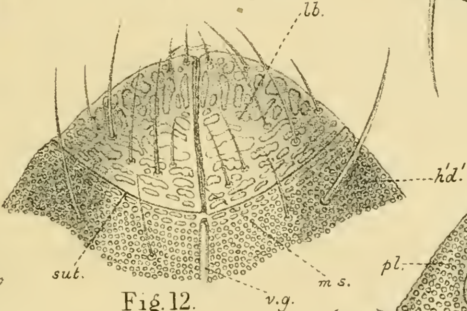


Fig. 6.

Fig. 2.



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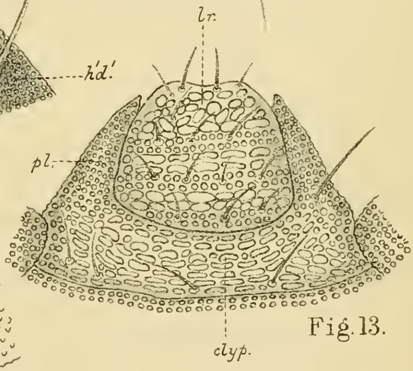

Fig. 13.

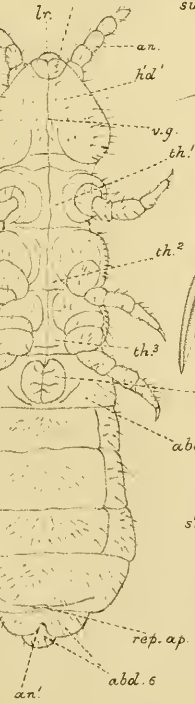

Fig. 3.

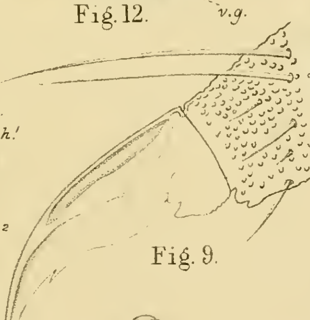

Fig. 9.

Fig. 8.

Fig. 7.

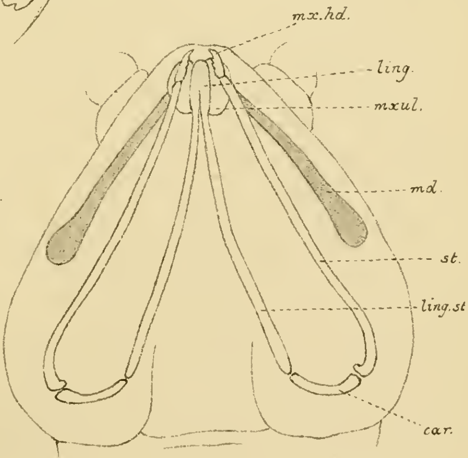

Fig. 11.

A. D. Imms. del

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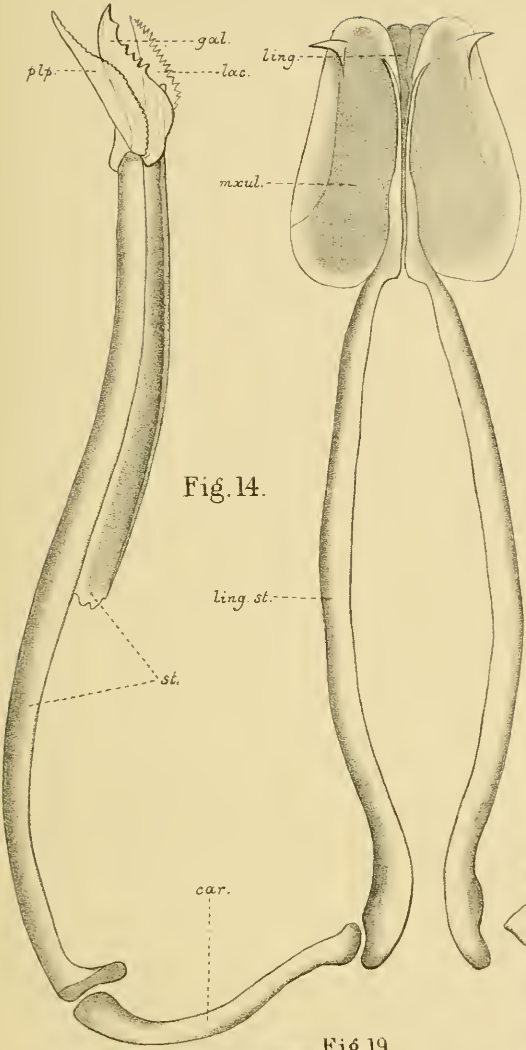

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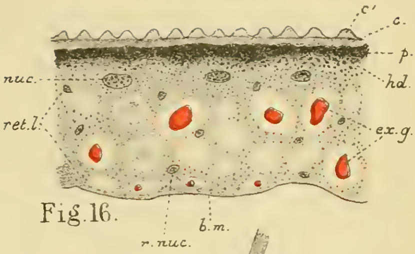

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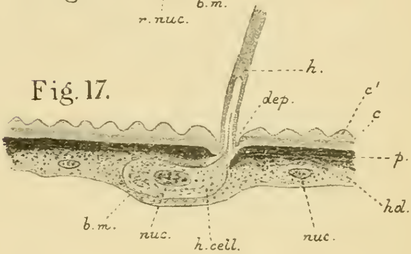
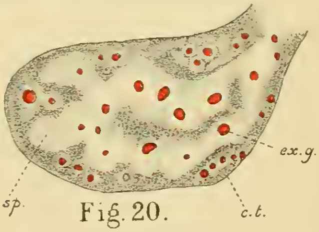


Fig. 17.

Fig. 18.



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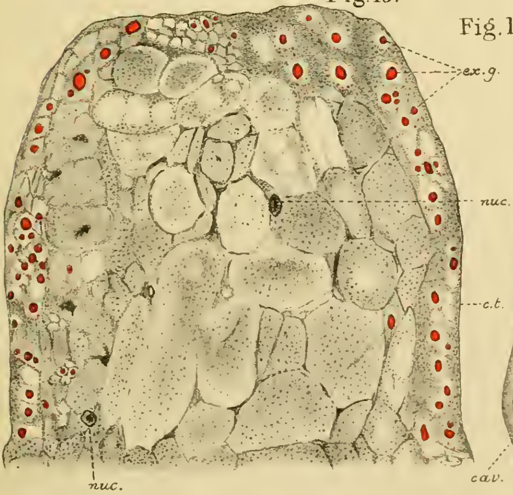

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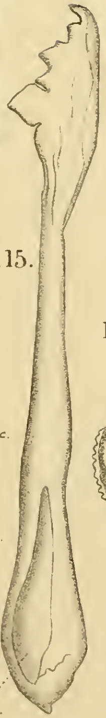
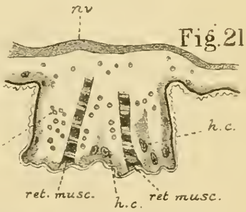


Fig. 15.

Fig. 22.



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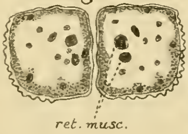

Fig. 23.

Fig. 24.

Fig. 25.

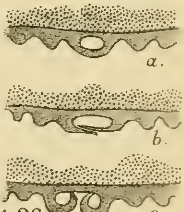

Fig. 26.

A. D. Imms, del.

McFarlane & Erskine, Lith. Edinr

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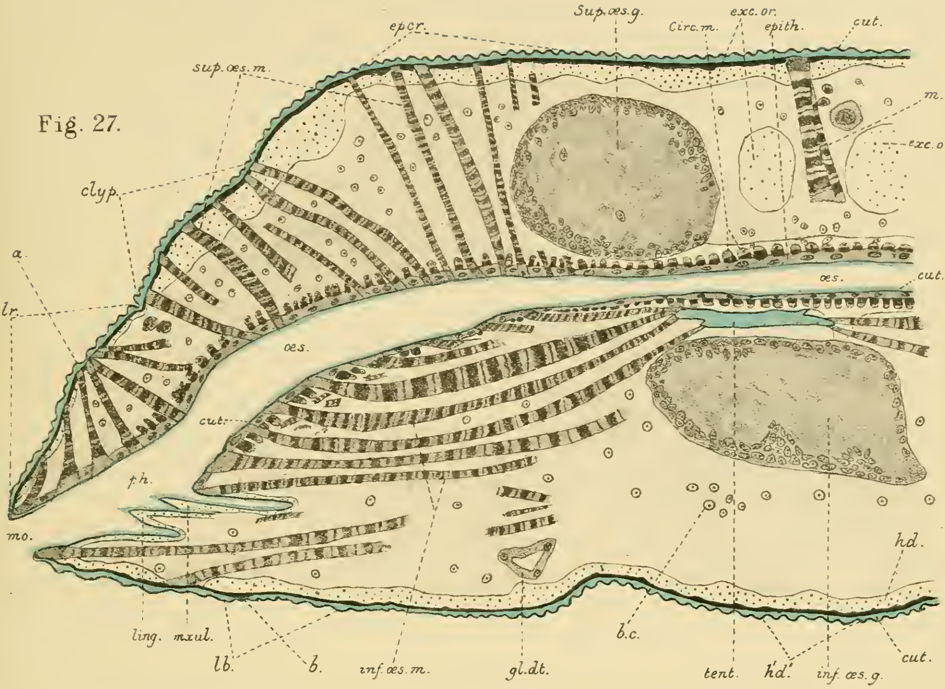
Fig. 27.



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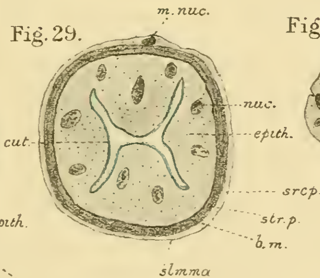

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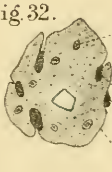


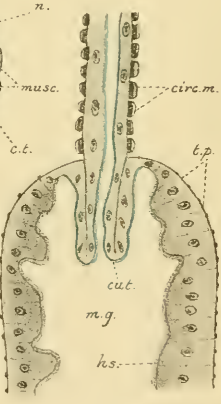
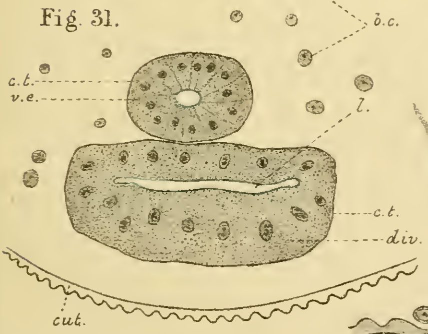


Fig. 28.

Fig. 31.



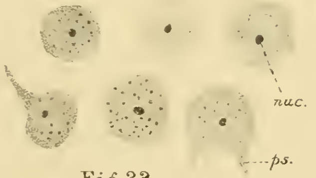
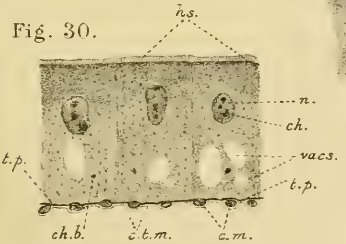


Fig. 33.

Fig. 30.



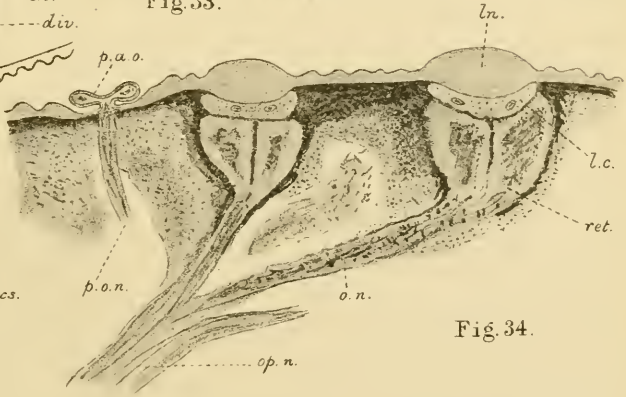


Fig. 34.

A. D. Imms, del.

McFarlane & Erskine, Lith Edinr.

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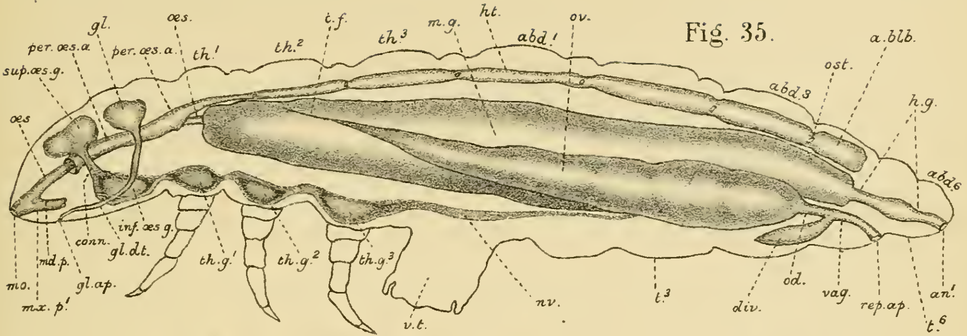
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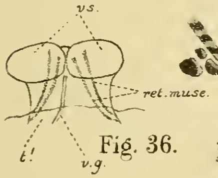
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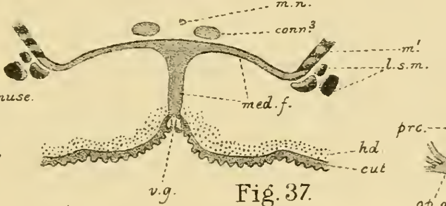
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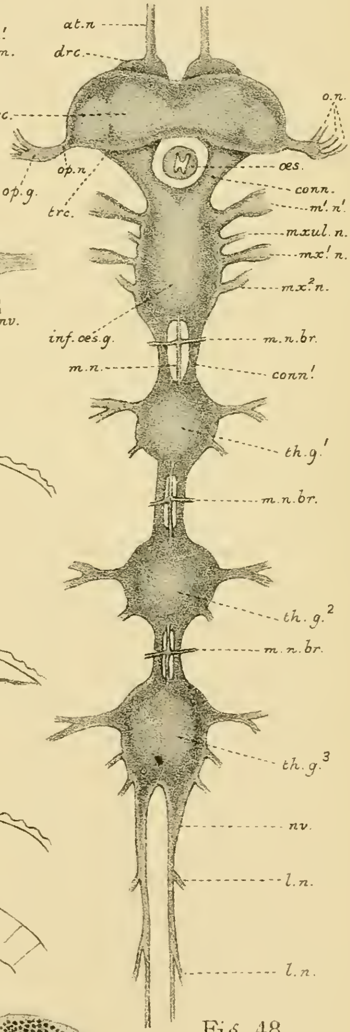
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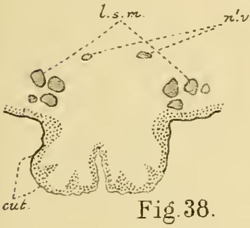
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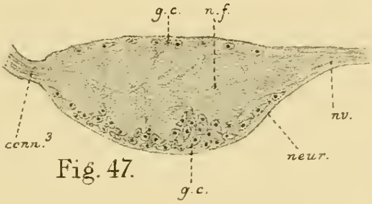
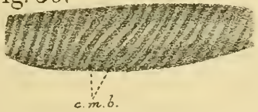
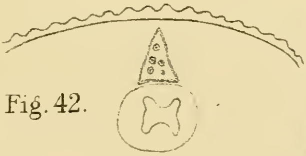


Fig. 47.

Fig. 39.

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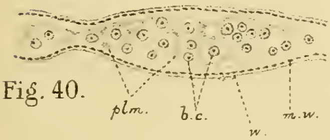
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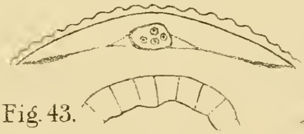
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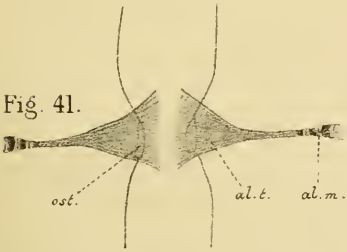
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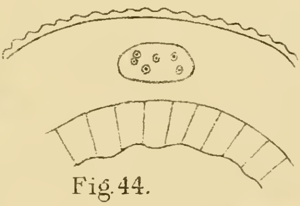
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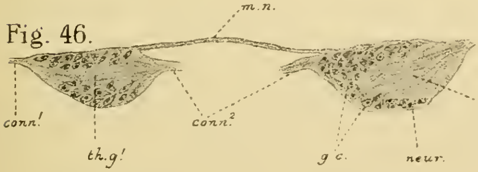
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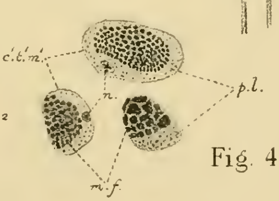
Fig. 45.

A. D Imms, del.

McFarlane & Erskine, Lith Edinʳ

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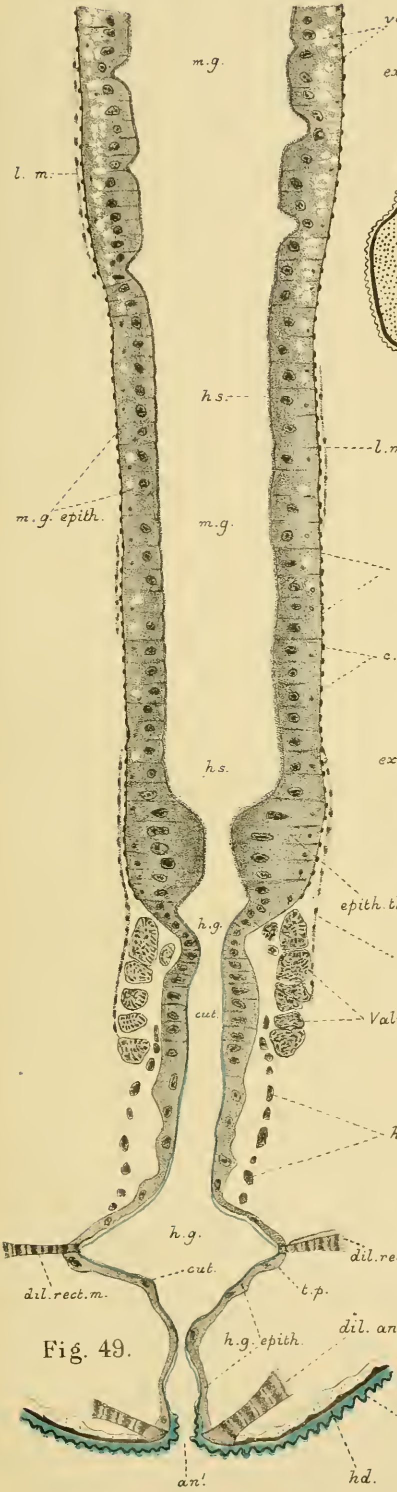

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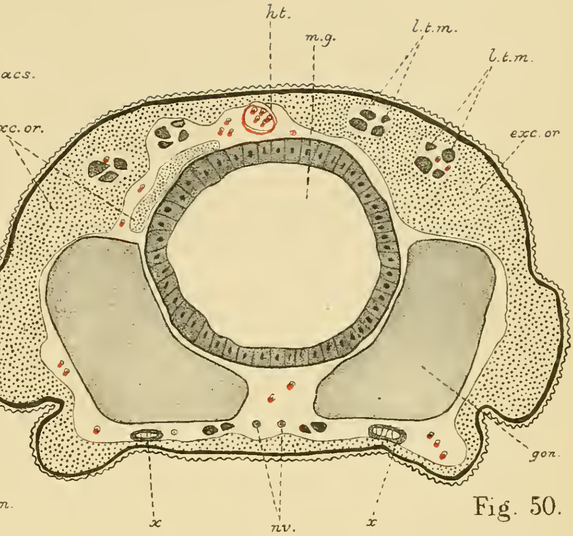

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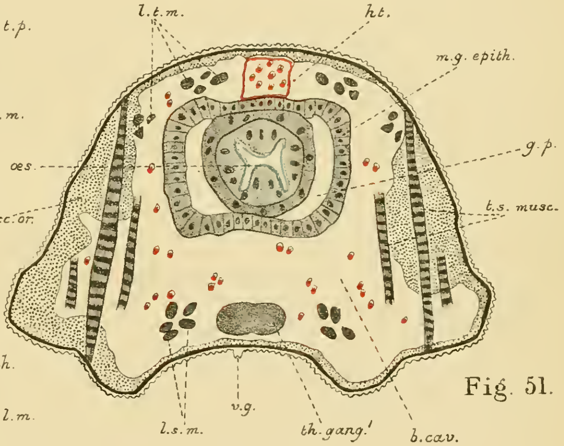

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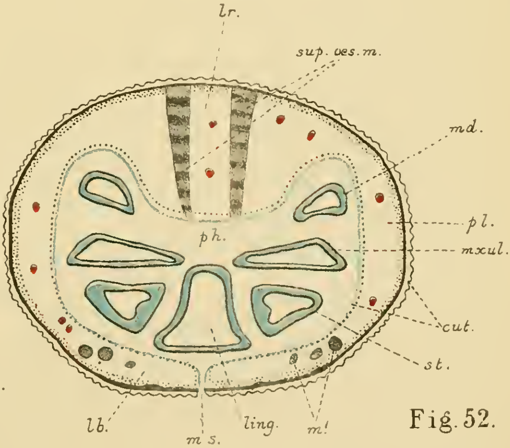
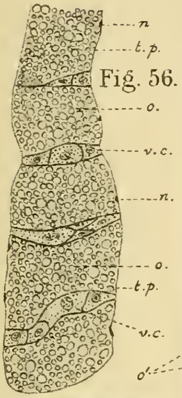


Fig. 52.

A. D. Imms, del.

McFarlane & Erskine, Lith Edinr

ANURIDA.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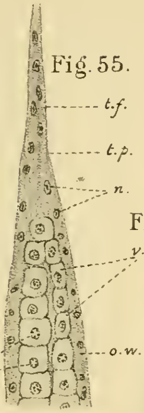
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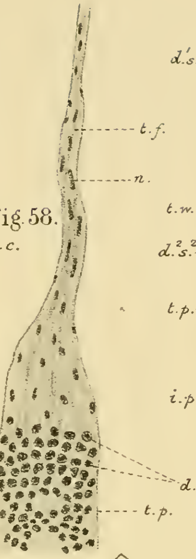
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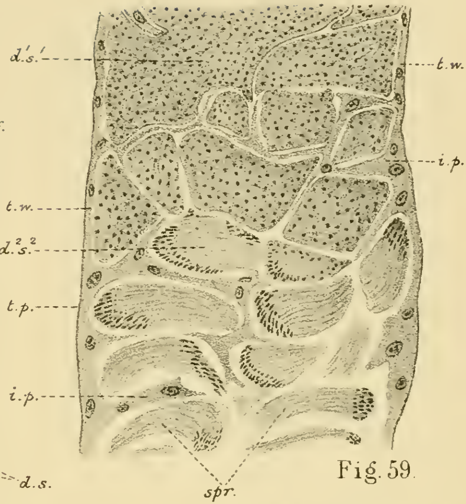
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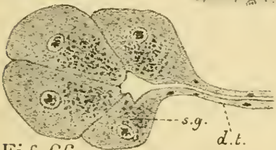
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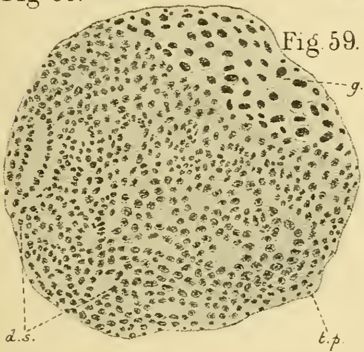
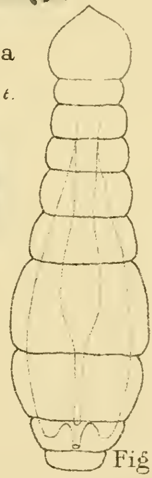


Fig. 59. a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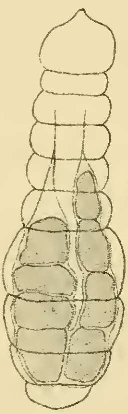
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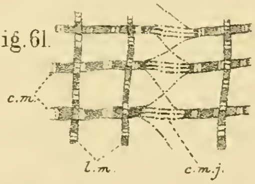
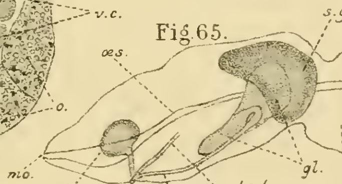


Fig. 61.


Fig. 62.


Fig. 57.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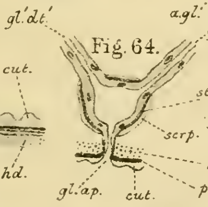
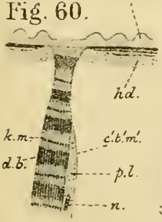


Fig. 64.


Fig. 68.


Fig. 67.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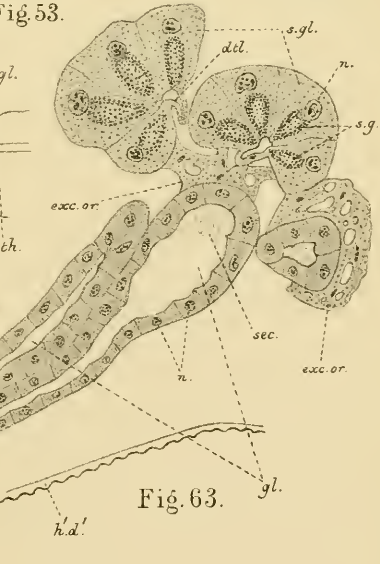
Fig. 63.

A. D. Imms, del.

McFarlane & Erskine, Lith. Edinr

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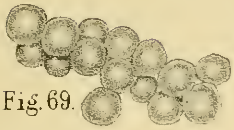

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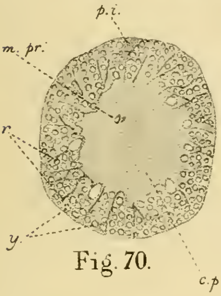

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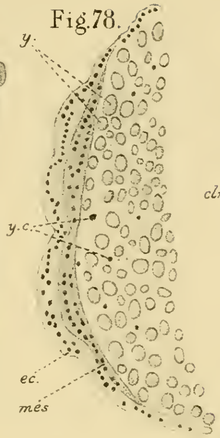

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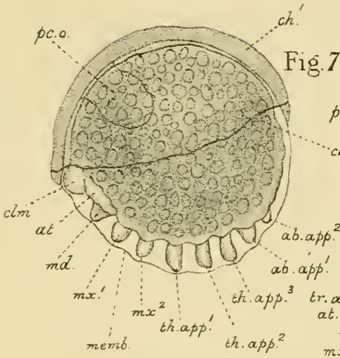

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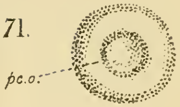

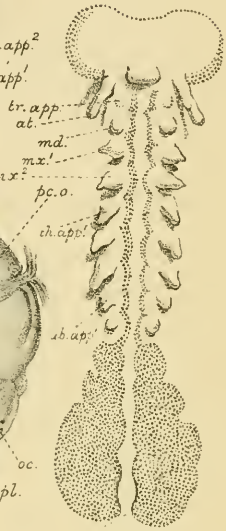

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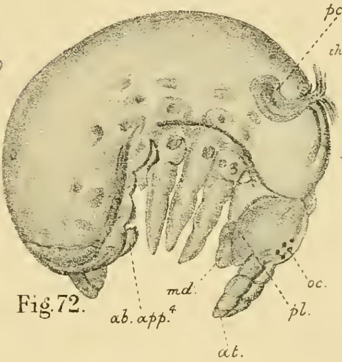

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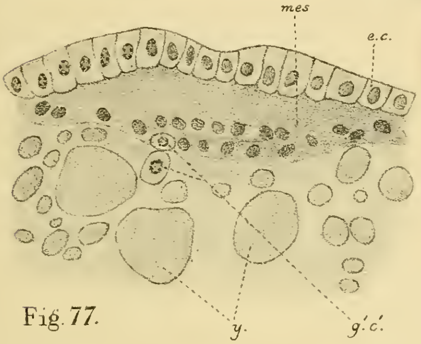

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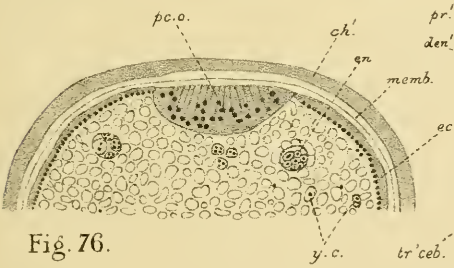

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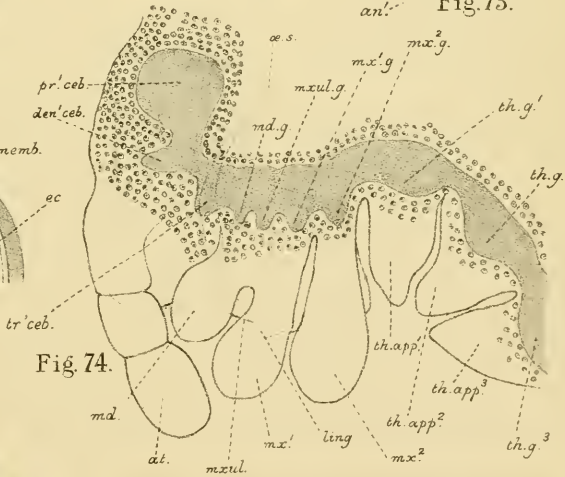

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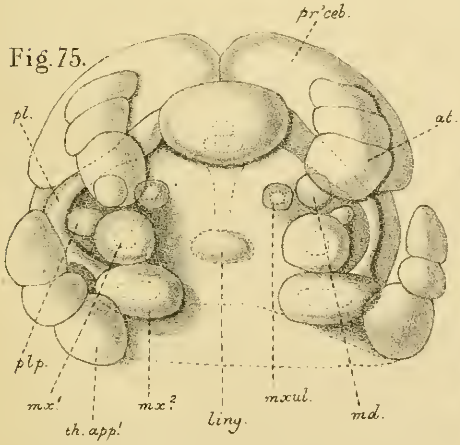

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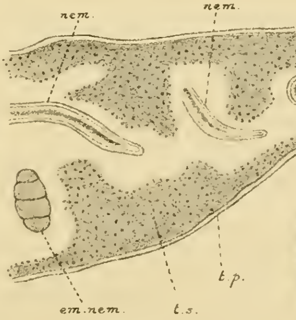

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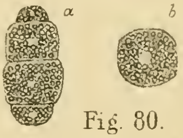

Fig. 80.

A. D. Imms del. Figs. 69, 71, 79, 80.

McFarlane & Erskine Lith Edinr

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