On the Antennal Musculature in Insects and other Arthropods.

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With 25 Text-figures.

CONTENTS.

INTRODUCTION AND METHODS.

IT is well known that in the Insecta each antenna is moved by extrinsic muscles which are inserted into the base of the scape or first segment. These muscles are levators and depressors which have their origins on the dorsal and anterior arms of the tentorium. They bring about movements of the whole antenna. The only other antennal muscles are intrinsic, viz. the flexors and extensors of the flagellum. The origins of these muscles are within the base of the scape and their insertions are on the base of the pedicel (or second antennal segment). The remainder of the antenna, often termed the flagellum, is devoid of muscles.

A few years ago, when dissecting an example of Heterojapyx sp. obtained by the late R. J. Tillyard in Australia, I was surprised to find that an elaborate system of intrinsic muscles is present in each segment of the antenna and that these muscles extend to the apex of the appendage. Further investigation revealed the presence of an elaborate musculature also in the antennae of Japyx and Campodea, among Thysanura and in Scutigerella, and in Hanseniella among the Symphyla. These facts led me to explore the subject to some extent in the Chilopoda and Diplopoda, and to note the occurrence of diverse types of antennal musculature in Crustacea. The outcome of this investigation has been to record certain new morphological data bearing upon antennal structure and evolution.

Four methods of investigating the antennal muscles were used. (*a*) Stained whole mounts. (*b*) Prepared whole mounts examined under polarized light. (*c*) Serial microtome sections, and (*d*) dissections.

(*a*) For whole mounts the material was fixed either in hot 70 per cent. alcohol or in an alcoholic solution of mercuric chloride. In most cases bleaching was necessary, and this was done by subjecting the specimens to chlorine vapour in a small, tightly closed vessel. Staining was by means of Mayer's para-carmine and any excess was washed out in acid alcohol. The specimens were examined in cedar wood oil, or permanently mounted in canada balsam.

(*b*) Advantage was taken of the well-known fact that muscles are anisotropic when viewed with polarized light. With the nicol prisms in the crossed position the antennal and other muscles have the appearance of self-luminous objects in a dark field (Text-figs. 13 and 14). The application of polarized light is especially useful in the case of very small specimens: it also has the advantage of enabling material to be examined with the minimum of previous treatment. Under a polarizing microscope small muscles betray themselves with clarity whereas they are not easily identified with certainty by other methods should they fail to stain readily.

It will be obvious that the medium itself in which the specimens are examined must be free from polarization. Also the fixation, or other prior treatment, must be such as will not modify or destroy the anisotropic property of the muscles. Material fixed in hot 70 per cent. alcohol gave satisfactory results when examined in cedar-wood oil or mounted in canada balsam. Unless the cuticle be transparent as in Campodea, for example, bleaching is usually necessary, and for this purpose chlorine vapour was used.

(*c*) Various methods of treatment for section cutting were tried. For Chilopoda and Diplopoda, in particular, whose cuticle becomes greatly hardened in the process, the following method proved suitable. Collected material underwent a preliminary fixation in hot 70 per cent. alcohol. After this had cooled, the heads were cut off with a sharp razor blade, and transferred to warm cupric trinitrophenol, made up as given by Petrunkevitsch (1933), viz. 60 per cent. alcohol 100 c.c., nitric acid 3 c.c., ether 5 c.c., cupric nitrate 2 gm., picric acid 0·5 gm. This solution imparts an elastic texture to the tissues and prevents excessive hardness or brittleness of the cuticle. After being kept in the solution for 12 hours the specimens were washed in three changes of 70 per cent. alcohol. They were then passed through 90 per cent. alcohol to methyl benzoate containing 1 per cent. celloidin, and were kept there for 24 hours. They were then transferred to benzole for an hour and then changed into fresh benzole for a similar period. Wax was then added to the benzole and the receptacle was kept for 3 hours on the top of a warm embedding oven. Final embedding was in wax of 56° C. melting-point for 12 hours. The most satisfactory stain proved to be Mallory's triple stain, which gave good differentiation of the muscles in contrast to the surrounding tissues. Indebtedness is acknowledged to F. J. W. Bloy, research assistant, for the patience and skill which he exercised in obtaining good microtome sections.

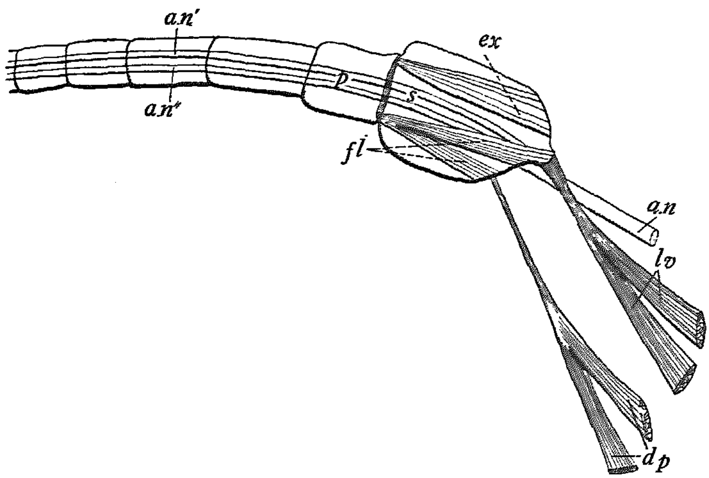
(*d*) For dissection the material was fixed in Pampel's fluid (Pampel, 1914) and afterwards embedded in paraffin. The dorsal or ventral wall of the head, as the case may be, was then removed to the required extent by slicing it away in a microtome. When sufficient of the head wall had been removed the wax was dissolved out and the specimens lightly stained with paracarmine. With this preliminary treatment dissection of the extrinsic muscles was considerably facilitated especially in the case of Lithobius and Japyx.

The terminology applied to the different muscles offers some difficulty. Among the components in a functional group, for example, it is often hard to determine whether such components are merely individual muscle bundles or represent separate muscles. Furthermore, in naming the various muscles their functions have been, in most cases, the guiding principle. In determining the effect of the action of any given muscle its individual action alone has been considered. It is, however, obvious that the effects of the action of a muscle may differ according to whether or not other muscles act in conjunction with it.

It needs to be emphasized that the present communication is of an essentially preliminary character. Many details of the musculature are not dealt with, while the subject of the innervation of the different muscles is omitted. The aim of the paper is to call attention to an unexplored aspect of morphology and thereby, it is hoped, lead to its being more adequately studied in the future.

Insecta Pterygota.

Morphologically the insectan antenna consists of a basal segment or scape which bears an annulated flagellum. This type of antenna prevails throughout the Pterygota among which it presents almost innumerable modifications of form and structure. The general arrangement of the extrinsic and intrinsic antennal muscles in the Insecta has already been briefly referred to on p. 273 and is shown in Text-fig. 1. This disposition of the musculature has been described by many authors in very different orders including the Orthoptera (Du Porte, 1920; Snodgrass, 1928; Walker, 1931; Maki, 1935), Isoptera (Basch, 1865; Holmgren, 1909), Hemiptera (Miller, 1933), Anoplura (Florence, 1921; Keilin and Nuttall, 1930), Neuroptera (Miller, 1933; Maki, 1936), Coleoptera (Bauer, 1910), and Hymenoptera (Morison, 1927; Speicher and Miller, 1933). I have also examined the antennal musculature in a large number of different insects including Blatta, Gryllus, Forficula, Stenoperla, Embia, Archotermopsis, various Hemiptera, including Heteroptera and different members of the Aphididae, and a number of Lepidoptera, Hymenoptera, and Diptera Nematocera. In all cases the antennae were found to consist of an annulated flagellum devoid of any intrinsic muscles and articulating with a basal segment or scape. It is within the



TEXT-FIG. 1.

Lateral view of proximal portion of left antenna of an African migratory locust (Locusta migratoria migratorioides) showing extrinsic and intrinsic muscles. × *circa* 35. *a.n.*, antennal nerve and its branches *a.n.'*, *a.n.''*; *dp.*, depressor muscle; *ex.*, extensor muscle; *fl.*, flexor muscle; *lv.*, levator muscle; *s.*, scape; *p.*, pedicel.

scape that the flexor and extensor muscles, which effect the movements of the flagellum as a whole, take their origin. The typical insectan antenna, with its greatly reduced intrinsic musculature, may be contrasted with the segmented antennae of certain Thysanura (to be described below) in which a very complete intrinsic musculature is present.

In some Hemiptera intrinsic muscles are stated to be present in two basal segments of the antenna. Thus, Baker (1915) describes and figures intrinsic muscles in the first and second segments of the antenna in the wingless viviparous female of the Aphid, Eriosoma lanigerum. I have not been able to confirm this observation in English examples of the same species or in many other aphides, where intrinsic muscles are present only within the scape. In the closely allied species E. americana, Miller (1933) similarly finds intrinsic muscles within the scape only. According to Berlese (1893, 1895), in males of the Coccids Pseudococcus (Dactylopius) and Lepidosaphes (Mytilaspis) movements of the flagellum are effected by muscles which originate in the second segment or so-called pedicel. These muscles are termed by Berlese the adductor and abductor of the funiculus. Since the males of the Coccidae are highly specialized in almost every aspect of their anatomy, the condition described by Berlese cannot be regarded as of any phylogenetic or ancestral significance. It appears to have been brought about as a secondary development either by the subdivision of the original scape and its muscles, or by the development of a suture in association with its articulation with the head.

Statements have been made regarding the presence of muscles in the flagellum of the antennae among Pterygota. Thus Du Porte (1920) describes flexor and extensor muscles in the flagellum of the antenna of Gryllus domesticus. Basch (1865) likewise describes (and figures) a pair of longitudinal muscles extending through the flagellum of Termes. Reinvestigation of the antennae of both these insects has led me to the conclusion that these authors have unquestionably mistaken the two prominent rami of the antennal nerve for longitudinal muscles. An error of this kind has evidently resulted from observations made solely on unstained whole preparations.

Straus-Dürckheim (1828, p. 153) describes and figures (Pl. 3, fig. 1) two small muscles—the abductor and adductor—in each of the first three 'segments' of the antenna in the cockchafer, Melolontha melolontha. The famous anatomist also states that each pair of the above-mentioned muscles moves the segment which follows. While I am able to confirm Straus-Dürckheim's observation that a pair of muscles are located in the scape of the antenna of Melolontha, as in other Pterygota, I am quite unable to discover any evidence of muscles being present in the second or third divisions of the antenna. It seems very probable that the conspicuous branches of the antennal nerve were mistaken for muscles by this author.

Thysanura.

The division of the Thysanura into two groups, which some workers regard as representing separate orders, is fully substantiated by a study of the antennal musculature. These muscles are so very different in the Thysanura Ectognatha (Thysanura *sen.str.*) and the Thysanura Entognatha (Rhabdura or Diplura) that they are best considered separately under these two divisional headings.

A. Thysanura Ectognatha.

Petrobius (Machilis) maritimus and Lepisma saccharina were investigated as typical representatives of this division of the order. In both of these genera the antenna is composed of a large basal segment or scape followed by a smaller element or pedicel, which bears a long flagellum composed of numerous false segments or annuli. The musculature conforms to the general type prevailing in the antennae throughout the Pterygota. In a few words it may be said that in both Petrobius and Lepisma movements of the antennae are effected by extrinsic muscles arising on the endoskeleton of the head, and intrinsic muscles located within the scape: no other antennal muscles are present.

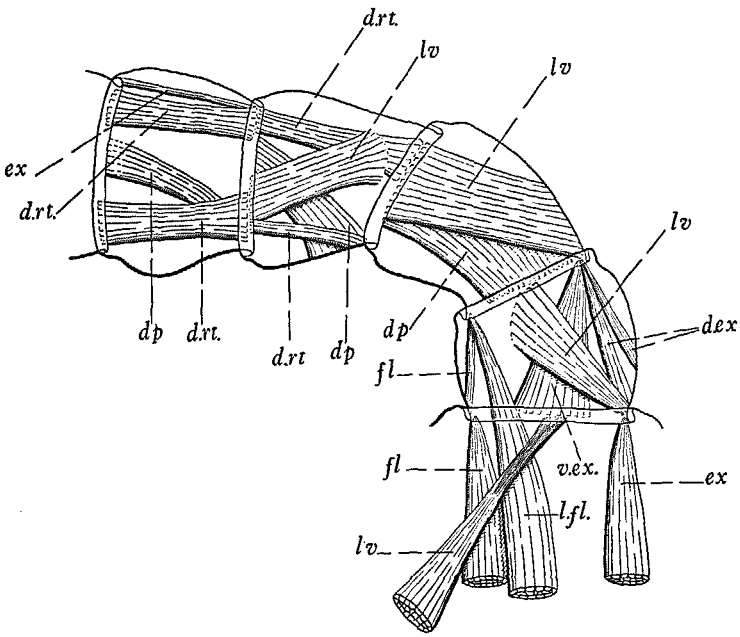
B. Thysanura Entognatha.

Three species belonging to this suborder were investigated, viz. Heterojapyx gallardi Till., Japyx sp., and Campodea lubbocki Silv.

Indebtedness is here expressed to Dr. S. M. Manton for a number of examples of Japyx sp. collected by herself in the Cape Province, South Africa; and also to the late Dr. R. J. Tillyard for two examples of Heterojapyx gallardi from Australia, and to Dr. R. S. Bagnall for naming the Campodea. Since there were no obvious differences to be detected in the antennal musculature of Japyx and Heterojapyx the account which follows is based upon a study of examples belonging to the first-named genus only, but the descriptions are applicable to both genera.

I. Japyx sp. (S. Africa).

a. The Extrinsic Muscles in Japyx (Text-fig. 2) are:



TEXT-FIG. 2.

Dorsal view of proximal portion of left antenna of Japyx sp. × 85. Extrinsic muscles: *ex.*, extensor of antenna; *fl.*, flexor of antenna; *l.fl.*, long flexor of segment II; *lv.*, levator of antenna. Intrinsic muscles: *d.ex.*, dorsal extensor of segment II; $dp._3$, $dp._4$, $dp._5$, depressors; $d.rt._4$, $d.rt._5$, dorsal retractors; $ex._5$, extensor; $fl._2$, flexor; $lv._2$, $lv._3$, $lv._4$, levators; *v.ex.*, ventral extensor of segment II.

(1) Levator of the Antenna (*lv.*).—An elongated muscle arising from about the middle of the side-wall of the head on a level with the hind border of the brain. It passes, obliquely inwards and forwards, alongside the brain and is

inserted by means of a well-developed tendon on the middle of the base of the first segment of the antenna, on the dorsal aspect.

(2) Flexor of the Antenna (*fl.*).—A stout muscle which arises from the hypopharyngeal apodeme of its side, behind the origin of the levator, and passing forward, above the zygomatic adductor muscle of the mandible, becomes inserted on the outer lateral margin of the base of the first segment of the antenna.

(3) Extensor of the Antenna (*ex.*).—A stout muscle which arises from the hypopharyngeal apodeme of its side and passing forward, beneath the zygomatic adductor muscle of the mandible, runs alongside the œsophagus to be inserted on the inner lateral margin of the base of the first segment of the antenna.

(4) Long Flexor of Segment II (*l.fl.*).—A long stout muscle which arises from the hypopharyngeal apodeme of its side and passes forwards, and slightly upwards, above the zygomatic adductor muscle of the mandible. It traverses the cavity of the first segment of the antenna, alongside the antennal nerve, and is attached to the outer margin of the base of the second segment of the antenna.

β. The Intrinsic Muscles (Text-figs. 2 to 5) are as follows:

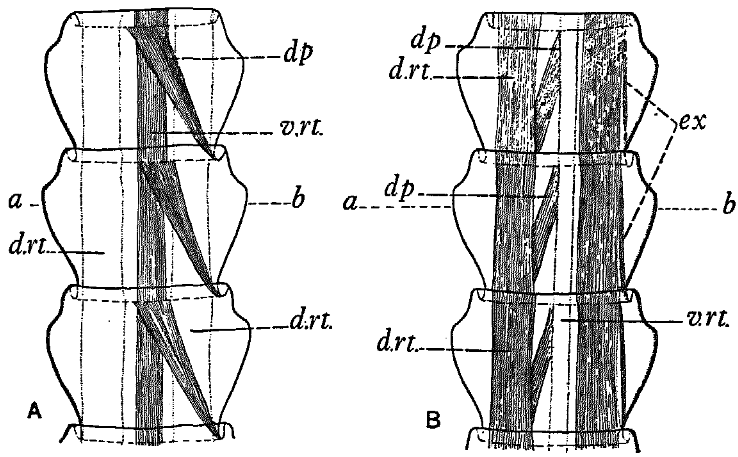
(1) Levator of Segment II ($lv._2$).—This muscle has its origin on the outer border of the base of the scape. It passes obliquely forwards and, spreading out in a fan-like manner, is inserted dorso-medially on to the base of the second segment and on the adjacent part of the scape.

The functions of this muscle are not wholly clear. Since some of its fibres are inserted on to the base of segment II it would appear that it acts partially as the levator of that segment. On the other hand, a large proportion of its fibres have their insertions of the dorsal wall of segment I and their origins are also in that same segment. It would seem, therefore, that when in a condition of tension it also serves to give extra rigidity and acts antagonistically to the pull exerted by the broad and powerful depressor muscle of segment III ($dp._3$).

(2) Flexor of Segment II ($fl._2$).—A slender muscle which arises from the outer aspect of the base of the first

antennal segment slightly distal to the insertion of the flexor muscle of the antenna. It passes forwards in the horizontal plane and is inserted on the outer margin of the base of the second segment of the antenna, proximal to the point of attachment of the levator muscle ($lv._3$).

(3) Dorsal Extensor of Segment II (*d.ex.*).—This muscle consists of two bundles, one of which arises from the



TEXT-FIG. 3.

A, ventral and B, dorsal view of segments VIII to X of the left antenna of Japyx sp. × 90. *dp.*, depressor; *d.rt.*, dorsal retractor; *ex.*, extensors; *v.rt.*, ventral retractor.

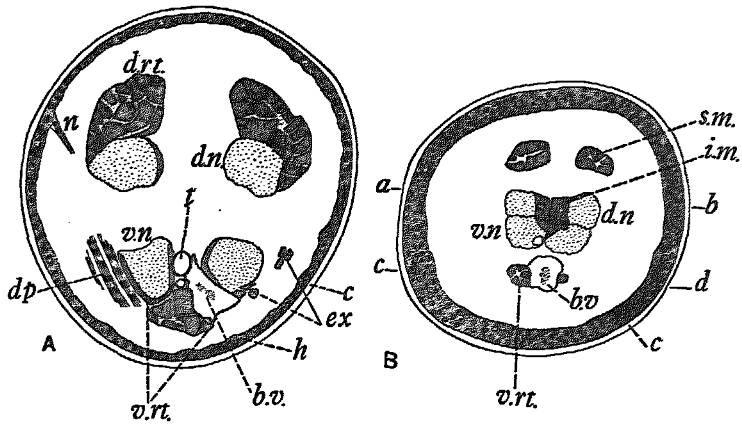
inner aspect of the base of the first segment and the other arises postero-laterally on the inner border of the same segment. Both bundles converge and become inserted on the inner aspect of the base of the second segment.

(4) Ventral Extensor of Segment II (*v.ex.*).—A broad, fan-like muscle which arises from the base of the first segment on the ventral aspect and passes directly forward to be attached to the inner aspect of the base of the second segment, beneath the insertion of the dorsal extensor.

(5) Levator of Segment III ($lv._3$). A broad muscle arising from the inner postero-lateral border of the second seg-

ment and with a very wide insertion on the base of the third segment.

(6) Depressor of Segment III ($dp._3$).—A broad muscle arising from the base of the second segment and, passing beneath the levator, has a wide attachment along the base of the third segment.



TEXT-FIG. 4.

A, transverse section through the eighth segment of the left antenna of Japyx sp. in the position indicated by *a* . . . *b* in Text-fig. 3. × 150. B, transverse section through the nineteenth segment of the left antenna of Japyx sp. × 150. *b.v.*, antennal artery; *c.*, cuticle; *d.n.*, dorsal branch of (right) antennal nerve; *dp.*, depressor muscle; *d.rt.*, dorsal retractor muscle; *ex.*, extensor muscle; *h.*, hypodermis; *i.m.*, inferior division of dorsal retractor muscle; *n.*, nerve branch; *s.m.*, superior division of dorsal retractor muscle; *v.n.*, ventral branch (left) of antennal nerve; *t.*, main trachea of antenna; *v.rt.*, ventral retractor muscle.

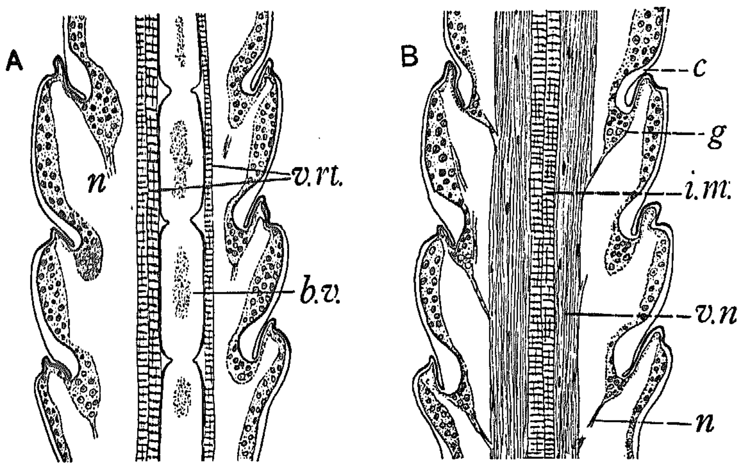
(7) Dorsal Retractors of Segment IV ($d.rt._4$).—A pair of longitudinal muscles arising from the base of the third segment and inserted into the base of the fourth segment.

(8) Levator of Segment IV ($lv._4$).—A broad muscle which arises on the dorso-posterior wall of the third segment and, passing obliquely outwards, has a broad insertion on the base of the fourth segment.

(9) Depressor of Segment IV ($dp._4$).—A broad muscle which arises from the postero-lateral aspect of the outer part

of the third segment and, passing beneath the levator muscle, becomes attached to the base of the fourth segment.

From the fourth to the seventeenth or eighteenth segments, each segment contains five muscles which originate on its base and are inserted on the base of the succeeding segment (Text-figs. 3, 4, and 5). These are (1) a pair of dorsal retractors (*d.rt.*) which lie above, and are in intimate contact with the



TEXT-FIG. 5.

Longitudinal sections through the left antenna of Japyx sp. A, at the level indicated by *c* . . . *d*, and B, at the level indicated by *a* . . . *b* in Text-fig. 4 B. *g.*, ganglionic enlargement of segmental nerve. Other lettering as in Text-fig. 4.

corresponding dorsal antennal nerves. These muscles form a continuous series with their insertions in close contact with the origins of the muscles in front. (2) An unpaired median ventral retractor (*v.rt.*), which is situated beneath the ventral nerves of the antenna and alongside the antennal artery (*b.v.*): the main trachea (*t.*) of the antenna runs in close association with, and just above, this muscle. (3) A depressor (*dp.*) whose origin is near the outer border of the base of its segment, near to and below that of the left dorsal retractor: passing obliquely upwards the depressor muscle is inserted near to the middle of the basal margin of the segment in front. (4) A slender extensor (*ex.*) which lies just externally to the right dorsal retractor muscle of its segment: it has its insertion in close association with that of the last-named muscle.

Traced forwards through the antennae the segmental muscles become progressively smaller. In the twelfth segment the depressor and extensor each become reduced to a slender bundle of one or two fibres and further forwards they are no longer evident. In the region of the eighteenth to twentieth segments, varying in different individual insects, the dorsal retractor muscles each separate into two bundles, forming superior and inferior components (Text-fig. 4 B). The superior retractors lie free from, and above, the antennal nerves, while the inferior retractors are seen to lie in close contact with the four antennal nerves which have become closely drawn together. Traced farther forwards, the superior retractor muscles disappear and the two inferior retractor muscles become closely approximated. They appear as a single median chain of longitudinal muscles which passes forwards directly from segment to segment and ends in the penultimate segment of the antenna. The ventral retractor muscle likewise becomes progressively reduced in calibre as it is traced forwards. Ultimately it becomes represented by a few slender fibres which disappear altogether, some two or three segments behind the apex of the antenna.

The movements capable of being effected by the three longitudinal segmental muscles are probably complex. Acting in unison, the contraction of these muscles through each segment would result in the retraction, or shortening, of the antenna. This is evident for the reason that the proximal half of each antennal segment is of markedly narrower diameter than the distal portion and thus allows of each segment being telescoped into the segment immediately behind (Text-fig. 3). Contraction of the two dorsal retractor muscles, throughout their course through the segments, would result in retraction and probably an upward inclination of the antenna. Contraction of the ventral retractor muscle would, similarly, impart a downward bending of the antenna. On the other hand, contraction of the dorsal retractor muscle of one side only through each segment of the antenna would result in the movement of that appendage in the horizontal plane. The outer, or post-axial, dorsal retractor muscles, by contracting simultaneously through each segment, would perform the function of a flexor by inclining the antenna outwards and backwards. Similarly, the independent contraction of the inner, or pre-axial dorsal retractor muscle, in each segment, would, by restoring the antenna to its normal position, function as an extensor.

Structure of the Antennae.—In almost all the antennal segments a girdle, in the form of a thickened epidermal layer, encircles each segment beneath the setiferous area. This thickened layer is mainly composed of numerous ordinary epidermal cells, trichogenous cells, and nerve-cells. The trichogenous cells are large and pyriform with a central vacuole. In association with many of the trichogenous cells there is a nerve fibril which passes into the base of the hair concerned. These fibrils are prolongations from the nerve-cells. The latter form the ends of segmental nerves which are given off from the main antennal nerves. In the distal two-fifths of the antenna each segmental branch from the main antennal nerves ends in a small ganglionic enlargement which gives off nerve-fibres innervating the sensory hairs of the segment in front (Text-fig. 5 B). These minute ganglionic centres are very evident in the distal segments where the muscles are reduced and much less prominent.

In conformity with the elaborate development of its musculature, the antenna is provided with a conspicuous median artery which evidently ensures an efficient blood-supply to that appendage. This vessel is conspicuous in transverse sections throughout the length of the antenna. In the proximal half of this appendage the walls of the artery are in intimate contact with the investing coats of the ventral antennal nerves and the ventral retractor muscle (Text-fig. 4 A). Traced farther forwards, the artery is no longer in contact with the antennal nerve and lies partially embedded between the fibres of the ventral retractor muscle (Text-fig. 5 A). The position of the artery in relation to this muscle is assymetrical, the majority of its fibres being situated on the outer or post-axial aspect of the artery (Text-figs. 4 B and 5 A). At the base of the antenna the artery lies free except for slight fibrous attachments to the antennal nerves. Along its course the artery is accompanied by the main antennal trachea which runs in close association with it along its outer or post-axial aspect (Text-fig. 4 A). The most striking feature shown by the antennal artery is its very clear division into a linear series of chambers, one for each segment of the antenna, throughout the greater part of the length of that appendage. Each chamber is marked off from its fellow by a well-defined constriction which is situated at the junction between two antennal segments (Text-fig. 5 A). The occurrence of these chambers is of mechanical advantage in connexion with the movements of the antennal segments. Since the constrictions are intersegmental in position, they have developed at positions where repeated flexion and extension of the segments would naturally result in repeated compression of the artery at those points. There is little doubt, furthermore, that the initial stimulus which impels the blood into the two antennal arteries is provided by the pulsations of the dorsal vessel. Since, however, the artery is attached to the ventral retractor muscle in each segment, the contraction and relaxation of the fibres of that muscle would directly influence the blood flow which might otherwise tend to be impeded at the constrictions.

The main antennal nerve, as is usual among many insects, divides into two branches. This division, in Japyx, takes place within the head, before the nerve enters the first segment of the antenna. In the second segment the antennal nerve is clearly seen to be composed of four subequal branches. This is brought about by the right and left branches subdividing so that each shows a dorsal and ventral component. The fourfold division of the antennal nerve is traceable almost to the apex of the appendage. In the region of the eighteenth or nineteenth segment the four branches of the antennal nerve become closely approximated so as to form an apparently single nerve. Its fourfold composition, however, is evident in transverse sections (Text-fig. 4 B) wherein each branch is seen to be clearly defined by its perineurium. Fine sensory branches are given off segmentally from each of the four nerves. These branches pass obliquely outwards to the integumental sensoria. They arise from the main antennal nerves in the segment proximal to the one which they innervate, and each ends in a small ganglionic enlargement (Text-fig. 5). It will be seen on reference to Text-figs. 4 and 5 B that the antennal nerves are also in intimate connexion with the longitudinal segmental muscles. They also give off branches to other of the antennal muscles and are, therefore, composed of both sensory and motor fibres. This condition sharply contrasts with what obtains in all pterygote insects.

B. Campodea lubbocki Silv. (Text-fig. 6).

Numerous examples of this species were obtained in the Botanical Gardens in Cambridge.

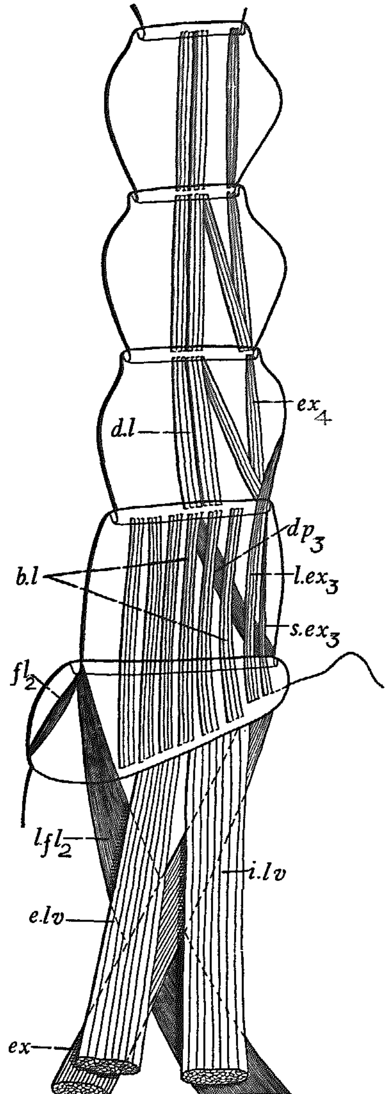
a. Extrinsic Muscles. These comprise five muscles as follows.

(1) External Levator of the Antenna (*e.lv.*).—An elongated muscle which arises from the anterior or lateral arm of the tentorium of its side. It passes upwards and slightly inwards, and is inserted dorsally on the proximal margin of the scape.

(2) Internal Levator of the Antenna (*i.lv.*).—An elongated and rather more slender muscle than (1): it arises from the transverse bar of the tentorium, close to the junction with the lateral arm of its side. Passing directly upwards and forwards, it becomes inserted on the dorsal aspect of the proximal margin of the scape, internal to the insertion of the external levator.

(3) Extensor of the Antenna (*ex.*).—This muscle arises ventrally to, but in close association with, the origin of the external levator. It passes obliquely forwards and inwards, becoming inserted on the inner lateral border of the proximal margin of the scape.

(4) Long Flexor of Segment II ($l.fl._2$).—This is a stout elongated muscle which has its origin, slightly to one side of the median line, on the transverse bar of the tentorium. It passes obliquely forward and outward beneath the muscles (1) to (3), and becomes inserted on the outer border of the base of the second segment of the antenna.



TEXT-FIG. 6.

Basal segments of left antenna of Campodea lubbocki, dorsal view. × 250. I. Extrinsic muscles: *ex.*, extensor of antenna; *e.lv.*, external levator of antenna; *i.lv.*, internal levator of antenna; *l.fl.*$_2$ long flexor of segment II. II. Intrinsic muscles: *b.l.*, basal longitudinal muscles; *d.l.*, dorsal longitudinal muscle; *dp.*$_3$, depressor of segment III; *ex.*$_4$, dorsal extensor of segment IV; *fl.*$_2$, flexor of segment II; *l.ex.*$_3$, long extensor of segment III; *s.ex.*$_3$, short extensor of segment III.

(5) Depressor of the Antenna.—A broad stout muscle which is deeply seated near the floor of the head. It arises from the transverse bar of the tentorium and, passing directly forwards, is inserted on the middle of the proximal margin of the scape. Being wholly ventral in location, it is not visible in Text-fig. 6.

β. Intrinsic Muscles. These consist of:

(1) Flexor of Segment II (*fl.*$_2$).—A small muscle which has its origin on the outer margin of the first segment of the antenna. It passes obliquely inwards and is inserted on the base of the second segment in close association with the attachment of the antennal flexor.

(2) Basal Longitudinal Muscles (*b.l.*).—These comprise a dorsal series of five or more groups of fibres which have their origins on the base of the scape and become attached dorsally to the base of segment III.

(3) Long Extensor of Segment III (*l.ex.*$_3$).—A long slender muscle which has its origin on the lateral apodeme of the base of the labrum. It is attached near the middle of the inner aspect of segment III.

(4) Short Extensor of Segment III (*s.ex.*$_3$).—A very slender muscle which has its origin in close association with that of muscle (3), and its insertion is on the base of segment III on the inner aspect.

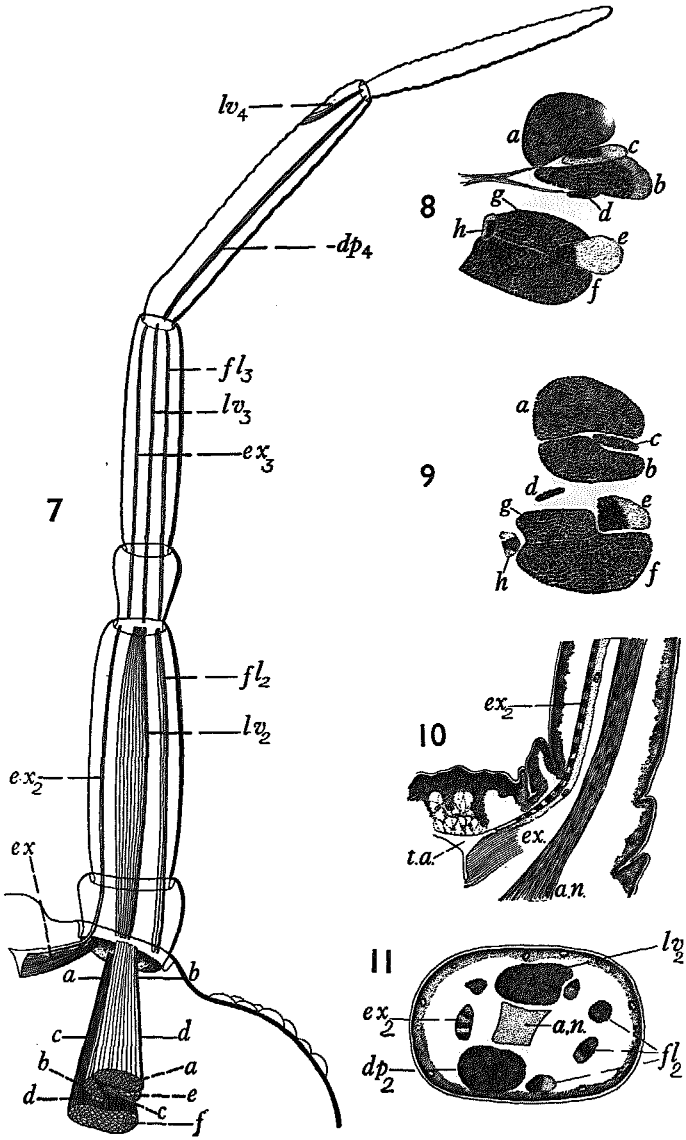
(5) Depressor of Segment III (*dp.*$_3$).—A ventral muscle which has its origin on the inner aspect of the base of segment II and its attachment on the base of segment III near the mid-ventral line.

From the third to the penultimate segment, inclusive, the following muscles are present. Dorsal and ventral longitudinal muscles (*d.l.*), situated in the mid-dorsal and mid-ventral positions respectively; and dorsal (*ex.*$_4$) and ventral extensors of slender calibre. In segments III and IV a depressor is also present. In each case the origins of these muscles are on the base of a segment and their insertions are on the base of the segment immediately in front.

Collembola (Text-figs. 7 to 14).

The species Orchesella villosa Geoff. was investigated in some detail as an example of this order. Isotomurus palustris (Müll.), Podura aquatica L. and Sminthurus viridis L. were also examined. O. villosa has the advantage of being among the largest of the British species of the order and is readily collected. On the other hand, the exceptional length of the antennae in this species, and the apparent 6-segmented condition of these appendages, are unusual and evidently specialized features among Collembola. Since this species regenerates its antennae with facility, some care is necessary to ensure that only individuals with the original fully segmented appendages are examined. The scape of the antenna is of a much larger diameter than the remaining segments, and is articulated with the head by means of a basal annulus or subsegment (Text-fig. 7). The second antennal segment is likewise basally articulated with the apex of the scape by a well-defined subsegment. These two subsegments have no special intrinsic muscles of their own and are obviously only secondarily demarcated parts of the bases of the segments to which they belong. Statements made in taxonomic works that the antennae on Orchesella are 6-segmented are consequently erroneous.

The only previous work in which detailed reference is made to the antennal musculature of Collembola is that of Denis (1928). This author, however, only describes the extrinsic muscles and gives no account of the intrinsic muscles of the antennal segments. The species he examined were Anurida maritima (Guer.), Onychiurus fimentarius (L.), and Tomocerus catalanus Denis. In each of these species the majority of the extrinsic muscles arise on the tentorium, while some take their origin on the dorsal region of the head or, more strictly, on the terminal branches of the 'trabécules tentoriaux'. In Anurida eight pairs of muscles are stated to have their origins on the tentorium: in Onychiurus certain of these muscles are undeveloped and only five pairs are described, while in Tomocerus no fewer than eleven pairs of extrinsic muscles, disposed in four groups, are recognized.



TEXT-FIGS. 7–11.

Fig. 7.—Orchesella villosa: right antenna, dorsal aspect showing extrinsic and intrinsic muscles. × 60.

The principal muscles concerned with the antennae in Orchesella villosa are as follows:

a. Extrinsic Muscles.—These number seven pairs which are divisible into two main groups—a dorsal and a ventral.

Group I comprises four dorsal muscles (*a*, *b*, *c*, *d*, in Text-figs. 7 to 9). They originate partly on the body of the tentorium and partly on the anterior tentorial arm of their side. They extend upwards and forwards, becoming closely inserted together on the dorsal border of the first segment of the antenna, slightly towards the outer margin. These muscles function in the main as levators of the antenna. They correspond with the muscles forming group II of Denis in Tomocerus.

Group II is chiefly composed of a very stout depressor of the antenna. This muscle has its origin on the posterior arm of the tentorium and, passing upwards and forwards, it separates slightly into a dorsal and a ventral component (*f*, *g* in Text-figs. 8 and 9). These have separate insertions on a prominent apodeme, or inflexion of the integument, on the base of the ventral border of the scape of the antenna, somewhat towards the inner aspect. A smaller muscle *e* arises from the tentorium in close association with the muscles of group I. It passes upwards and slightly outwards along the external border of the depressor muscle, and its attachment to the base of the antenna is between the points of insertion of the two

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Fig. 8.—Transverse section of the extrinsic antennal muscles of the right side and taken through the region *a* . . . *b* in Text-fig. 7. × 220.

Fig. 9.—Transverse section of the same muscles and taken through the region *c* . . . *d* in Text-fig. 7. × 220.

Fig. 10.—Longitudinal section through the base of the first segment of the antenna, showing the origins of the extensor muscles of the antenna and of segment II. × 80.

Fig. 11.—Transverse section of the first segment of the left antenna taken near the middle of its length. × 150.

a.b.c.d., extrinsic muscles of group I; *a.n.*, antennal nerve; *dp.*, depressor $dp._4$ of segments II and IV; *e.f.g.h.*, extrinsic muscles of group II; *ex.*, extensor of antenna; $ex._2$, $ex._3$, extensors of segments II and III; $fl._2$, $fl._3$, flexors of the same segments; $lv._2$, $lv._3$, $lv._4$, levators of segments II, III, and IV; *t.a.*, medio-dorsal apodeme.

components *f* and *g* of the depressor muscle. A small muscle (*h* in Text-figs. 8 and 9) is in close association with the depressor and lies along the inner border of the latter. The muscles of group II are apparently homologous with those forming group I of Denis.

Extensor of the Antenna (*ex.* in Text-figs. 7 and 10). A short stout muscle which has its origin on the medio-dorsal apodeme (*t.a.*) formed by extensions of the tentorium. Passing outwards and forwards, it becomes inserted on the ventral border of the scape close to the origin of the depressor of segment II.

β. Intrinsic Muscles comprise the following (Text-figs. 7 to 13):

(1) Levator of Segment II ($lv._2$).—A stout muscle which has its origin on the dorsal aspect of the scape in the median line: its insertion is in a similar position on the base of the second segment.

(2) Depressor of Segment II ($dp._2$).—A stout muscle which arises from the distal border of the apodeme (at the base of the scape) which also gives attachment to the depressor muscle of the antenna. It passes forwards ventrally somewhat towards the inner border of its segment, and is inserted ventrally on to the base of the second segment.

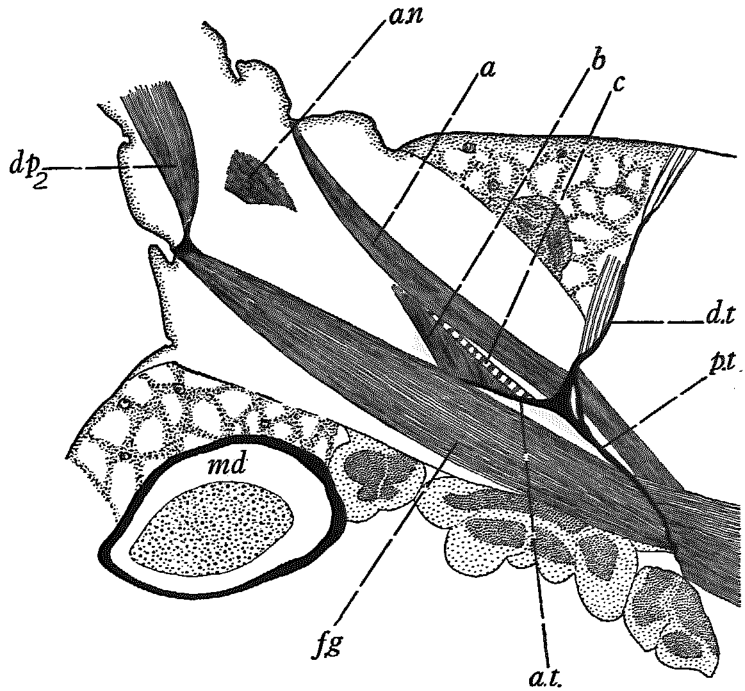
(3) Extensor of Segment II ($Ex._2$).—A slender strap-like muscle formed of three small bundles which have their origins on the mid-dorsal apodeme (*ap.*) in close association with those of the extensor muscle of the antenna. It traverses the whole length of the first antennal segment near its inner aspect, and lies just above the depressor muscle ($dp._2$): it is inserted on to the inner border of the base of segment II.

(4) Flexor of Segment II ($fl._2$).—Towards the outer border of the scape there are three or four slender muscle bundles, each composed of relatively few fibres: they evidently function as the flexor muscle of the second antennal segment.

(5) Levator of Segment III ($lv._3$).—A very slender mid-dorsal bundle of fibres which arises from the base of seg-

ment II and is inserted in a corresponding situation on the base of segment III.

(6) Extensor of Segment III ($ex._3$).—A ventro-lateral group of fibres along the inner side of segment II and inserted on the base of segment III.



TEXT-FIG. 12.

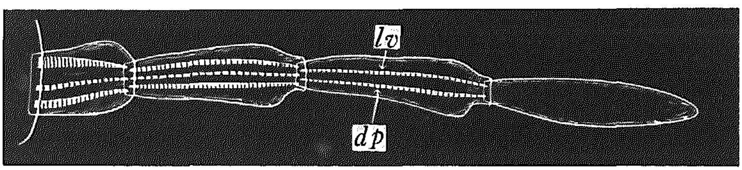
Orchesella villosa: Longitudinal and vertical section through the base of the left antenna and the tentorium, showing the origins of certain of the extrinsic antennal muscles. × 250. *a.b.c.*, extrinsic muscles of group I; *a.n.*, antennary nerve; *a.t.*, anterior arm of tentorium; *dp.*$_2$, depressor of segment II; *d.t.*, dorsal arm of tentorium; *f.g.*, extrinsic muscles of group II; *md.*, mandible; *p.t.*, posterior arm of tentorium.

(7) Flexor of Segment III ($fl._3$).—A corresponding muscle, equally slender and composed of but few fibres, which is inserted ventro-laterally on the outer aspect of the base of segment III.

(8) Depressor of Segment IV (*dp.*$_4$).—A narrow, band-like muscle arising laterally from the base of segment III and inserted ventrally into the base of segment IV.

(9) Levator of Segment IV (*lv.*$_4$).—A very short but conspicuous band of muscle which arises on the dorsal aspect of segment III, about one-quarter of the length of that segment from its apex. Extending obliquely downwards, it is inserted ventro-laterally on the base of segment IV.

The Antennal Muscles of other Collembola.—While, as has been previously mentioned, there are considerable

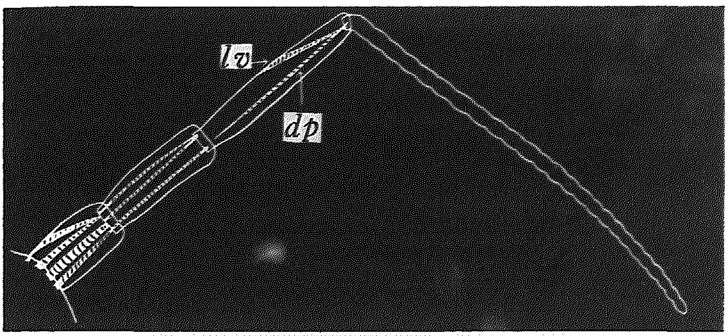


TEXT-FIG. 13.

Isotomurus palustris: antenna viewed with polarized light, showing intrinsic musculature. × 175. *dp.*, depressor, and *lv.*, levator of segment IV.

differences in the number and relationships of the extrinsic muscles among different genera of Collembola, the intrinsic muscles appear to be tolerably uniform. In the four genera examined, belonging to three different families, the most notable difference is in connexion with the levator muscle of segment IV (Text-figs. 13 and 14). In Isotomurus palustris and Podura aquatica this muscle has its origin on the dorsal aspect of the base of segment III. It traverses the whole length of segment III and is inserted on the base of segment IV. In Sminthurus viridis its origin takes place about the middle of segment III (Text-fig. 14) while, as already described in Orchesella, this muscle is still further shortened since it arises within the apical one-fourth of segment III. There is, therefore, a graded series in the shifting forward of the point of origin of the levator muscle of segment IV and in its consequent shortening in the species of Collembola mentioned.

It is noteworthy that in certain genera of Collembola an apparent initial stage in the development of the annulated type of antenna is present. Thus, in many of the Sminthuridae, together with such genera as Tomocerus and Orchesella, the terminal segment, and sometimes the penultimate segment



TEXT-FIG. 14.

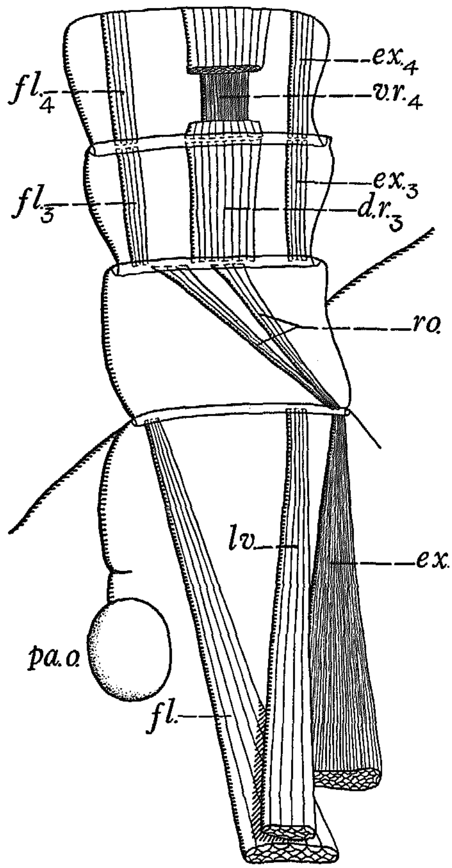
Sminthurus viridis: antenna viewed with polarized light, showing intrinsic musculature. × 170. *dp.*, depressor, and *lv.*, levator of segment IV.

also, is definitely annulated owing to the presence of numerous ring-like divisions.

Symphyla (Text-fig. 15).

In this subclass the species examined were Hanseniella capensis (Hans.) and Scutigerella immaculata (Newp.). No significant differences in the antennal musculature were observed in these examples and the account which follows is based upon observations made on Scutigerella. Indebtedness is here expressed to Dr. S. M. Manton for several well-preserved examples of Hanseniella from Cape Colony. As regards Scutigerella, its scarcity around Cambridge in 1937 made it necessary to obtain material from another district. A number of examples collected in glasshouses at Cheshunt (Herts.) were kindly sent to me by Mr. E. R. Speyer.

A survey of all the literature bearing upon the Symphyla reveals the complete absence of any description of the antennal musculature in the group: an incidental reference to the presence



TEXT-FIG. 15.

Scutigerella immaculata: base of left antenna, dorsal aspect. × 500. *d.r.*$_3$, dorsal retractor of segment III; *ex.*, extensor of the antenna; *ex.*$_3$, *ex.*$_4$, extensors of segments III and IV; *fl.*, flexor of the antenna; *fl.*$_3$, *fl.*$_4$, flexors of segments III and IV; *lv.*, levator of the antenna; *pa.o.*, post-antennal organ; *ro.*, rotator; *v.r.*$_4$, ventral retractor of segment IV.

of segmental muscles is made by Verhoeff in his account of the Symphyla in Bronn's 'Tierreich' (1933).

a. Extrinsic Muscles.

The extrinsic muscles are divisible into a dorsal and a ventral series. The dorsal muscles are two in number on either side and lie above the antennal nerve.

Levator of the Antenna (*lv.*).—A long slender muscle which arises, in close association with its fellow of the opposite side, near to the median line, from the hinder part of the roof of the head-capsule. It passes forwards, and somewhat outwards, in the horizontal plane and becomes inserted on the dorsal aspect of the base of the first segment of the antenna.

Flexor of the Antenna (*fl.*).—This long and slender muscle arises in close association with the levator of its side. It passes forwards and outwards in a slightly lower plane than the levator, which crosses it proximally, and is inserted on the outer aspect of the base of the first segment of the antenna.

The ventral muscles are three in number and are situated below the antennal nerve.

Extensor of the Antenna (*ex.*).—A rather broad muscle which arises from the posterior region of the floor of the head. It passes directly forwards and is inserted ventrally on the inner aspect of the basal segment of the antenna.

Depressors of the Antenna.—These are two muscles which arise, in close association, just to one side of the median line on the transverse apodeme of the cranium and behind the origin of the extensor muscle. They pass forwards and have two separate points of insertion which are located close together on the ventral border of the basal segment of the antenna.

These muscles are termed depressors with some reservation; but, since their insertions are internal to that of the extensor muscle of the same side, their contraction would most likely have the effect of pulling the antenna downwards.

It is noteworthy that while the flexor and levator muscles are located dorsally to the antennal nerves they are overhung by the proto-cerebral lobes of the brain. A deep sinus or space between the proto- and deuto-cerebral lobes is traversed by these two muscles.

β. Intrinsic Muscles.

Rotator of the Antenna (*ro.*).—A slender dorsal muscle which has a narrow point of origin on the inner aspect of the base of the first antennal segment. It extends obliquely outwards and forwards, dividing into two distally separated bundles. These bundles have separate points of insertion on the dorsal aspect of the basal margin of the second segment of the antenna.

The contraction of this muscle apparently has the effect of rotating the antenna, the basal segment of the latter functioning as a pivot for that purpose. The absence of the usual segmental muscles from this segment appears to be in correlation with the function suggested.

Within the second segment and each segment which follows, up to and including the penultimate segment there, are four muscles. These muscles differ but little from segment to segment with the exception that they become less pronounced in their development as the apex of the antenna is approached. These segmental muscles, as exemplified by those in connexion with the second and third and third and fourth antennal segments, are as follows:

Dorsal Retractors (*d.r.*$_3$).—These are broad median dorsal longitudinal muscles.

Ventral retractors (*v.r.*$_4$).—Each is a median ventral longitudinal muscle of slightly smaller calibre than its dorsal counterpart.

Flexors (*fl.*$_3$, *fl.*$_4$).—Longitudinal muscles situated towards the outer border of each segment.

Extensors (*ex.*$_3$, *ex.*$_4$).—Corresponding muscles to the flexors and located towards the inner border of the segments.

The above muscles have their origins at the base of a segment, and their insertions are in corresponding positions on the base of the segment which immediately follows and whose movements they effect.

CHILOPODA.

Representatives of the three main divisions of the Chilopoda were examined in connexion with the present work, viz. Anamorpha—Lithobius forficatus, numerous examples from Cambridge; Epimorpha—Cryptops hortensis Leach, several specimens, Cambridge; Schizotarsia—

Scutigera longicornis F., two examples collected by myself at Allahabad, India, a number of years ago, and several specimens from the Malay States in the Cambridge University Museum of Zoology; also a single example of an unidentified species collected in Brazil by Mr. H. E. Hinton, to whom I am indebted for the specimen.

The only study of the antennal musculature in the Chilopoda is the account given by Meinert (1883) of the head of Scolopendra. In this memoir a description of the extrinsic antennal muscles is given. Incidental reference to the antennal musculature of Lithobius is made by Bogdanof (1880), who, in his brief account, figures the antennal flexors, and by Fuhrmann (1921). The last-named writer, in his account of the antennal sensoria of Myriapoda, refers to the presence of segmental antennal muscles. Snodgrass (1928) refers to and figures extrinsic antennal muscles in Scutigera forceps, and remarks that these muscles have their origins on the wall of the head and not on the tentorium as in insects.

a. Lithobius forficatus (Text-figs. 16–18).

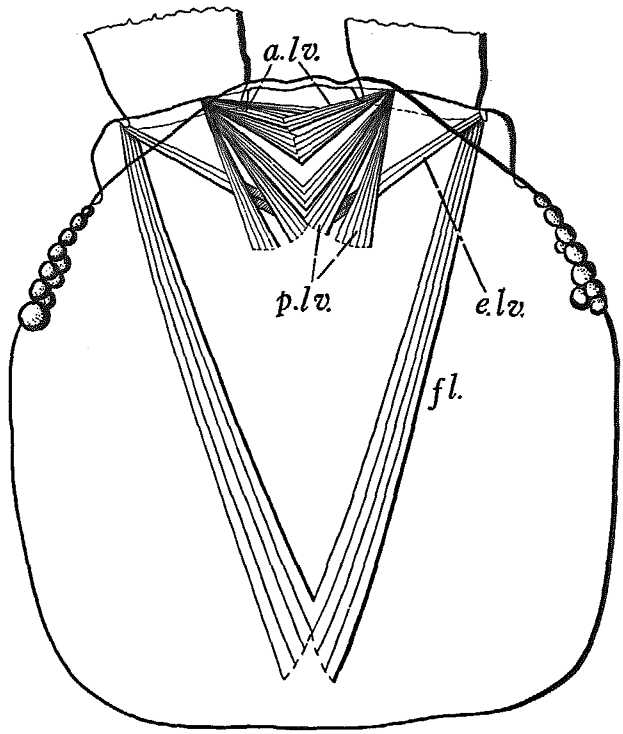
The extrinsic antennal muscles of Lithobius differ considerably from those described by Meinert in Scolopendra. For one thing, Meinert recognizes eleven pairs of these muscles whereas I have only been able to identify with certainty eight pairs in Lithobius. Furthermore, the topographical relations of these muscles show marked differences in the two cases. The relations of the following muscles were determined (Text-figs. 16, 17).

(1) Flexor (*fl.*).—A powerful muscle composed of at least six distinct bundles of fibres. It arises, in close association with its fellow, from the roof of the cranium behind the brain and near the hind margin of the head. Passing obliquely downwards and outwards it is inserted on the outer border of the base of the first segment of the antenna. The two flexors correspond with the adductores antennarium perlongi of Meinert in Scolopendra.

(2) Anterior levator (*a.lv.*) is a fan-like muscle which arises from the dorsal wall of the head in front of the brain.

Its fibres pass downwards and converge to become inserted dorsally on the base of the first segment of the antenna.

(3) Posterior levator (*p.lv.*) is a larger muscle than the



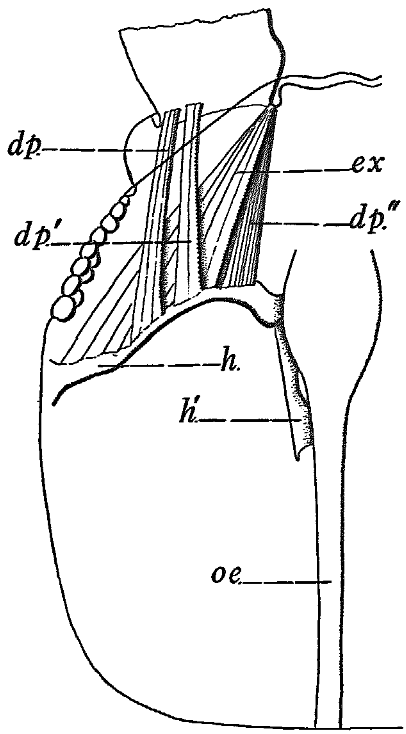
TEXT-FIG. 16.

Dorsal extrinsic antennal muscles of Lithobius forficatus. × 32. *a.lv.*, anterior levator; *e.lv.*, external levator; *fl.*, flexor; *p.lv.*, posterior levator.

anterior levator and consists of more numerous bundles of fibres. It arises just above the brain, and its insertion is in common with that of the anterior levator.

(4) External Levator (*e.lv.*) is a slender dorsal muscle composed of two bundles of fibres. It arises, in close contact with its fellow of the opposite side, from the roof of the cranium immediately in front of the brain. Extending outwards, and

somewhat downwards, it is inserted on the outer border of the base of the first segment of the antenna. Its insertion is in connexion with that of the flexor muscle and is dorsal to it.



TEXT-FIG. 17.

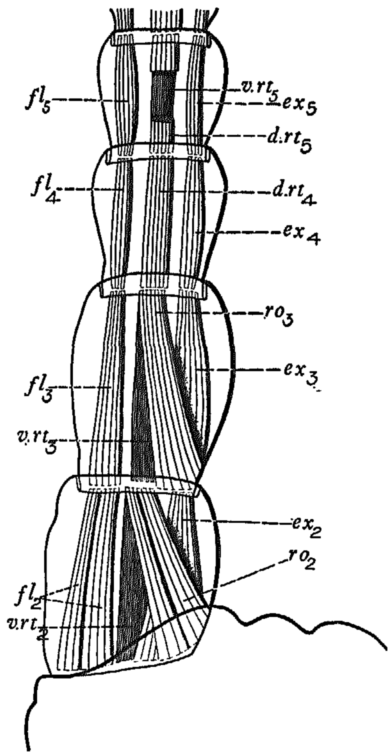
Dissection of head of Lithobius forficatus, showing the more deeply seated extrinsic antennal muscles of the left side. × 32. *dp.*, *dp'*, *dp"*, outer, middle, and inner depressors; *ex.*, extensor; *h.*, suspensorial bar or plate of the hypopharynx; *h'*, hypopharyngeal apophysis; *oe.*, oesophagus.

These levator muscles correspond functionally with the six pairs of reflexors figured by Meinert in Scolopendra.

(5) Extensor (*ex.*).—A large sheet of muscle which has a broad seat of origin on the suspensorial bar or plate (*h.*) of the hypopharynx. It passes obliquely forwards to be inserted

ventrally on the inner margin of the base of the first segment of the antenna.

(6) Outer Depressor (*dp.*).—This muscle arises from the



TEXT-FIG. 18.

Lithobius forficatus; basal segments of left antenna, dorsal aspect. × 32. *d.rt.*, dorsal retractors; *ex.*, extensors; *fl.*, flexors; *ro.*, rotators; *v.rt.*, ventral retractors. The numerals refer to the respective segments of the antenna.

suspensorial plate of the hypopharynx dorsal to the extensor muscle, and is attached ventrally to the outer margin of the base of the first antennal segment.

(7) Middle Depressor (*dp′.*).—The origin of this muscle is from the suspensorial plate of the hyphopharynx further in-

wards than that of the outer depressor. Its insertion is on the ventral wall of the base of the first segment of the antenna.

(8) Inner Depressor (*dp''.*).—A stout muscle arising from the apex of the bend of the suspensorial plate of the hypopharynx. Its insertion is beneath, but in close association with, that of the extensor muscle.

The above depressor muscles evidently correspond in part with adductores parvi, absconditi, and inferiores of Meinert. While they may function to some extent as 'adductors' or flexors their relations appear to indicate that they mainly operate as depressors.

The intrinsic muscles of Lithobius are arranged on a generalized and relatively simple plan (Text-fig. 18). There are four muscles in each segment of the antenna, and these have their origins on the base of that segment. In the scape, or first segment of the antenna, the following muscles are present.

1. Dorsal Oblique or Rotator of Segment II (*ro.2*).—This muscle is composed of several bundles, and has a broad seat of origin on the inner aspect of the base of the scape. It passes forwards somewhat obliquely, and is inserted on to the base of the second segment of the antenna in the mid-dorsal line. This muscle, which is evidently homologous with the dorsal retractor of the segments which follow, appears to function as a rotator.

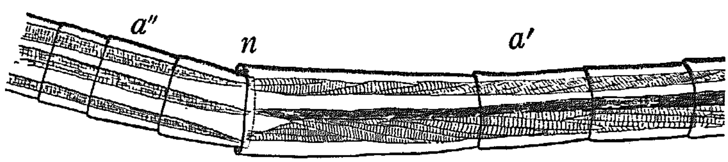
2. Extensor of Segment II (*ex.2*),—A muscle composed of a number of distinct and separated bundles of fibres which are disposed in two groups with a dorsal and ventral origin respectively. The fibres of both groups converge, and have a common insertion on the inner aspect of the base of the second segment of the antenna.

3. Flexor of Segment II (*fl.2*).—This muscle is similarly composed of a number of bundles: it has a broad base of origin on the outer margin of the base of the scape.

4. Ventral Retractor of Segment II (*v.rt.2*).—This muscle is located along the median line of the floor of its segment.

In the second segment of the antenna the arrangement of the muscles is essentially similar to that of the scape (Text-fig. 18).

In the third and following segments there are four clearly defined segmental muscles each composed of several bundles. These muscles are a flexor (*fl.4*) and extensor (*ex.4*), a dorsal retractor (*d.rt.4*), and a ventral retractor (*v.rt.4*). This disposition is continued into the penultimate segment. The muscles which have their origins in the last-named segment are concerned with the movement of the apex of the antenna.



TEXT-FIG. 19.

Scutigera longicornis: portion of left antenna, in the region of the first nodus, showing intrinsic muscles. × 40. *a′*, *a″*, first and second series of annuli with 'nodus', *n*.

b. Scutigera longicornis (Text-fig. 19).

Scutigera longicornis, like other members of the Schizotarsia, has extremely elongated, filiform antennae, which are composed of a two-segmented peduncle, or scape, and a flagellum made up of 300 or more annuli. The antenna is divisible into three regions, each region being demarcated by a joint or 'nodus' and composed of annuli of progressively smaller calibre. The antenna is moved, as a whole, by extrinsic muscles which arise from the head capsule and are attached to the base of the peduncle. The flagellum is capable of a wide range of movement which is effected by a remarkable series of longitudinal intrinsic muscles. These muscles are coincident with almost the whole length of the appendage. The first region of the antenna (i.e. up to the first 'nodus') comprises, in the specimens examined, between 54 and 64 annuli. It is traversed by a prominent dorsal or levator muscle which arises within the peduncle and is attached to the basal annulus of the second region. Two lateral muscles—i.e. a flexor and an extensor—take their origins, not from the peduncle, but from the distal half of the first region of the antenna. They are likewise attached to the basal annulus of the second region. Each of the two succeeding regions of the antenna is traversed by a similar series of longitudinal muscles and those of the third region become extremely attenuated towards the apex of the appendage. When an antenna is cleared in cedar wood oil and examined under polarized light, each muscle is seen to be largely composed of a number of closely arranged oblique bundles of fibres.

Diplopoda (Text-fig. 20).

The only description known to me of the antennal musculature of a Diplopod is by Silvestri (1903) in his memoir on the anatomy of the subclass. In this work a brief account is given of the extrinsic and intrinsic antennal muscles in the species Plusioporus salvadorii (Spirostreptidae).

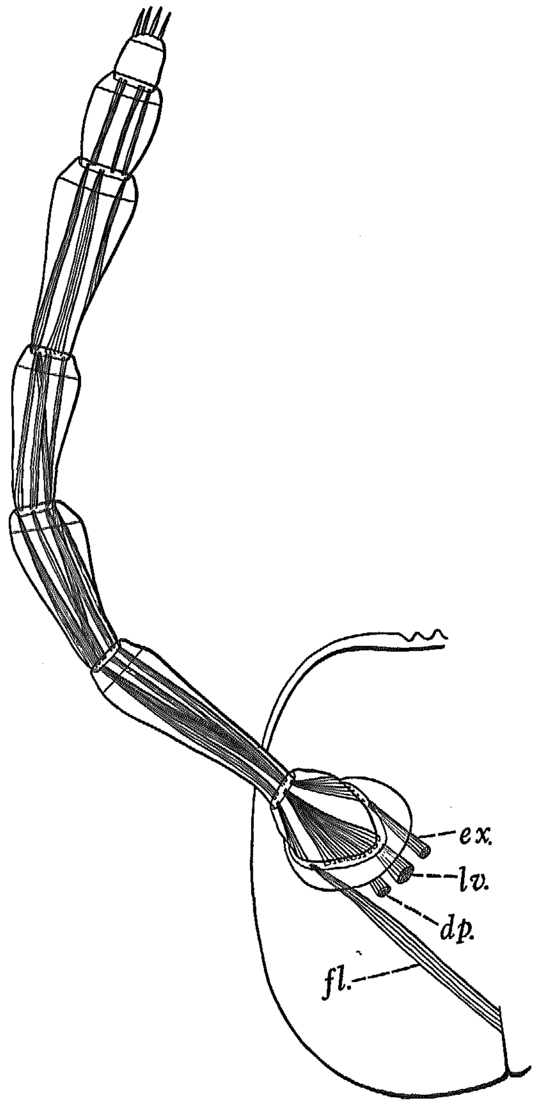
The species investigated in connexion with the present work belong to the family Julidae. They are Cylindroiulus punctatus (Leach) and Ophyiulus pilosus (Nwpt.) for whose identification I am indebted to Dr. S. G. Brade-Birks. Since there are no evident differences of importance in the musculature of these two species the description is confined to Cylindroiulus punctatus. This species is common and readily found between the bark and wood of decaying trees. The antennal musculature in the Julidae shows the same general plan of arrangement as described by Silvestri in Plusioporus.

The extrinsic muscles are four in number, as follows:

1. Flexor (*fl.*).—This muscle arises from an inflexion of the median suture of the vertex at its anterior end and is inserted post-axially on to the base of the scape of the antenna. It is the same muscle as is termed by Silvestri the abductor.

2. Extensor (*ex.*).—It arises from the transverse bar or arm of the tentorium of its side and is inserted on the pre-axial border of the base of the scape. It represents the adductor of Silvestri.

3. Levator (*lv.*).—It has its origin in close association with that of the extensor muscle, and is inserted on the dorsal margin of the base of the scape.



TEXT-FIG. 20.

Cylindroiulus punctatus: dorso-lateral view of left antenna, showing the musculature. × 60. *dp.*, depressor; *ex.*, extensor; *fl.*, flexor; and *lv.*, levator muscles of the antenna.

4. Depressor (*dp.*).—This muscle originates as the transverse bar of the tentorium in close connexion with the origins of the extensor and levator muscles, and has its insertion on the ventral aspect of the base of the scape.

The intrinsic muscles have their origins in the base of each segment of the antenna, while their insertions are on the base of the segment immediately in front. They are composed of four groups of muscle-fibres which function as extensors, flexors, levators, and depressors of segments 2 to 6. Those which originate in the scape have broad bases, and their fibres converge distally to narrow points of insertion. The muscles in the remaining segments are composed of more slender groups of fibres and pursue a longitudinal course. Inserted on to the apical or reduced seventh segment of the antenna are slender muscles which arise from the base of the sixth segment: these muscles apparently function as retractors of segment VII.

PAUROPODA (Text-fig. 21).

Silvestri (1902) describes and figures the antennal musculature in the species Allopauropus brevisetus Silv. He recognizes the following pairs of muscles: the names given in brackets are those used by this author.

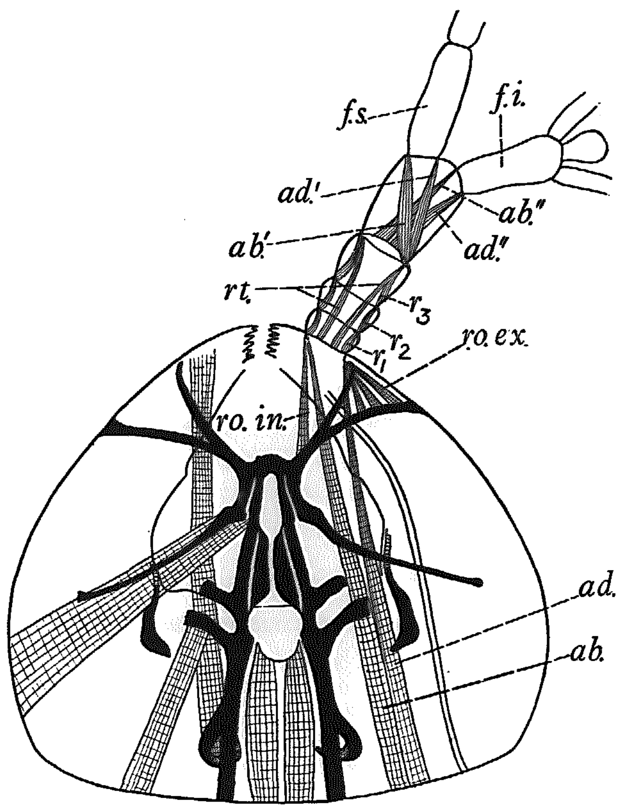
a. Extrinsic Muscles.

Flexors (*ab.*, abductores antennarum).—These arise from the dorso-posterior region of the head-capsule, and are attached post-axially to the base of the first segment of the antenna.

Extensors (*ad.*, adductores antennarum).—The origins of these muscles are in close association with those of the flexors, and their insertions are on the pre-axial border of the base of the first segment of the antenna.

External Rotators (*ro.ex.*, rotatores antennarum externi).—These muscles have their origins on the anterior external arms of the endoskeleton, and they are inserted superiorly on the post-axial border of the first antennal segment.

Internal Rotators (*ro.in.*, rotatores antennarum interni).—The origins of these muscles are on the anterior arms



TEXT-FIG. 21.

Allopauropus brevisetus, antennal musculature from the ventral aspect. Adapted from Silvestri. *ab.*, extensor of antenna; *ad.*, flexor of antenna; $r._1$, $r._2$, $r._3$, retractors of segments II, III, and IV; *ro.ex.*, external rotator of antenna; *ro.in.*, internal rotator of antenna; *rt.*, rotator of segment IV; *ab'*, *ad'*, extensor and flexor of superior ramus; *f.s.*, *ab''*, *ad''*, extensor and flexor of inferior ramus, *f.i.* (The endoskeleton is represented in deep black.)

of the endoskeleton, and their insertions are superiorly on the pre-axial margin of the first antennal segment.

β. Intrinsic Muscles.

Retractors (r_1–r_3, retractores antennarum articuli singuli).

These arise from the base of a segment and are inserted into the base of the segment immediately in front.

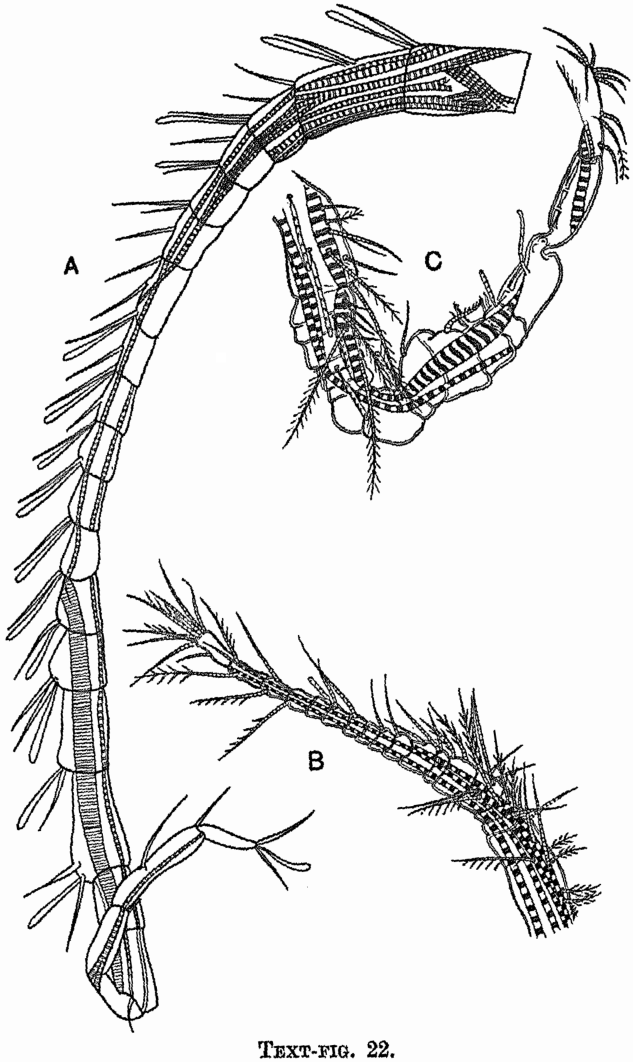
Rotators of Segment IV (*rt.*, rotatores articuli quarti).—They arise from the head capsule and are attached to the proximal border of segment IV.

Flexors and Extensors of the Rami (*ad′*, *ad″*, *ab′*, *ab″*, abductor and adductor flagelli).—There is a pair of these muscles in each ramus (*fi.*, *fs.*) of the antenna. They arise from the base of the fourth segment of the antenna, and are inserted on the post- and pre-axial margins respectively of the antennal rami.

Crustacea.

The first antennae, and also the second antennae, were examined in the following Crustacea: Branchiopoda—Chirocephalus, Daphnia; Ostracoda—Cypridae; Copepoda—Calanus, Neocalanus, Eucalanus, Euaugraptilus, Cyclops; Leptostraca—Nebalia; Stomatopoda—Squilla; Syncarida—Anaspides; Pericarida—Mysis, Diastylis, Tanais, Asellus, Gammarus; Eucarida—Potamobius (Astacus), Crangon, Cancer, Eupagurus. Also a number of the leading illustrated memoirs and monographs were consulted.

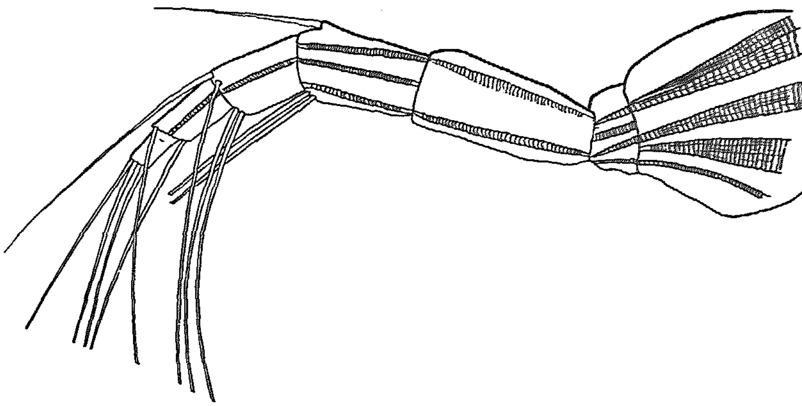
Among the lower Crustacea first antennae, of a presumably primitive type, are present in the Copepoda and Ostracoda. In both of these subclasses the first antennae, in the more generalized families, show clear differentiation into segments with well-developed intrinsic muscles. In the Copepoda the 25-segmented appendage of the Gymnoploea (Text-fig. 22) represents, according to Calman (1909), the primitive arrangement for that group while other types of first antennae have been derived from it by segment reduction. Several genera of the family Calanidae, including Neocalanus, Eucalanus, and Euaugraptilus were examined in specimens kindly provided by Dr. Seymour Sewell, F.R.S. In each case there were found to be only relatively slight differences in the musculature of the first antennae. Each segment, excepting the apical component, is provided with an intrinsic musculature.



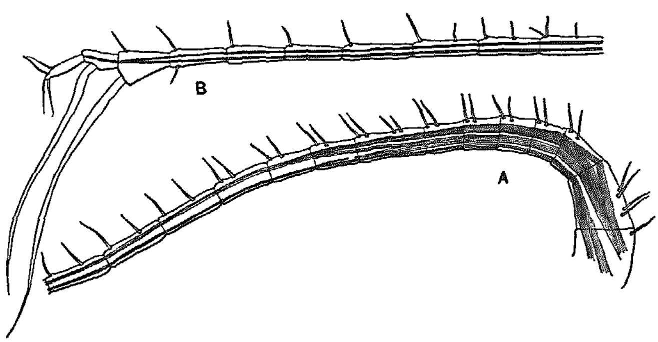
TEXT-FIG. 22.

First antenna of Copepoda. A, *Halitemora longicornis*, right. × 160. After Giesbrecht. B, *Cyclops brevicornis* ♀, right. After Hartog. C, *Clycops brevicornis*, ♂, right. After Hartog.

In the larger or proximal segments the muscles are grouped more or less in a circular zone or ring in each segment. In the



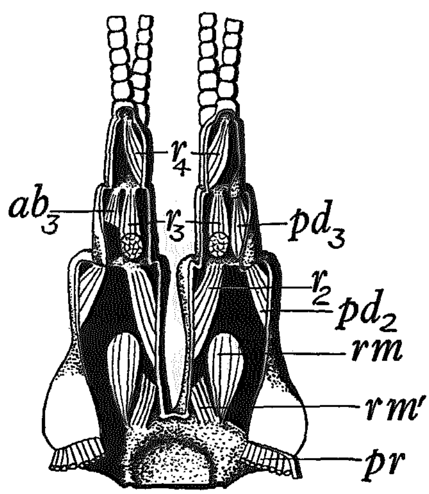
TEXT-FIG. 23.
Left first antenna of an unnamed species of Cypridae (Ostracoda), showing the intrinsic musculature.



TEXT-FIG. 24.
A, proximal, and B, distal halves of left first antenna of the Copepod, Neocalanus robustior Giesb. ♀, showing the intrinsic musculature. × 80.

middle and distal regions of the appendage the musculature is reduced and, in each segment, only a single pair of muscles is present (Text-fig. 24). In Cyclops and other genera of Copepoda, where there is marked sexual dimorphism in the first antennae, the number of individual segments is reduced. The intrinsic musculature likewise has undergone specialization and, in particular, in the geniculate first antennae of the males (Text-fig. 24 c).

In the Ostracoda the first antennae have fewer segments than in the Copepoda, the maximum number, according to Calman, being eight. Intrinsic segmental muscles are clearly evident, however, as is shown in Text-fig. 23. In the other classes of the



TEXT-FIG. 25.

First antennae of Potamobius astacus, dorsal aspect, showing musculature. Adapted from Schmidt. *Ab.*$_3$, abductor of segment III; *pd.*$_2$, *pd.*$_3$, productors of segments II and III; *pr.*, promotor of antenna; *r.*$_2$, *r.*$_3$, reductors of segments II and III; r_4, reductor of dorsal flagellum; *rm.*, *rm'*, remotors of antenna.

so-called 'Entomostraca' the first antennae are either much reduced and modified or wanting altogether. In the Branchiopoda, it may be mentioned, these appendages are evident in such forms as Chirocephalus, but are obviously degenerate and are devoid of segmentation. On the other hand, they have developed an imperfect annulation and have retained some of the original intrinsic musculature.

The second antennae, and other of the biramous appendages, in the more generalized groups of the 'Entomostraca' show well-developed intrinsic muscles not only in the protopodite but also in the segments of the exopodite and the endopodite. These muscles are clearly evident in the Copepoda, and are shown in many of the illustrations in Giesbrecht's memoir (1881), and also in the second antennae of Daphnia (vide Binder, 1931).

It is well known that throughout the Malacostraca the typical form of first antenna is an appendage with a 3-segmented peduncle bearing a pair of annulated flagelliform rami; or less frequently a single flagellum as in Nebalia. Representatives of the main divisions of the Malacostraca were examined, and in all cases intrinsic muscles were found only in connexion with the segments of the peduncle. The same applies to the second antennae whether the peduncle be composed of two or as many as six segments. Since these muscles have been studied in detail by Schmidt (1915) in Potamobius (Astacus), by Berkeley (1928) in Pandalus, and by Wetzel (1937) in Caprella, no further account is needed here. The movements of the flagella in both pairs of antennae are effected by muscles whose origins are in the distal segment of the peduncle (Text-fig. 25).

Discussion.

It will be evident from the foregoing account that there are two prevalent types of first antennae among the Arthropoda. They may be conveniently referred to as segmented antennae and annulated antennae, as the case may be.

Segmented Antennae are composed of a variable number of elements or segments, each having its intrinsic musculature. This kind of antenna is typical of the Chilopoda, Diplopoda, Pauropoda, Symphyla, Collembola, and Thysanura Entognatha, besides occurring in many of the Copepoda and Ostracoda among Crustacea. It is, therefore, the prevalent type of antenna among the lower Arthropoda. In the search for food, or security, or for maintaining relations with individuals of their own kind; these animals are primarily concerned with the perception of stimuli in their immediate vicinity. The antennal sensoria are of a simple kind and mainly consist of organs of the trichoid type. Specialized sensoria, so abundant on the antennae of many pterygote Insecta, for example, are either almost entirely wanting or are relatively few in number.

In their simplest development the segmental muscles of the arthropod first antenna are disposed more or less in a ring-like series around each segment. Functionally these muscles act as levators, depressors, flexors, extensors, and retractors. In all the groups of Arthropoda wherein this segmented type of antenna prevails the musculature of that appendage is derivable with greater or lesser modification from this generalized condition.

The presence of true segmented antennae in the Thysanura Entognatha is a hitherto unknown feature of considerable phylogenetic significance. In the first place it provides additional data in support of the contention that the entognath Thysanura represent a separate order of insects, entirely distinct from the Thysanura Ectognatha. In their antennal structure and musculature the last-named group exhibits characters which ally them more closely with the Insecta Pterygota. The second noteworthy feature is that the presence of segmented antennae in the entognath Thysanura provides still another character found also in the Symphyla and, consequently, lends additional support to the Symphylan theory of insect descent (Imms, 1936; Calman, 1936).

Annulated Antennae are composed of a peduncle, or protopodite, consisting of from one to four segments, each with its intrinsic musculature: distally the peduncle carries an elongated flagellum, or a pair of flagella, devoid of intrinsic muscles, and whose movements are effected by muscles originating in the peduncle. The separate components of the flagellum may be termed annuli (or 'flagellomeres') and they appear to be of a morphological value or category different from the musculated divisions, or segments, of the first-named type of antenna. Annulated first antennae are found throughout the Crustacea Malacostraca, in the Thysanura Ectognatha, and in all the Insecta Pterygota. The essential feature of this type of appendage is the multiannulate flagellum which is only capable of movement as a whole. The antennal nerve is entirely sensory in function and innervates numerous and often highly specialized sensoria which may amount to several thousand on a single appendage. By means of its basal muscles the flagellum is capable of being oriented in any required direction, and is thereby particularly well adapted for testing and exploring the surrounding medium for the perception of stimuli operating from a distance.

There can be little doubt that segmented antennae are the more primitive of the two types of these appendages. An apparently transitional form, between these two types, occurs in the Schizotarsia which possess annulated antennae of a highly specialized kind. These appendages are unique, not only in their extreme length and the great number of annuli present, but more especially owing to the fact that they possess an elaborate series of intrinsic flagellar muscles. The possession of these muscles allows of an exceptional range and flexibility of movement.

While it may be reasonably claimed that the annulated type of antenna is a derivative of the segmented appendage, it is noteworthy that the absence of intrinsic muscles, in the flagellum of the first-named organ, appears to be irreversible in the sense that such muscles are never re-acquired. No instance is known to me throughout the Insecta Pterygota and the Crustacea Malacostraca of the retention or the re-acquisition of the intrinsic muscles in the antennal flagellum. Facts of this kind have a direct bearing upon the generalization known as Dollo's 'Law'. On the basis of extensive data, drawn from both vertebrates and invertebrates, Dollo concluded that while evolution is reversible, in the sense that organs and structures that have developed may become lost, it is, on the other hand, irreversible in the sense that such organs or structures, once they have become lost, are never regained or regenerated. The loss of the intrinsic muscles in the flagellum of the annulated type of antenna affords, therefore, direct support to Dollo's contention.[1]

The factor or factors which have brought about the loss of the segmented type of antenna among the most highly evolved of

[1] Evidence of a biochemical and physiological character which confirms Dollo's Law has recently been assembled by Needham (1938).

the Arthropoda are obscure. The primary changes have been the loss of the intrinsic musculature, together with the motor fibres of the main antennary nerve, and the development of an appendage whose component parts or annuli are individually immovable.

Summary of Conclusions.

The first antennae of arthropods are divisible into two main types, viz. (1) segmented antennae and (2) annulated antennae. In the first type the antenna consists of a variable number of segments, each having intrinsic musculature. The antennae of the Chilopoda, Diplopoda, Pauropoda, Symphyla, Collembola, and Thysanura Entognatha all pertain to this type; also, the first antennae of many Copepoda and Ostracoda.

In the second type the antenna consists of a peduncle or protopodite composed of one or more segments, each with intrinsic musculature. Distally it bears an annulated flagellum, or a pair of flagella, devoid of intrinsic muscles and whose movements are effected by muscles originating within the peduncle. The first antennae of the Crustacea Malacostraca and the antennae of the Thysanura Ectognatha and of all the Insecta Pterygota belong to this type.

The greatly elongated antennae of the Schizotarsia are intermediate between these two types. They are composed of an immense number of small annuli and an elaborate intrinsic musculature is present, thus allowing these appendages a wide range and flexibility of movement.

The absence of intrinsic muscles in the antennal flagellum throughout the Insecta Pterygota and the Malacostraca appears to be irreversible in the sense that such muscles are never re-acquired. It thus lends support to the generalization known as Dollo's Law.

The presence of segmented antennae in the Thysanura Entognatha affords additional evidence in support of the Symphylan theory of the ancestry of insects.

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