MANDIBULAR MECHANISMS AND THE EVOLUTION OF ARTHROPODS

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[Plate 1]

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(1) A functional and comparative study has been made of the jaw mechanisms of representatives of the major classes of arthropods, covering, where appropriate, the whole endoskeletal systems of the head and the form and function of other mouth parts, hypopharynx, etc.

(2) Mandibles are developed embryologically, and presumably phylogenetically also, in one or other of two ways. Type A, in which the biting structures are developed from a proximal endite or gnathobase (Crustacea, Chelicerata), and type B, in which the mandible is developed from a whole limb, the tip of which and not the base is used for gnathal purposes (Onychophora, Myriapoda, Hexapoda).

(3) Two types of movement typical of the more primitive ambulatory trunk limbs have been exploited in mandibular evolution. Type I mandibular movement uses the promotor-remotor swing of an ambulatory or swimming coxa on the body, but the axis of swing may be shifted in various ways (Crustacea, Thysanura), and type II mandibular movement uses the prehensile action in the transverse plane of a coxa or coxa and telopodite. Type II is found in Myriapoda, where segmentation of the whole-limb mandible is essential, and direct transverse gnathobasic biting is employed by *Limulus*. Mandibles of types I and II appear to have evolved independently in the named examples.

(4) The more primitive examples of type II mandibles suit fine food feeding and the scratching of food surfaces. The gape is small, biting, if any, is weak, and added hydraulic efficiencies enable fine particles to be sucked up by terrestrial types (*Chirocephalus*, *Hemimysis*, *Paranaspides*, *Petrobius*).

(5) Biting in the transverse plane is not a primitive attribute of the Arthropoda outside the Chelicerata and certain Myriapoda. In the more primitive Crustacea and Hexapoda transverse biting is absent and there is little basic adduction and abduction. Transverse muscles primarily serve promotor-remotor rolling movements. No example has been found of a so-called monocondylic mandible of a crustacean or of a hexapod which exhibits freedom of movement in all directions

from this point and a basic power of transverse adduction, whether or not the mandible possesses a formed dorsal articulation.

(6) Strong biting in the transverse plane suiting hard or large food is a repeated end term in arthropodan evolution. The examples considered are: some Decapoda, Peracarida, Pterygota, Diplopoda and Symphyla. Adduction in the transverse plane is mechanically simple, but abduction presents great problems, hitherto not appreciated, which have had to be resolved by every group of animals attempting to evolve such mandibles. The resolutions of the difficulty are various, mutually exclusive, and independently evolved by mandibles of all types.

(7) The feeding mechanism of *Limulus* is described. The jaw mechanisms of *Limulus* and of Crustacea are fundamentally different and have probably been evolved in independence.

(8) The validity of the evidence for the existence of a pre-coxal segment in Xiphosura needs reconsideration.

(9) The rolling whole-limb mandibles of *Petrobius* are not far removed from a central type which could have given rise to the various mandibles occurring throughout the Hexapoda. It is shown in some detail how this mechanism is parallel to but different from that of the rolling gnathobasic mandibles of the more primitive Crustacea. Differences between the mandibles of Hexapoda and Crustacea concern mandibular form, musculature, movement and derivation; the head endoskeleton, and the form and movements of maxilla 1 are also different. The superficial resemblances are considered to be due to convergence between mandibles of unlike origin which utilize the same type of movement of an ambulatory limb.

(10) Present-day animals show how the *Petrobius*-type of jaw mechanism could have given rise to (i) the strong transverse biting of the Lepismatidae and Pterygota with loss of hydraulic efficiency of the *Petrobius* type and to (ii) a further development of the rolling movement, together with protrusibility of mandibles, which has been made possible by entognathy in the Apterygota. These two trends are mutually exclusive.

(11) Entognathy is a condition permitting great proximal mobility of the mandible and hence confers the powers of mandibular protrusion which are absent in strong closely articulated mandibles. Entognathy in essentially similar form, but differing in details, has been evolved in Onychophora, Chilopoda, Pauropoda, Collembola, Diplura and Protura. The 'Entognatha' is not considered to be a valid taxonomic group but one of convergence.

(12) A basic pattern of: mandibular structure, musculature, movements, associated head endoskeleton, and of the structure and movements of maxilla 1 is recognizable throughout the less specialized Pterygota, Thysanura, Collembola and Diplura, so linking these groups together by characters having nothing to do with the possession of three pairs of legs. This basic pattern of mandible and maxilla 1 is not found in the Myriapoda.

(13) A unified system of skeletal tendons and apodemes exists within the Arthropoda which has hitherto been imperfectly described. Anterior and posterior tentorial apodemes are present throughout the less specialized of the Hexapoda in essentially similar form. The segmental tendon system, present embryologically in all body segments in many animals, occurs in the adult hexapod head except where strong transverse biting has been evolved, and its presence then is consequently not required. Hexapod-like tentorial apodemes are absent in Crustacea, but homologous anterior tentorial apodemes are present in Myriapoda where their mobility is enhanced. Rigidity of tentorial apodemes is found in hexapods where strong transverse biting has been evolved (Pterygota).

(14) The details of the feeding mechanism of a chilopod are described. The mandibular mechanism has clearly been derived from the same basic transversely moving mandibles of the type seen in Diplopoda and Symphyla, but modified by the development of entognathy to give a highly specialized mechanism suiting carnivorous feeding and crevice living, and not found in any other group.

(15) The Chilopoda, Diplopoda and Symphyla all appear to have obtained direct transverse biting without any preliminary rolling mandible such as seen in Thysanura, but segmentation of their mandibles is essential. All have used the mobility of the anterior tentorial apodemes to provide (Diplopoda) or enhance (Symphyla and Chilopoda) the abductor force which opens the jaws. The differences between the mandibular mechanisms of Chilopoda, Diplopoda and Symphyla indicate independent evolution from a common type and no one of these three classes could readily give rise to the mandibular mechanisms present in either of the other two. The term Myriapoda,

indicating affinity between Chilopoda, Diplopoda, Symphyla and Pauropoda deserves to be reinstated.

(16) The symphylan mandibular mechanism, together with the structure and use of maxilla 1, the mobility of the anterior tentorial apodeme, and the presence of the myriapodan maxilla 1 salivary gland, are so entirely opposed both to the thysanuran condition and to the directions of evolutionary change seen in the Pterygota and entognathous Apterygota (whose basis appears to lie in the Thysanura) as to make the symphylan theory of insect origin untenable.

(17) It is concluded that jaws have evolved independently in (i) the Chelicerata, (ii) the Crustacea and (iii) the Onychophora–Myriapoda–Hexapoda series. Within the latter the jaws in the Onychophora must have evolved very early, before much cephalization had taken place. The mandibular mechanisms of the Myriapoda and Hexapoda are so different as to indicate that there can be no close connexion between these two groups of classes apart from a very distant common origin. The parallel evolution of jaws in arthropods must date from the earliest differentiation of the major classes. The Mandibulata cannot be regarded as a related group, but the term may serve to indicate a Grade of advancement. The bearing of these results on taxonomic systems is discussed.

1. Introduction

Habits of life, 'which have not been directly imposed by any properties of the environment, may persist for very long periods' (Watson 1949). Such habits have been shown to have been of paramount importance in the evolutionary divergence of large taxonomic categories of animals as far removed from one another as Plesiosauria (Watson 1949) and the Onychophora and myriapodan classes (Manton 1952 to 1961). This generalization is applicable presumably to many other groups of animals. Locomotory and feeding habits, together with behaviour patterns leading to reproduction, are all important both for survival and for evolutionary progress. A substantial start has been made in disclosing the correlations which exist between diagnostic trunk structure of certain classes and orders of land arthropods and the several types of locomotory and burrowing techniques which these animals exercise. This functional interpretation of structure is throwing much light on the probable evolutionary history of these groups of animals (Manton 1950 to 1961 and future parts of the Evolution of Arthropodan Locomotory Mechanisms series). But arthropods can be classified on their head structure alone. Since feeding habits depend in large measure upon head structure, a comparative and functional study of the head with particular reference to jaws is now desirable.

The evidence concerning the monophyletic, di- or polyphyletic derivation of the Arthropoda has been reviewed (Tiegs & Manton 1958). Very brief reference was made to the probable parallel evolution of mandibles within the phylum, and the theory of a monophyletic derivation of the arthropods was rejected. Certain so-called resemblances between the mandibles of various classes and of their supposed modes of action has led to the erection of a taxonomic category, the Mandibulata (Snodgrass 1938 to 1960) comprising the Crustacea, Myriapoda and Insecta. This category has found its way into recent text-books such as Kaestner's *Lehrbuch der Speciellen Zoologie* (1959, Teil 1, 4). A search for fuller evidence concerning the evolution of mandibles has disclosed a surprising absence of essential knowledge of both structure and mode of action of head skeleto-muscular systems in almost every class of arthropods except for certain insects, the 'higher' Malacostraca and Ostracoda.

A functional and comparative study has therefore been made on the jaw mechanisms of a series of animals which have been obtained in the living state and which represent relatively unspecialized members of the classes to which they belong. In addition some specialized Malacostraca are included for comparison both with the less specialized Crustacea and with terrestrial arthropods. The animals considered here are:

Crustacea: *Chirocephalus diaphanus* Prevost, *Paranaspides lacustris* Smith, *Anaspides tasmaniae* Thomson, *Ligia oceanica* Roux, *Astacus fluviatilis* (*Potamobius astacus* L.), *Carcinus meanus* (L.).

Chelicerata: *Tachypleus tridentatus* Leach (dead), *Limulus polyphemus* L.

Thysanura: *Petrobius brevistylis* Carpenter, *Ctenolepisma ciliata* Dufour, *Thermobia domestica* (Packard).

Pterygota: *Locusta migratoria* L.

Onychophora: *Peripatopsis Sedgewicki* Purc.

Collembola: *Tomocerus longicornis* (Müller), *Orchesella villosa* (Geoffroy).

Diplura: *Campodea staphylinus* West.

Diplopoda: *Poratophilus punctatus Attems, Cylindroilus punctatus* Leach.

Symphyla: *Scutigerella immaculata* Newport.

Chilopoda: *Cormocephalus nitidosus* Por, *Scolopendra cingulata* Latrielle, *Scolopendra subspinipes* Leach.

This study does not substantiate 'the essential likeness in structure and musculature of the mandibles in all mandibulate arthropods' (Snodgrass 1950). On the contrary it shows the fundamental differences. Certain jaw mechanisms, which have been considered to be basic, do not work in the manner supposed. It is essential to recognize the mechanical difficulties which have confronted all arthropods during their attainment of biting jaws capable of dealing with hard and large food. These micro-engineering problems have been resolved in different ways by the various classes of arthropods. Sometimes the resolutions show convergent resemblances, superimposed upon different basic morphologies, and, as with locomotory and burrowing mechanisms, the anatomical changes which become associated with each type of resolution of the biting problem become evolutionary one-way streets.

An appreciation of the mode of action of skeleto-muscular systems needs detailed knowledge of anatomy as well as observations on the living animals. Much of the obscurity which envelops jaw mechanisms and many of the erroneous statements which abound in the literature stem from anatomical complexity which is both difficult to apprehend and to portray, and from a lack of reference to living movements. Further errors have been due to the widespread belief in the existence of an elastic force, located in arthrodial membranes between head and limb, being sufficiently strong to promote a recovery swing and to elongate a mass of contracted muscles. When antagonistic muscles have not been recognized, elasticity has been invoked as the agent which reverses the effective movement, for example: the gnathobase of *Limulus*, the anostracan mandible (Snodgrass 1952) and maxilla 1 of *Thermobia* (Chaudonneret 1951, p. 210). Hydrostatic pressure has also been postulated as alone effecting recovery movements of mouth parts when the musculature has been ill assessed, although hydrostatic pressure is sometimes most important in causing limb movements (Cannon 1940, 1947).

In no animal used for the present study have recovery movements of mandibles been found to be caused by cuticular elasticity or by hydrostatic pressure, direct or indirect muscular action being responsible for them in each case. Elasticity of arthrodial membranes is minimal; if it were not so the effective movements of mouth parts, which are promoted by muscles, would be hindered. A few cases exist of elastic forces being of service in the movement of mouth parts, but the elasticity resides in sclerotized scutes and not in arthrodial membranes. In *Ligia*, for example, Jackson (1926) showed how the maxillulary sclerite and the basal sclerite of the maxillule are deformed on the effective stroke and then by their elasticity promote abduction of the inner and outer endites; and Eastham (1955) has demonstrated how elasticity of sclerotized cuticle is utilized in the rolling and unrolling of the butterfly proboscis, and he has also shown the limitations in the service of hydrostatic pressure.

The structural basis of only a few of the jaw mechanisms considered here have been accurately described in the literature and, apart from the higher Crustacea and pterygote insects, no illustrations exist which are sufficient and all embracing enough to enable the reader to grasp the basis of observable movements. And inaccurate descriptions and simplified drawings depicting no functional realities have been copied from one publication to another. Since it is not easy to visualize the large amount of anatomical detail which is needed for an understanding of mandibular mechanisms and of their probable evolution, illustrations have been prepared from the chosen series of animals, which give the detail as accurately and without simplification as the plane of the paper will allow, omissions in the drawings being confined to muscles whose functions lie outside the jaw mechanisms. Where necessary drawings are given at successive levels in the head. The recognition of endoskeletal structures on the figures of the various arthropods is facilitated by the use of blue for segmental tendons and their derivatives and red for the anterior and posterior tentorial apodemes of myriapods and insects. Red is also used to depict the major head apodeme of *Ligia* although it is not homologous with a tentorial apodeme. The use of solid colour on some figures and of coloured stipple on others is a matter of publisher's convenience and has no zoological significance.

Full diagnoses of the muscles seen here for the first time, and revisions of existing descriptions of muscles, will not be given because of their length. Instead the drawings and legends to the figures are intended to provide the requisite data (see pp. 114–183).

2. METHODS

The methods used for elucidating anatomy, namely serial sections stained with Mallory's triple stain or Azan, to differentiate segmental tendons from apodemes and muscles; dissections; 'steaks' prepared in chosen planes with a microtome; and the examination of preparations in benzyl alcohol, with or without the use of polaroids, have already been described (Manton 1961 *b*). Carnivorous aquatic and terrestrial animals, such as Crustacea and scolopendromorph centipedes, are not difficult to observe closely when feeding, but it is necessary to work out the anatomy and musculature first. Herbivores and omnivores are usually less hungry when caught and much more difficult to observe feeding, unless they are filter or continuous feeders. Animals which normally feed in the dark, and many entognathous types in which the head is opaque, are very difficult to watch feeding. Living animals have been confined in various ways for direct observation, sometimes using a right-angled prism in order to obtain a ventral view, and cinematography sometimes has been helpful. Manipulation of anaesthetized or freshly killed animals is useful for ascertaining what movements are and are not possible to the animal.

3. TYPES OF ARTHROPODAN MANDIBLES AND MANDIBULAR MOVEMENTS

Arthropodan mandibles and the corresponding structures in Chelicerata are developed embryologically in two different ways, and their basic movements are of two different kinds.

(i) *Types of mandibular movements*

Arthropodan jaws are used for scratching the surface of food, for squeezing or grinding small particles without biting, for cutting, holding, biting and for piercing. The strongest holding and biting movements in all classes usually take place in the transverse plane and represent end terms in jaw evolution.

Mandibular movements are derivatives of those of walking legs. The backward slicing of the jaws of Peripatus, each moving in opposite phase from its fellow, differs in no essentials from the walking leg movements of Onychophora. Two types of mandibular movement exist:

Type I

The rolling together in unison of paired asymmetrical gnathal surfaces gives a squeezing and grinding action, and movements which are slightly out of phase with one another or asymmetrical enhance the grinding (see also Fryer 1963). Each mandible mainly performs rotatory and counter-rotatory movements about its long axis which is set roughly dorso-ventrally (§§ 5, 8 and 17). The rolling of the mandible resembles in essentials the backward and forward swing of a trunk limb coxa on the body during normal running or swimming, and has probably been directly derived therefrom (§ 7 (i)). This rolling mandibular movement will be referred to as a promotor (abductor)-remotor (adductor) roll. The molar areas may be slightly parted on the promotor roll and squeezed together on the remotor roll, or parts of their surfaces may be in contact throughout the whole cycle. This type of movement occurs in the Branchiopoda, the less specialized Malacostraca, *Petrobius*, etc. (see below).

Type II

The bringing together in the transverse plane of squeezing gnathal surfaces, or of cutting cusps and blades, provides mechanically stronger crushing, gripping or cutting (§§ 10, 12, 19, 24–31). This movement takes place at right angles to the dorso-ventral axis of the promotor (abductor)-remotor (adductor) roll, and will be referred to as a direct or primary abductor-adductor movement. Type II mandibular movements have arisen in two different ways; in Myriapoda and Chelicerata directly from a movement resembling the transverse gripping exercised by paired trunk limbs, and in the more specialized Crustacea and Hexapoda secondarily, by independent modification of the rolling type I movement.

Strongly cutting or crushing mandibles are generally acknowledged to be an evolutionary advance on mandibles capable of weaker movements associated with soft or with fine food feeding. But the feeding mechanisms of present-day fine food feeders are often as advanced and specialized along their own lines as those of any other type of specialized feeder. However, the mandibular movements of fine food feeders often clearly indicate how their mandibles have evolved. A large pair of jaws extending across the whole width of the head provides (1) an extensive gnathal face, (2) large internal and/or marginal surfaces for muscle attachments, (3) the muscles can be as long as head depth and width will allow, long muscles most easily giving large displacements of the hard parts and, (4) if suitably hinged, such mandibles can provide the widest gape. Muscular adduction of such mandibles is easy, but abduction by muscles of a mandible which forms the most lateral part of the head presents difficulties. This problem has faced all evolving 'mandibulates' in their acquisition of the ability to tackle hard or large food. The resolutions are sometimes simple, but are often extremely elaborate; they are varied and mutually exclusive. Ram rods are employed by myriapods which utilize the anterior tentorial apodeme, and sometimes maxilla 1 also, for abducting the mandibles. Direct abductor muscles are used in addition by the Symphyla but at poor mechanical advantage. The simplest resolution of the abductor difficulty, by couples of antagonistic muscles, as in the Pterygota and higher Crustacea, is not primitive but derived from rolling type I mandibles (§§ 10 to 13, and 19 to 21).

(ii) *Types of mandibular structure*

Although the diversity of form of arthropodan mandibles is very great their basic morphology is of two types.

Type A

The present-day series of mandibles of larval and of adult Crustacea shows the unquestionable derivation of the mandible in this class from the proximal endite or gnathobase and the proximal part of the coxa, the distal telopodite in the adult being reduced to a bi- or a uniramous palp, or absent. Biting is similarly done by the leg base in *Limulus* and in the Arachnida and the embryonic derivation is the same.

Type B

In the Onychophora–Myriapoda–Hexapoda assemblage the mandible, on the contrary, is formed from the whole of an embryonic limb. In the Onychophora even the two terminal jaw blades resemble the two claws on each walking leg. The unsegmented mandibles of insects are developed from a whole limb rudiment, the most distal part forming the gnathal armature or mandibular tip. Most of the myriapod classes possess jointed mandibles, a feature correlated with the manner of use of the mandibles and providing flexures serving adduction in the transverse plane, as in a telopodite. There is no reason to suppose that myriapod and insect mandibles are not of the same whole limb type, although the differences in the mechanisms of movement and in details of morphology are so great as to preclude the origin of the one from the other (see further in § 33).

4. TYPES OF ARTHROPODAN EXO- AND ENDOSKELETON OF THE HEAD

The body wall and endoskeleton play an integral part in the mechanisms of jaws and other mouth parts, but the component structures are ill recognized and confusedly and inaccurately described. Mouth parts resemble trunk legs in utilizing (i) the ectodermal basement membrane of the body wall, (ii) segmental tendinous bars and (iii) cuticular apodemes, for their muscle insertions. Tendons are glistening white when large enough for direct observation, they are flexible, unless very thick, while apodemes are stiffer. In section the tendons stain blue with Mallory's triple stain or with Azan, as described by Cannon (1931), while apodemes stain as does the surface cuticle, red-orange in whole or in part in classes where sclerotization rather than calcification is the main stiffening agent, more blue when calcification is heavy, as in Diplopoda. Basement membrane and its outpushings appear blue or grey with Mallory, fibrillar processes often staining pink and blue in a patchy manner. Basement membrane, fibrils and tendons are soluble after prolonged boiling in potash.

(i) *Body wall skeleton*

Onychophoran cuticle resembles that of other arthropods but it is thin and much furrowed. Sheets of sub-ectodermal tendinous fibrils invest the body and legs. The fibrils lie in many directions and probably do not stretch, and, like coelenterate mesogloea, permit great deformations of the body yet provide firm attachments for the muscles, which are inserted upon this layer or on to extensions from it. The body wall of other Arthropoda does not permit such great deformations and the habits of life do not require it (Manton 1961 *a*).

Besides secreting the external cuticle, arthropodan ectoderm usually forms a skeletal basement membrane, as in Chilopoda (Fahlander 1938) and anostracan Crustacea (figures 3 *b* and 4 *c*), on to which muscles are attached. The basement membrane is linked in places to the surface cuticle by fine or by substantial intracellular fibrils (as seen in figure 4 *c*), which resemble the fine links which exist between the cuticle and sub-ectodermal connective tissue of Onychophora and of Annelida, such as *Scoloplos*. Where scutes are present fibrils from some muscles and from tendinous endoskeletal units appear to pass right through the ectoderm to insert upon the inner face of the cuticle (see the mandibular muscles on figure 4 *b*), but the electron microscope shows the myofibrils and tonofibrils to be discontinuous (Hinton, personal communication). Other myofibrils insert upon the basement membrane and are unsupported by tonofibrils (figure 4 *c*). Sometimes the basement membrane forms cuticle-like thickenings used for muscle attachments, as in *Scutigera* (Fahlander 1938), and mid-dorsally in the head of *Cryptops* a narrow sub-ectodermal rod carries the dorsal pharyngeal muscles. *Chirocephalus* possesses outgrowths from the basement membrane which form longitudinal tendinous endoskeletal rods through the head (figure 3), and these bear fibrillar suspensory processes staining much as do the suspensory processes of the segmental tendons (figure 3 B).

Embryologically the sub-ectodermal connective tissue fibrils of Onychophora and of the annelid *Scoloplos* (Anderson, personal communication) seem to be of ectodermal origin, first appearing close against the ectoderm just before the muscle cells become differentiated, the muscle primordia then being discontinuous. Arthropodan ectoderm thus has the potentiality of giving internal and external skeletal structures, besides muscles and other fibrils (Cannon 1927 *a*, 1940; Manton 1928, 1934), and the onychophoran massive development of sub-ectodermal connective tissue fibrils is not a unique arthropodan condition, but an elaboration suiting particular habits of life (Manton 1961 *a*).

(ii) *Tendinous endoskeleton* (*blue on the figures*)

The presence of a series of transverse segmental bars composed of tendinous fibrils is widespread in the head and trunk of arthropods and serves for muscle attachments. The assumption has often been made that because these structures are discontinuous with the ectoderm in the adult, they are mesodermal in origin (e.g. Pringle 1961; Tuxen 1959, etc.). However, these segmental bars or sheets of tendon originate from intersegmental ectoderm in the only animals in which their development has been followed (*Hemimysis* and *Nebalia*, Manton 1928*a*, 1934). Later the tendons separate from the ectoderm and grow with the animal.* They become more or less segmental in position (possibly the shift is not always in the same direction in all animals), and very large in the mandibular segment in many classes of arthropods. The term 'mandibular adductor tendon', customarily used for the Crustacea, will be amended here to 'transverse mandibular tendon' because the tendon is clearly homologous from group to group, yet it carries mandibular muscles of various functions (p. 95). Segmental tendons are present along the trunk of the adult diplopod *Polyxenus* where they carry dorso-ventral and other trunk muscles besides extrinsic limb muscles (Manton 1956, 1961*b*, text-fig. 34). In Malacostraca the trunk tendinous bars of the embryo are utilized by the longitudinal and oblique trunk muscles, first as embryonic scaffolding which becomes reduced to thin sheets of fascia uniting the muscular components of the two sides of the body, later the bars may disappear entirely. The elaborate segmental tendons within the lateral and ventral longitudinal muscles of chilopods (see Manton 1964), which carry some extrinsic leg muscles also, are probably homologous structures.

In the head the transverse segmental tendons may remain separate from one another, but often they link together, sometimes lightly (see the median fibres between the mandibular and maxillary tendons of *Petrobius*, figures 20 and 24H), or these two bars may largely fuse as in Campodea (figure 44). All the head bars are linked by paired longitudinal connectives in many 'lower' Malacostraca, the whole forming a lattice with considerable stability (figures 8 and 9 and Manton 1934, text-fig. 17). Comparable expansions continuous with the mandibular tendon form the endosternite of the ostracod *Doloria* (Cannon 1931), and in *Limulus* the endosternite presumably represents the fused transverse tendons of at least five prosomal segments (figures 14 to 16). Patten & Redenbaugh (1899, 1900) correctly appreciated the basic similarity between the endosternite of *Limulus* and the head tendons of *Apus*, but at that date little was known of the widespread occurrence of such structures throughout the Arthropoda. Where transverse tendons are large and carry many muscles, additional support is gained by outgrowths or struts which insert on the dorsal and lateral basement membrane below the ectoderm of the head. One pair of struts links the mandibular tendon with the lateral head wall in *Scolopendra*, many struts fan out to the dorsal head wall in *Scutigera* (Fahlander 1938, where the transverse

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* The ectodermal origin of tendinous endoskeleton in certain Crustacea (Manton 1928, 1934) does not necessarily imply that such tendons are invariably ectodermal in all arthropods as Fahlander's comments (1938) upon my work seem to suggest. Crustacean ectoderm can form anything from cuticle to basement membrane, striated muscle and other fibrils. But muscles which are of ectodermal origin in some Crustacea are of mesodermal origin in others (Cannon 1940, p. 148) thus prohibiting generalizations concerning ectodermal structures.

mandibular tendon is unfortunately termed a tentorium) and in *Anaspides* the links with the body wall are seven (figures 7 and 8, i to vii). The *Limulus* endosternite possesses muscular ties to the carapace (figure 16) from the anterior, lateral and dorsal cornua of Benham (Lankester, Benham & Beck 1885). Head segmental tendons, and the transverse muscles which they bear, become reduced or disappear when transverse biting is secondarily developed in Decapoda, Isopoda and the Pterygota, so permitting a large gape (see p. 19). Segmental tendons are wide in the transverse plane of the head, the transverse muscles being short and converging on the tendon, when the jaws perform rolling movements as in *Limulus*, *Chirocephalus*, *Petrobius* and *Campodea*. And the tendons form a thin median sheet of fascia uniting long transverse muscles when the functions of the latter are mainly stabilizing, as in *Tomocerus* and *Scolopendra*.

(iii) *Head apodemes* (*red or white on the figures*)

Hollow cuticular apodemes are usually paired in the head. They arise as an intersegmental series in *Pieris* (Eastham 1930) from the hinder edge of the antennal, premandibular, mandibular and maxilla 1 segments. The first and last of these form the anterior and posterior tentorial apodemes, and the premandibular and mandibular intuckings form apodemes carrying the mandibular abductor and adductor muscles respectively. One or both of the tentorial apodemes are present also in the apterygote and myriapod classes (§§ 17 (i), 22 (i), 25 (ii), 27 (i), 31 (i)), in spite of the conflicting statements which have been made on these imperfectly known structures. Tentorial apodemes are attached to the transverse segmental tendon system in *Petrobius*, *Tomocerus* and *Scutigerella* (figures 22, 33 and 57). Additional apodemes situated elsewhere in the head serve muscles other than those originating on the mandibles.

The Crustacea possess no common basic plan to their head apodemes. *Chirocephalus* has no apodemes. The very simple endophragmal skeleton of *Hemimysis* is initiated by paired latero-ventral intuckings at the maxilla 1–2 intersegment, the external openings of the apodemes spreading half across the embryonic maxillulary segment (Manton 1928*a*, text-figs. 22*d*; 1934, text-fig. 17). Each apodeme grows forwards and unites with its fellow and with the maxillulary transverse tendon. These same apodemes are further elaborated in the higher Peracarida (see *Ligia*, figures 11 and 12) but are small in *Paranaspides* and *Anaspides*, and a much more elaborate endophragmal skeleton exists in the Decapoda. The head apodemes of the Ostracoda are also elaborate, the anterior hypostomal and the antenno-labral attaching to the transverse mandibular tendon (Cannon 1940). However, the head apodemes of none of these Crustacea bears close resemblance to the basic tentorial apodemes of the myriapod-insect assemblage, even when an apodeme arises at the maxilla 1–2 intersegment, the position of origin of the posterior tentorial apodeme.

The three types of head endoskeleton in Crustacea give stability and strength to the movements of the jaws and other mouth parts. Tendinous and apodemal endoskeletons are, however, mutually interchangeable in animals within the same division (Peracarida) and sub-class (Malacostraca), as shown by the presence of both in a mysid, the elimination of tendinous and elaboration of the apodemal endoskeleton in an isopod and the presence of a largely tendinous endoskeleton in a syncarid crustacean (Manton 1934). And lateral thoracic tendinous nodes, which are united with the head skeleton of *Anaspides* (figure 8), are represented by calcified cuticle in *Palinurus* (Parker & Rich 1893). Since both types of structure are of ectodermal origin these transformations are probably of little phylogenetic significance, the larger animals and/or those using the more forceful actions employing apodemes most fully. But in the myriapod-hexapod series the composition of the head skeleton is much more uniform.

5. THE MANDIBULAR MECHANISM OF *CHIROCEPHALUS DIAPHANUS* PREVOST

Although the complexities of branchiopodan feeding mechanisms are becoming known, little has been recorded of the mandibular movements other than reference to their grinding activities (the observations of Mahoon (1960) are referred to below). That the large transverse muscle filling the open concavity of the mandible is a simple adductor is implicit in various works on mandibles which are not based upon direct observations. Abductor muscles have been stated to be absent (Snodgrass 1950). These views are not confirmed.

The mandible of *Chirocephalus* is shown in side view and from the transverse plane in figures 1 *a* and *c* (interrupted ruling). The lateral open part of the mandible is set dorsoventrally on the head and the molar area is carried inwards and forwards on the free ventral lobe as shown. The mandible is loosely articulated at its dorsal extremity where arthrodial membrane is short (marked by a cross on figure 1 and see figure 4*c*). A short sclerotized rib, shown in black, lies in the cuticle at the ends of the cervical groove and supports the articulation. Elsewhere ample arthrodial membrane links the mandibular margins with the cuticle of the head. Each mandible rocks backwards and forwards about an axis situated a little lateral to the line joining the black cross and black spot on figure 1 *c*. The end of the forward roll is shown in figure 1 *a*, where a lateral hollow is exposed above the maxillule and below the bulge housing the maxillary gland. In figure 1 *b* the mandible, at the end of the backward roll, now occupies much of this hollow and the straight anterior margin of the mandible is now visible. This backward roll brings the molar areas forcibly together, and on the forward roll they abduct slightly. When a little out of phase the molar areas rub across each other.

Cardboard shapes representing the frontal aspect of a pair of mandibles are shown in figure 2 rotating through 50° about a vertical axis. From the forward position of the lateral parts of the mandible (*a*) to their backward position (*c*) the molar surfaces are rolled against each other. The reverse movement parts the molar surfaces slightly, an effect due to the shape of the cards. *Chirocephalus* can at times abduct the mandible to a greater extent than would be possible if its movements were just such a simple roll, and at other moments abduction may be absent. In *Daphnia* the labrum does not obscure a ventral view of the mandibles, and for long periods the promotor-remotor swings can be seen to roll the molar faces back and forth across each other, some parts always being in contact. Food material flows into the space *x* (figure 2 *a*), is crushed and emerges into the space *y* (figure 2 *c*) at the end of the remotor roll, and is then sucked into the mouth. The asymmetry of the molar lobes enhances this grinding action. At other times the mandibles abduct clear of one another. The mandibular cycle of movements has a much lower frequency than that of the filtering trunk limbs.

(i) *The head endoskeleton of* Chirocephalus diaphanus *Prevost*

The skeleto-musculature of the mandibles of *Chirocephalus* is seen in figure 3 at progressively more posterior levels (A to E), and a diagrammatic frontal view is shown in 2*d*. The very large transverse mandibular tendon is anchored dorsally and ventrally to the ectodermal basement membrane. Paired suspensory processes insert dorsally upon thickened basement membrane below the cervical groove. The processes are composed of fibrils lacking cross striations and readily stain pink in parts with Mallory's triple stain. The cervical groove braces the dorsal body wall against potential buckling caused by the pull of muscles on the tendon, just as do many other furrows and sutures on the heads of arthropods (Strenger 1952 and see pp. 20, and 37).

From the posterior face of the mandibular tendon a median connexion passes ventrally to join a complex formed by paired longitudinal endoskeletal bars (figure 3D, E). The principal origin of these bars lies laterally, just in front of the mandible and above the level of the nerve cord. Here the basement membrane bears ingrowths which unite together behind the oesophagus forming a transverse partly hollow plate (figure 3B). From it a pair of longitudinal extensions or bars passes forwards and backwards on either side (figure 3C to E). They soon become solid. The anterior bars extend forwards lateral to the oesophagus, below the digestive diverticula, and anchor on the front of the head. The posterior extensions pass above the nerve cords as flat plates to the maxillulary segment, where they unite with the lateral parts of the maxillulary transverse tendon. Behind the mandible the posterior extensions join together forming a median bridge which sends a supporting flange to the groove between the paragnaths (figures 3D, E). Ventral longitudinal muscles from the trunk and oesophageal dilators round the mouth insert upon these endoskeletal bars which firmly anchor the transverse mandibular tendon. The superficial similarity of these paired cephalic longitudinal elaborations of the basement membrane to the tendinous bars of *Paranaspides* and the apodemes of *Ligia* indicates similar functional needs.

The transverse mandibular tendon expands into an oblique dorso-ventral pillar within the mandible (see figure 3C, D). This pillar forms the axis of the rolling movements, and bears muscles which fan outwards, forwards and backwards over the inner face of the mandible. The frontal view in figure 2*d* shows the tendinous pillar to be closer to the anterior than the posterior face of the mandible and muscles 5*a* and 5*b* to be antagonistic to one another. The manner in which the mandible bulges back over its posterior marginal attachment to the body is seen in the frontal view; it is a device which gives maximum bulk and length to muscles 5*a* and easy mobility to the mandible on the head.

(ii) *Mandibular musculature and movements of* Chirocephalus diaphanus *Prevost*

The conspicuous promotor roll of the mandible must be caused by the pull of muscles 3 from its anterior margin to the dorsal basement membrane in front of the cervical groove, and of muscles 5*b* from the pillar of the tendon. The stronger remotor roll must be caused by the pull of: muscles 4 from the posterior mandibular margin to the dorsal cuticle of the head behind the cervical groove; muscle 4*a* from the posterior mandibular margin to the transverse tendon; muscles 5*a* from the posterior face of the mandible to the tendinous pillar; and by the direct muscles 5*c* uniting the posterior margins of the two mandibles. It is not surprising that the muscles causing the backward remotor roll (4, 4*a*, 5*a* and 5*c*) are much more bulky than those causing the recovery promotor roll (3 and 5*b*) since the former promotes the major squeezing and grinding by the molar areas.*

Additional but small direct adductor movements are possible during the backward roll and direct abductor movements during the forward roll, that is movements in a plane at right angles to that of the promotor-remotor roll. The muscle fibres from the lateral faces of the mandibles (5*d* in figures 2*d* and 3D) fanning on to the tendinous pillars must adduct the mandibles swinging them from their dorsal point of closest union with the head (the black cross), and fibres 5*e* must give a levator action to the ventral part of the mandible (level D), so bringing the molar areas close to each other and to the mouth. Slight direct abduction must be effected by muscle 6 (level D) which runs from a short stout tendinous junction close to the dorsal mandibular articulation and inserts high up on the transverse tendon. The looseness of the dorsal mandibular articulation (figure 4*c*) permits the dorsal end of the mandible to be pulled inwards and downwards a trifle, a movement giving slight abduction of the molar end of the mandible. Muscle 6 works at a very poor mechanical advantage, but it has only to stretch contracted muscle and not to do outside work. The abductors of *Scutigerella* also work at a very poor mechanical advantage § 27 (iii)). Muscle fibres 5*f* from the dorsal part of the mandible to the tip of the tendinous pillar (level D) probably assists muscle 6.

That the so-called 'mandibular adductor' fibres (5*a* to 5*f*) do not all contract together, as has previously been implied, has not been proved directly. It is the correspondence between observable mandibular movements and the positions of the several muscles which shows that they work as promotor, remotor, adductor, abductor and levator units. And the muscles which should provide the greater force have in fact the greater bulk, the larger transverse sectional area and the better mechanical advantage. It will be noted that this skeleto-muscular set up allows considerable flexibility in effects, and that the mandibles need not work quite synchronously. Such flexibility characterizes the movements of the living animal.

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* Binder (1931) describes an essentially similar musculature for *Daphnia*, and correctly stresses the rolling movement caused by the dorsally inserted extrinsic muscles. The two muscles of *Daphnia* corresponding with 5*c* of *Chirocephalus* are considered by Binder to be direct transverse adductors which reduce the tension on the transverse mandibular tendon, and tend to cause its buckling. However, muscle 5*c* does not pull squarely on the mandible, but from its posterior border, and cannot do other than roll the outer face of the mandible backwards. Binder clearly draws muscles for *Daphnia* corresponding with 5*a* and 5*b* of *Chirocephalus*, and these muscles similarly contribute to the remotor and promotor roll of the mandible. Thus it is unlikely that there is a lessening of tension or a crumpling on the transverse mandibular tendon, a condition found in no arthropod studied here (see also p. 12).

Mahoon (1960) gives an outline of the mandibular muscles of *Daphnia*, but in less detail than given by Binder (1931), whose work was not considered. Mahoon's account of the mandibles of *Chirocephalus* and *Artemia* is based upon an incomplete appreciation of both the morphology and the movements. I do not consider that the whole promotor roll of the branchiopod mandible is mainly concerned with a slow bringing together of the anterior tips of the molar lobes, although the activities of the mandibles are sufficiently varied for an extreme promotor position to have such an action (see figure 6 left-hand diagram). The promotor roll appears to represent the recovery movement, associated or not with slight abduction, and is preparatory for the strong, remotor roll which closes the molar areas on food material arriving from behind.

6. CONCLUSIONS CONCERNING THE ANOSTRACAN CRUSTACEA

Thus it is clear that the anostracan mandible is not worked by three primitive muscles comprising no abductor, and phylogenetic schemes based upon such a concept (Snodgrass 1950, 1952) must be abandoned. The mandibles of *Chirocephalus* are essentially rubbing, grinding and squeezing organs and they do not exert a cutting action. Their effects depend mainly upon a wide antero-posterior rolling of the lateral muscular parts of the mandible about a dorso-ventral axis so moving the molar areas in the opposite direction. Small direct adductor and abductor movements are superimposed upon the backward and forward roll respectively. The approximately vertical position of the axis of movement permits the use of a maximum area of molar armature for grinding. When this axis becomes oblique and finally horizontal in certain higher Malacostraca the triturative molar area becomes progressively reduced, because only a smaller part of the mandible can be rolled across its fellow (as in *Ligia*, p. 25), and triturition on the promotor roll becomes impossible. Muscles are present which are appropriate in position and size to cause all the observed movements. The rolling action directly resembles the promotor and remotor swing of the coxa of a walking leg, and has presumably been derived therefrom (see below). All muscles, except 4*a*, are recognizable in the Syncarida and Mysidacea.

7. MODE OF INITIATION OF TRANSVERSE BITING IN CRUSTACEA

Chirocephalus has no need of a biting mandible since finely divided or soft food reaches the molar areas from behind, close to the body (Cannon 1933*a*), as shown by the arrow on figure 5*e*. But many Crustacea combine fine food feeding with an ability to deal with larger particles. The fine food of *Hemimysis* and *Paranaspides*, for example (Cannon & Manton 1927, 1929; Manton 1930), reaches the molar areas from behind and close to the body (but by setal action instead of by a water current as in *Chirocephalus*), shown by the upper arrow in figure 5*f*. In addition large food can be bitten into by incisor processes of the mandibles situated ventral to the molar area. The route for the larger food particles is roughly from below upwards, as shown by the lower arrow on figure 5*f*. *Ligia*, on the contrary, feeds only on large food which enters the preoral space from below as shown by the arrows in figure 5*g*.

That a mandible is a modified segmental appendage is undoubted, but in order to appreciate the relationship between the mandibular mechanism of *Chirocephalus* and that of a trunk limb, and to understand the modes of initiation of biting mechanisms, it is necessary to consider the coxa-body joint of trunk limbs. The coxa-body joint is common to mandibles of all kinds whether they bite with the tip or with the base.

(i) *The coxa-body joints of arthropod legs*

The swimming and ambulatory limbs of typical members of most arthropodan classes swing forwards and backwards at the coxa-body joint about an axis lying approximately transverse to the body, and little or no levator or depressor movements are possible. This axis (dotted line in figure 5*a* to *d*) is ventrally placed in most Crustacea and Diplopoda, it is a little oblique, extending laterally just on to the pleuron in Symphyla and it extends further up the pleuron in Chilopoda and *Limulus*. These positions suit the locomotory habits of the owners. The ventral or slightly ventro-lateral position, as seen in *Peripatus*, is probably more primitive than the lateral one because the former more readily raises the body off the ground (Manton 1952*a*) and the latter in extant examples show so many obvious specializations: *Limulus* (§ 14), and the Chilopoda (Manton 1958*a*, 1964), and the arachnid coxa (spider and scorpion) swings but little and also has many specializations (Manton, 1958*b* and a future Part of 'The evolution of arthropodan locomotory mechanisms'). The insect coxa-body joint is far from primitive, in a beetle, for example, an essentially rotatory movement provides promotor and remotor effects (Evans 1961).

The essential form of a simple coxa-body joint in arthropods is shown in end-on view in figure 5*d*. Little arthrodial membrane (white stipple) links the lateral and mesial margins of the coxa with the trunk cuticle (marked by crosses) while ample arthrodial membrane lies fore and aft. Consequently the movement at the joint is restricted by the skeleton to one plane, and all available muscle can facilitate the strong remotor and weaker promotor movement by pulling on the anterior and posterior rims of the coxa. Articulating facets of stiff cuticle formed on either side of the short arthrodial membrane strengthen the joint and localize the movement and may be simple or most elaborate in construction. In some small aquatic arthropods the coxa-body joint possesses no articulating facets and the proximal rim of the coxa fades into arthrodial membrane and body cuticle.

Usually the internal face of the coxa provides insertion sites for intrinsic leg muscles only, and the extrinsic muscles arise from the proximal rim of the coxa, as in the Copepoda, Malacostraca, Diplopoda and Symphyla. But in small animals possessing wide leg bases with no firm articulation at the coxa-body joint, the extrinsic limb muscles arise from the internal face of the coxa, as in the Branchiopoda and Cephalocarida (*Hutchinsoniella*, see Hessler, in preparation). The extrinsic muscles in these groups insert upon the body wall and the segmental tendons, as also in *Polyxenus* (Diplopoda, Manton 1956) and Chilopoda.

A restriction of the two close articulations (short arthrodial membrane) to a single point serves special purposes and enhances the range of possible movements, but more muscular energy is then tied up in producing stability and less is available for causing direct movement. An outer articulation is present alone on the maxillipede of *Calanus* (Perryman 1961) and on the prosomal limbs of *Limulus* (figure 14) and a close mesial union occurs alone in the trunk limbs of Chilopoda and in a spider (Manton 1958*b*).

(ii) *Derivation of the* Chirocephalus *type of jaw mechanism*

The rolling of the anostracan mandible represents the backward and forward swing of an ambulatory or swimming leg, and muscles 3, 4 and 4*a* represent the promotor and remotor muscles attached to the proximal rim of a trunk limb coxa. The mandibular roll moves the lateral part of the jaw from a transverse to a posterior position, so bringing the molar processes well towards the mouth at the end of the backward movement. Such a range characterizes many trunk limbs also and is seen in *Chirocephalus* itself.

The mandibular advances of *Chirocephalus* on a trunk limb coxal mechanism are: (1) the enlargement of the mandible and its extension up the pleuron; (2) the mesial freedom of the mandible from the head, no close articulation lying near the black spot on figure 1*c*;

and (3) the abundance of muscles originating from the inner surface of the mandibular cuticle and inserting on the transverse mandibular tendon. Most trunk limbs lack such muscles, but they arise in *Hutchinsoniella* from the internal face both of the mandible and of all post-oral limbs, and insert upon the transverse segmental tendon (Hessler, in preparation). The trunk limbs of *Chirocephalus* also possess extrinsic muscles which arise from the internal face of the limbs and insert both dorso-laterally on the body wall and on to elaborate transverse segmental tendons. In the mandible the greater part of the transverse muscles provides strength to the backward and forward roll and the lesser part contributes to small direct adductor-abductor movements. Direct adductor and abductor movements are carried out on a grand scale by *Limulus* (§ 14 (ii)) but Crustacea achieve their transverse biting quite differently.

(iii) *Derivation of biting by incisor processes in Crustacea*

The leg of a iuliform diplopod swings back and forth on an axis the lateral end of which is tilted upwards and backwards a little. Consequently the spines (Manton 1958*a*; text-fig. 7, *v.s.*), carried on an inwardly directed coxal bulge, meet their fellows in the middle line at the end of the backstroke and are far apart at the end of the forward swing. Such a movement could readily lead to that of the anostracan mandible. If the *Chirocephalus* type of mandible was provided with an incisor process, suitably shaped and set well away from the axis of movement, and if the dorsal end of this axis was shifted posteriorly, as in figure 5*f*, the same mandibular roll would produce adduction and abduction of the incisor processes in the transverse plane. Such a mandible is present in a mysid, *Anaspides* and *Paranaspides*. The axis of movement, the interrupted line between the cross and the black spot on figures 5*f* and 7, lies nearer to the anterior margin of the mandible than in *Chirocephalus*, thereby enhancing the range of movement of the parts of the mandible most distant from this axis. Figure 6 shows a ventral view of the mandible of *Anaspides*, the dorsal point of union with the head is marked by a cross. On the left the mandible is at the end of an extreme forward roll about the axis of movement; see the base of the arrow. The molar areas are well open one from another and are visible behind the labrum. The incisor processes are far apart near the lateral limit of the labrum. No mandibles of any arthropod have been found which open wider than the lateral limit of the labrum. Positions *b* to *d* show the backward roll of the mandible, see the same base of the arrow. The incisor processes come together in a transverse plane until they meet above the labral margin, and the molar areas come together and tuck well over the posterior face of the labrum. The biting by the incisor processes is clearly a derivative of the rolling movement about the long axis of the mandible and not an exaggeration of the small direct adductor and abductor movements shown by *Chirocephalus*. The musculature of the Syncarida is capable of providing small contributions to the adductor-abductor movements as in *Chirocephalus*.

A more extreme backward shift of the dorsal end of the axis of mandibular movement results in the *Ligia* condition (figure 5*g*). The axis is now a skeletal hinge formed at the morphological anterior border of the mandible between the black cross and spot. Movement about this axis results in direct adduction and abduction in the transverse plane. Much musculature now works at a more favourable mechanical advantage, giving stronger transverse biting movements than in *Paranaspides* by the utilization of long adductor and abductor apodemes.

Mandibles with large transverse muscles filling their cavities and inserting upon a transverse mandibular tendon do not abduct far. To do so would require considerable variations in length of these muscles, and all muscles work most economically when deformations are minimal. Fine food feeders do not require the wide gape which is serviceable to large food feeders. The reduction and disappearance of the transverse mandibular muscles in various higher Malacostraca has been noted by Snodgrass (1950), and the mandibular cavity becomes empty of muscles (figure 12*a*). This change is correlated with the simplification of the primitive marginal musculature which now works on two strong apodemes (§ 10), and the disappearance of the transverse muscles permits the use of a wide gape. The existence of a series of animals showing intermediate stages between those of the *Paranaspides* type and those of the large food feeding Malacostraca indicates that the end term simplicity is not a primitive one.

The details upon which the above conclusions are based can now briefly be considered.

8. The mandibular mechanism of *Paranaspides lacustris* Smith, *Anaspides tasmaniae* Thomson and *Hemimysis lamornae* (Couch)

The mandibular mechanisms of these filter- and large-food-feeding Malacostraca (Cannon & Manton 1927, 1929; Manton 1930) have not hitherto been described with accuracy, either from the morphological or functional aspect, beyond drawings of the entire mandible and of its gnathal edge. These mandibular mechanisms are essentially similar, and that of *Hemimysis* shows the closest resemblance to *Chirocephalus*. All employ the same basic rolling movement, seen in *Chirocephalus*, but are adapted to give transverse biting of incisor processes, as indicated above: by the oblique set of the mandible on the head; by the presence of incisor processes; by the axis of movement lying near to the anterior margin of the mandible, so allowing the bulk of the muscles originating on the inner face and posterior margin of the mandible to apply their pulling forces far from the axis and so to contribute strength to the backward roll; and by a more extensive and robust endoskeletal system, although *Paranaspides* and *Hemimysis* are not larger animals than *Chirocephalus*. The elaboration of the head endoskeleton is related also to the strong movements of maxillules and maxillae.

The ventral end of the axis of movement of the mandible lies at the side of the mouth at the point marked by a black spot on figures 7, 8 and 9A close to an extension from the transverse mandibular tendon. Ample arthrodial membrane links the head with the molar process giving free movement. The dorsal end of the axis, marked by a cross, is not an articulation, but a union of thickened mandibular cuticle to the thin head cuticle lining the pleural fold (*Hemimysis*, figure 4*b*). The mandible is here suspended by stout fibrils passing upwards to insert upon thickened basement membrane of the lateral head ectoderm. This arrangement gives free rocking of the mandible on the head and limited movement in other directions. The axis of movement is less oblique in *Hemimysis* than in the Syncarida, a condition favouring grinding by the molar areas but giving less effective biting by incisor processes.

(i) *The endoskeleton of* Paranaspides lacustris *Smith,* Anaspides tasmaniae *Thomson and* Hemimysis lamornae (*Couch*)

The endoskeleton of these two Syncarida is similar and mainly tendinous (figure 8). Paired longitudinal bars are anchored anteriorly to the surface cuticle at i and ii. Union iii lies at the side of the mouth (figure 9A). A stout upward strut from each longitudinal bar unites with one arm of the suspension of the transverse mandibular tendon, and inserts by a double ending iv on the dorso-lateral head wall (figure 9D). A median ventral union vi between the paragnaths is muscular in *Hemimysis* and mostly tendinous in *Paranaspides,* as it is in *Chirocephalus.* A posterior connexion vii anchors each bar to the maxillae 1–2 intersegment, and two fine strands pass out to the first of a series of segmental endoskeletal nodes as shown in figure 8. These nodes are tendinous in *Paranaspides* and *Anaspides* but cuticular in *Palinurus* (Parker & Rich 1893). The mandibular tendon is stabilized by a paired dorso-lateral suspension much as in *Chirocephalus,* but each divides and inserts dorso-laterally on the cervical groove by two endings v (figures 7, 8 and 9D), and the groove itself is doubtless intrasegmental and serves the same purpose as in the Anostraca (p. 14). An anterior transverse connexion between the two longitudinal bars takes the pull from mandibular promotor (abductor) 6 (figure 9*c,* and Manton 1934, text-fig. 17*e*). A stout apodeme leaves the posterior margin of the mandible (figures 7, 8 and 9D) giving strength to remotor (adductor) muscle 4 and providing a large surface for the origin of its fibres. This apodeme is present in most Malacostraca and in the cladoceran *Eurycercus* (Fryer 1963) but absent in the soft food feeding *Chirocephalus.* The endoskeleton of *Hemimysis* is shown by Manton (1928, text-fig. 22*d*; 1934, text-fig. 17), the endoskeletal strut e in the latter figure being the posterior mandibular apodeme bearing dorsal remotor muscles 4. The small apodemes from the maxilla 1–2 intersegment of the Syncarida are much larger in the Mysidacea where they unite in the middle line, and take the place of the long paired tendinous bars of the Syncarida.

(ii) *Musculature of* Paranaspides lacustris *Smith,* Anaspides tasmaniae *Thomson and* Hemimysis lamornae (*Couch*)

Again mandibular movements are not produced by three simple muscles comprising no abductors, as claimed by Snodgrass (1950). A similar set of mandibular muscles with diversified functions is recognizable in large measure throughout the Malacostraca. The muscles arise from the only possible sites, the anterior and posterior margins and from the concavity of the mandible, and only in that sense can they be reduced to three basic groups. The muscle numbering used on the figures is an extension of that employed by Snodgrass for the muscles of decapods described by Schmidt (1915), Parker & Rich (1893) etc.

Most mandibular muscles originate directly under the stiff mandibular cuticle, but some pull from arthrodial membrane near the margin of the mandible (for example, promotor (abductor) 3 in figure 9C). There are many comparable cases among arthropods where angular displacements of the hard parts are great, for example sternite 1 muscle *d* in *Cylindroiulus* and the deep dorso-ventral muscles of *Siphonotus* (Manton 1961 *b*) pull on arthrodial membranes, and the deformations at the insertion of the muscle are thereby reduced since the membranes bend freely. Similarly the muscles flexing the patella of a spider's leg, by pulling on the swinging arcuate sclerite in the arthrodial membrane, avoid the deformations of muscle insertions operating at the patella margin (Manton 1958*b*).

Muscles which cause the promotor roll of the mandible are: muscle 3 from the anterior margin, as in *Chirocephalus*; muscle 6 pulling on the anterior margin in the Syncarida (figures 8 and 9C); and muscles 5*b*, the smaller portion of the transverse muscles which lies antero-dorsal to the main part of the transverse tendon (figures 7 and 9B, C and E), which act exactly as in *Chirocephalus*. Muscle 6 in *Chirocephalus* and in *Hemimysis* arises close to the dorsal apex of the mandible, from its posterior margin, and inserts high up on the tendinous skeletal complex at the base of the dorsal suspensory arms, a most strikingly detailed similarity. The muscles in both cause slight direct abduction (see below).

Muscles which cause the remotor roll of the mandible, and consequently effect grinding by the molar processes and biting by the incisor processes, are: the very large muscle 4 from the posterior apodeme which fans in several sections to the dorsal head wall, spreading both in front and behind the cervical groove; the greater part of the transverse muscles, 5*a*, situated posterior to the transverse tendon (figures 7 and 9B, C and E), and acting as in *Chirocephalus*; and the direct transverse muscle 5*c* uniting the posterior margins of the two mandibles (figures 7 and 9E), the great thickness of this muscle in the Syncarida is shown by its sagittal section in figure 8 where it lies just behind the transverse tendon, as in *Chirocephalus*.) An additional muscle 2, not present in *Chirocephalus*, passes outwards to the lateral wall of the head from the anterior border of the mandible, in *Hemimysis* from the ventral end of the anterior border; this muscle represents adductors 1 and 2 of *Astacus* and crab (figures 7, 9B, 13). The most ventral parts of the remotor 5*a* musculature must cause some direct adduction of the ventral end of the mandible. This movement will be reversed by the promotor muscles and by muscle 6 in particular.

9. CONCLUSIONS CONCERNING THE MORE PRIMITIVE MALACOSTRACAN CRUSTACEA

Thus the mandibular mechanisms of *Chirocephalus*, *Hemimysis* and *Paranaspides* are essentially similar in that all are dependent upon the dorsally inserting promotor and remotor muscles 3 and 4 giving movements similar to those of a trunk limb. The short transverse muscles between the mandibles and the wide transverse tendon, muscles 5*a* being more bulky and longer than 5*b*, primarily serve the rolling movement and only secondarily do they promote transverse biting by the incisor processes. The direct transverse muscle 5*c* strengthens the remotor roll.

The direct abductor muscle 6 of *Chirocephalus* and *Hemimysis* is a very small component of the whole mandibular musculature, and with muscles 5*d* and 5*e* promotes movements at right angles to the main mandibular roll. It is this direct movement in the transverse plane which is further developed by the Chelicerata in achieving strong transverse biting. In the Decapoda, Amphipoda and Isopoda, on the contrary, a modification of the promotor-remotor roll leads to strong transverse biting. The origin of muscle 6 from the anterior mandibular margin in the Syncarida (cf. *Hemimysis*) gives assistance to the promotor roll. This muscle becomes the principal promotor (secondary abductor) of the Decapoda (§§ 12 and 13). The addition of remotor muscle 2 in the mysid and Syncarida is a tendency carried further by the Decapoda and increases the strength of the remotor roll, the muscle becoming one of the principal but secondary adductors of the crab.

Among the more primitive Malacostraca here examined, the mandibular mechanism of *Hemimysis* appears to be the most primitive and to have most in common with *Chirocephalus*. An examination of the leptostracan *Nebalia bipes* (O. Fabricius) shows divergence from the basic plan. The incisor process of this animal bears only one cusp and the axis of mandibular movement is not oblique but vertical, thus suiting a largely grinding and squeezing action. Muscles 4, 5*a*, 5*b* and 5*c* are typical, but muscles 3 and 6 are unusual and an additional muscle is present.*

The copepod mandible does not spread so far up the sides of the head as do those of the Branchiopoda and the more primitive Malacostraca, but a close lateral articulation is present, representing the dorsal point of the mandibles so far described. The effective *Calanus* 'bite' is caused by a remotor roll in which the gnathal surfaces are swept forwards, upwards and together (Perryman 1961), a movement comparable to those of *Chirocephalus* and *Hemimysis* (see p. 98).

Since Anostraca, Mysidacea and *Paranaspides* represent some of the least advanced of modern Crustacea, the similarity in their mandibular mechanisms possibly reflects a basic type of crustacean mandible. However, *Hutchinsoniella* may represent an even more primitive condition in that all extrinsic mandibular muscles arise from the face of mandible and none from the proximal edge; but such a condition, related as it is to the absence of basal articulations on all the limbs, is only suitable for a small animal in which the limb movements are not rapid.

Much more elaborate mandibles with diverse functions are found in the Ostracoda, for example (Cannon 1931, 1933*b*, 1940), but it is the modifications present in some of the higher Malacostraca which are informative for the present purposes, because they convergently resemble some hexapods.

10. THE MANDIBULAR MECHANISM OF *LIGIA OCEANICA* ROUX

As is well known, the Isopoda and Amphipoda represent two specialized and divergent lines of peracaridan evolution. Isopoda are typically large-food feeders, the route for the food to the mouth being from below upwards, as shown in figure 5*g*. *Ligia* feeds between tide marks under aerial conditions, and it possesses a median hypopharynx-like process from the ventral head wall, present also in *Porcellio*, as noted by Snodgrass (1950, 1951). This median lobe (figures 10*b* and 11) contains much glandular tissue situated below the ectodermal epithelium. This organ is absent both in the typically aquatic isopod *Idotea* and in the aquatic and terrestrial amphipods *Orchestia* and *Talitrus*; thus it is not typical

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* In *Nebalia bipes* the probable homologue of muscle 3 forms a dorsal suspension of the mandible, in place of suspensory fibrils such as those of *Hemimysis* (figure 4*b*). The muscle arises antero-dorsally and passes directly upwards to the dorsal head wall. The muscle appears to be abductor as well as suspensory in function.

The probable homologue of muscle 6 inserts upon the base of the suspensory arms of the transverse mandibular tendon, exactly as in *Chirocephalus* and *Hemimysis*. The muscle lies in two sectors, one above the other, arising from the upper part of the posterior mandibular margin dorsal to the direct transverse muscle 5*c*. Muscle 6 therefore appears to be remotor in function and not promotor as is usual. An additional promotor muscle arises from the arthrodial membrane near the antero-ventral mandibular margin and inserts in the middle of the anterior face of the transverse mandibular tendon. This muscle and muscle 6 must be antagonists, and must fortify the roll caused by the normal complement of muscles already mentioned, thus furthering the squeezing and grinding efficiency of the mandibles.

of all Isopoda or of Crustacea in general, but is probably related to aerial feeding (see further below). The mandibular mechanism of *Ligia* will be considered because of certain similarities it appears to share with hexapods.

(i) *Morphological basis of the feeding mechanism of* Ligia oceanica *Roux*

The skeleto-muscular system of the head of *Ligia* has been described by Jackson (1926) and his terminology is employed here. The cranial exoskeleton bears many shallow folds, an occipital groove and marginal, frontal and supra-antennal lines (figure 10*a*), which internally provide strong cuticular insertions for muscles and give rigidity to the cranial insertions of mandibular adductor 4 in particular. The tergal ala is a deeper intucking at the maxilla 2–maxillipedal intersegment.

The head of *Ligia* is short antero-posteriorly although it is fused with the maxillipedal segment; mobility of the head occurs at the joint between first and second thoracic segments. The mouthparts are set close together, no suction chamber between maxillules and maxillae being present as in filtratory Peracarida. The bases of the maxillules and maxillae extend far back to the posterior limit of the head, so providing plenty of surface for the origin of muscles, the stronger maxillule projecting behind and lateral to the maxilla (figures 10*a*, *b*).

The paragnaths are short antero-posteriorly compared with *Anaspides* (cf. figures 8 and 11). Laterally each paragnath is expanded into a lobe which closely hugs the mandible (figures 10*a*, *b*), and on this lateral edge ends the bifurcation of 'the median bar' of the ventral exoskeletal system. In the fork from the median exoskeletal bar lies the median lobe from the ventral head wall, referred to above, projecting between the free parts of the maxillule and maxilla (figures 10*b*, 11). The three long soft spines from the proximal maxillulary endite and the two soft spines from the maxilla extend into the gulley between this median lobe and the paragnath on either side, so directing particles to the molar process of the mandible. The maxillae fit closely against the median lobe which prevents escape of food material close to the body. The distal (outer) endite of the maxillule, which is strongly biting, operates level with the mandibular incisor processes by movements in opposite phase to those of the mandibles. The distal ends of the maxillae and paragnaths prevents escape of food at this level. The gnathobases of the 6th legs of *Limulus* (figures 68 and 69, plate 1, facing p. 30) fit round the chilaria just as the maxillae of *Ligia* fit round the median lobe, and in both animals backwards escape of food material is thereby prevented.

In *Idotea* the maxillae reach the middle line, fitting closely against the median exoskeletal bar, a structure less heavily built than in *Ligia* and also bifurcating to end on the paragnaths. No median lobe projects between this skeletal fork and distally the maxillae meet together in the middle line (see also Naylor 1955, fig. 1). Some structures functionally a little like the median lobe of *Ligia* can be found occasionally in large food feeding Crustacea. The predatory mysid *Lophogaster*, in which filter feeding is absent and the mouth parts correspondingly different from most mysids, shows a transverse fold projecting from the body behind maxillae 2 (Manton 1928*b*, pls. II–III, unlabelled on fig. 6 and marked *m.p.* on fig. 5). The median largest part of this projection must assist in keeping food from escaping behind the maxillae 2, but less effectively than in *Ligia*. These crustacean median lobes of the body wall project behind the 'bite' of both maxillae 1 and 2 while the hypopharynx of hexapods projects in front of the labium (maxillae 2). The similarity, as far as it goes, between *Ligia* and hexapods is probably due to convergence under the influence of rather similar feeding habits.

Ventrally the head of *Ligia* is almost uncalcified except for the 'maxillo-sternal framework' (Jackson 1926) of strongly sclerotized and calcified creases which form ribs supporting the mouth parts. The median bar (figure 10*b*) and its anterior bifurcation to the paragnaths give paired branches: the maxillularly sclerite, forming the outer and anterior margin of the maxillulary socket and passing along the proximal maxillulary endite; a short branch to the median lobe supporting a curious paired projection; the maxillary sclerite lying between the bases of the maxillule and maxilla and forming almost a circle round the latter, running along the edge of the median bar; the alar bar passing out to the lateral notch at the back of the head (ringed round in figure 10*a*); and the maxillipedal sclerite. These bars, except for the maxillipedal sclerite, do not carry limb muscles other than a maxillipedal muscle to the alar bar. Anteriorly a stout tendon leaves the fork at the base of each paragnath, and from it muscles extend upwards to the tergal ala (figure 11, 'exoskeletal muscle'). These muscles control the position of the 'maxillo-sternal framework', paragnaths and median hypopharynx-like process.

This curious form of the ventral head wall provides strength to the closely set mouth parts and an elastic mechanism promoting abduction of the maxillule (Jackson 1926). These superficial skeletal folds of cuticle show no basic resemblance to either the anterior or posterior tentorial apodemes of myriapods and hexapods, which primarily serve muscle insertions, frequently support the basal articulation of the maxilla 1 and in myriapods cause or assist mandibular movements (§§ 17 (i), 19 (i), 22 (i), 25 (ii), 27 (i), 31 (i)). No support has been found for the contrary view of Snodgrass (1950, 1952).

The head endoskeleton proper of *Ligia* represents an elaboration of the simple paired maxilla 1–2 apodeme of a mysid and a syncarid (Manton 1928*a*, text-fig. 22*d*; 1934, text-fig. 17 *Paranaspides*) and typical of all Peracarida. These apodemes take the place of the longitudinal tendinous bars uniting the segmental tendons of *Paranaspides* and *Anaspides* (blue in figure 8). The paired apodemes in *Ligia* (red in figure 11) arise from wide slit-like intuckings at the maxilla 1–2 intersegment. The walls of these intuckings are membranous (white stipple) except for two sclerotized ribs, the outer angle being formed by the inferior lateral pterygoid process, attached at its outer end to the lateral part of the cranium at the point surrounded by a circle (figures 10*a* and 11). The inner angle forms the maxillary pterygoid process which is continuous with the maxillary sclerite. From the tip of this intucking the main apodeme, hollow and sclerotized, passes inwards and forwards as the sternal ala of Jackson. It is anchored to the frontal line by the pharyngeal process of Jackson, (ii on figure 11) resembling the attachments i and ii of the tendinous bar of *Anaspides* (figures 8, 9*a*). A downwardly directed process (the superior tendinous process of Jackson) bears mandibular muscles 5*a* (see below).

(ii) *Structure, musculature and mode of action of the mandible of* Ligia oceanica *Roux*

The mandible of *Ligia* is shaped as shown in figures 10 to 12, and its derivation has been considered in § 7 (iii). The axis of movement, between the cross and black spot, is almost horizontal, very close to the morphologically anterior mandibular margin which forms a hinge-like articulation extending along the dotted line (figure 10*a*). This allows direct adductor and abductor movements in the transverse plane. The apodeme from the posterior margin of the mandible (typical of all Malacostraca) is very large and its remotor (adductor) muscle 4 fills much of the head cavity, passing to the tergal ala and fanning over the whole dorsal cranium, one sector passing to the supra-antennal line. The remains of the muscles from the mandibular concavity, 5*a* inserting on to the longitudinal endoskeletal bar, contribute a small adductor force.

The abductor mechanism is 'ingeniously' contrived. From the small preaxial, anterior, margin of the mandible an apodeme extends upwards and outwards into the 'cheeks' of the head below the eye (figures 10*a*, 12*a*), and from its tip three muscles (in four sectors) pass upwards and inwards to the tergal ala, cranium and marginal line. Contraction of these muscles pulls the apodeme towards the middle line, thereby abducting the mandible, the apodeme working at a poor mechanical advantage since its origin is so close to the hinge. The muscles are the homologues of the simple mandibular promotor (abductor) 3 of *Anaspides*. Promotor (abductors) 5*b* and 6 and remotor (adductors) 2 and 5*c* are absent. Thus the mandible of *Ligia* is almost empty of muscles, as are those of other arthropods which have achieved transverse biting by comparable means (Decapoda and Pterygota; see below).

The gnathal armature of the mandible remains typically peracaridan but the incisor process is very strong. The molar process is suitably modified for the transverse instead of the rolling movement. The area of fine cuticular serrations is restricted to the inner upper part of the molar area, the corners of which are brought together by adduction, and slight asymmetry of the mandibles probably gives a rubbing effect between the opposing faces. The rest of the molar area is densely clothed with hairs which on adduction reach the middle line and are directed towards the mouth. These hairs must push food towards the small areas of contact between the molar lobes and press it forwards into the mouth. Much greater modification of the gnathal edge is found in the more specialized Decapoda.

11. Conclusions concerning the more specialized Peracarida

The vertical position of the axis of mandibular roll in *Chirocephalus* and *Nebalia* favours a maximum capacity for molar trituition of fine material. A slightly oblique axis in *Hemimysis* reduces the grinding capacity, but permits incisor process biting as well. This tendency is carried further by *Paranaspides* and *Anaspides* with a more oblique axis. The horizontal axis of *Ligia* increases the efficiency of incisor process biting to a maximum, but at the expense of the trituritive ability of the molar areas.

The absence in *Ligia* of a transverse mandibular tendon, such as seen in *Chirocephalus* and the more primitive malacostracan *Anaspides*, is correlated with the disappearance of most of the transverse mandibular muscles except for a remnant of remotor muscle 5*a*, which now inserts upon a process from the sternal ala apodeme. Comparable transfers of transverse muscles to head apodemes occur in decapods and in *Ctenolepisma* (see §§ 12 and 19 (ii)) and have been noted by Snodgrass (1950) in Amphipoda and Decapoda. The functional significance of these changes is now apparent. The elimination of a transverse tendon and its muscles permits easy wide movements of the mandible and a wide gape (for the reason given on p. 19) which are serviceable in large-food feeding. A strongly biting mandible projecting as far from the body as shown in figure 12*a* (cf. figure 3C, D) is dependent upon the absence of transverse ties, the great elaboration of muscle systems 3 and 4 and their apodemes, and the strengthening of the head wall. Such changes do not support the view that evolutionary advance in muscular systems takes place mainly by simplification (Applegarth 1952), although only two principal, but complex, muscle systems remain compared with a greater number in primitive Malacostraca. The mandible of *Ligia* is independent of the head endoskeleton owing to the ample support given by the hinge. The main head apodeme (sternal ala of Jackson) remains as the primary site of insertion of the extrinsic maxilla 1 and maxilla 2 muscles whose positions are roughly indicated by the arrow on figure 11.

The mandibular mechanism of *Ligia* bears a superficial resemblance to that of the Pterygota, and those of the more primitive Crustacea, *Chirocephalus* and *Anaspides* (see above) show a resemblance to that of *Petrobius*, but the similarities in all cases are considered to be due to convergence (§§ 21 and 33 (iii)).

12. THE MANDIBULAR MECHANISMS OF CRAYFISH *ASTACUS FLUVIATILIS* (*POTAMOBIUS ASTACUS* L.) AND CRAB (*CARCINUS MAENAS* L.)

The mandibles of a number of decapod Crustacea are well known, and it will be sufficient here to refer to the mandibular skeleto-muscular systems of the crayfish (Schmidt 1915) which resembles that of *Palinurus* (Parker & Rich 1893) and to the shore crab *Carcinus maenas* (Borradaile 1922; Snodgrass 1950) which resembles *Cancer* (Pearson 1908). In both these decapods the whole gnathal edge of the mandibles forms a strong gripping or cutting blade and the grinding molar area of more primitive Crustacea, which is still present in *Ligia*, is absent. The labrum does not overhang the mandibles, as in most arthropods with strongly biting mandibles, it tucks between the gnathal edges in front of the mouth, the mandibular palps preventing antero-lateral escape of food. The mandibles receive food from the maxillipeds and chelipeds for holding, crushing and cutting, and do not bite into the food mass alternately with the maxillules as in *Ligia*. The mandibles are relatively smaller than in *Ligia*.

Figures 13*a* and *b* show side views of the mandibles of the crayfish and crab with the lateral parts of the head removed as far as the union of the mandible with the head. The axis of swing of the mandibles is marked by a dotted line between the cross and spot, as in figures 5 and 7; here it is oblique because of the backward position of the dorsal articulation, marked by a cross. In both decapods a hinge is formed which allows biting in the transverse plane, and there is no freedom at the point marked by the black spot, as in the rolling type of mandible (*Chirocephalus* and *Anaspides*). The main hinge in the crayfish is formed by an elongation of the dorsal articulation along the anterior margin. In the crab the dorsal articulation is very weak and a strong anterior articulation (near the black spot) lies between epistome and the mandible at the base of the mandibular palp. The corresponding anterior articulation in the crayfish is weak and lies further from the mandibular biting edge. The mandibular movements in these decapods are clearly derivable from that of the *Anaspides* type by the formation of an anterior hinge. The muscular system of *Anaspides* is also clearly recognizable in both decapods, but additional apodemes are present. A small one projects from the anterior margin of the mandible in crayfish and a much longer one in the crab (white in figures 13*a*, *b*, *c* and *d*). In the crab the anterior ventral position of the hinge enables the morphologically dorsal part of the mandible to be in line with the anterior apodeme so that the two form a very long lever (as noted by Snodgrass (1950)) which is responsible for the strong 'bite' of the crab.

The modifications of the remotor (adductor) musculature of the two decapods differs from that of *Ligia*, although all are based upon the same plan found in *Anaspides* and other primitive Malacostraca. Muscle 4 becomes the principal adductor in the crayfish, but is very small in the crab, and a strong calcified articulated apodeme in both carries the muscle towards the dorsal surface, but in a more posterior position than in *Anaspides* giving suitable leverage to the more obliquely set mandible. Remotor (adductor) 2 (adductor lateralis mandibulae of Schmidt) from the anterior apodeme passes outwards to the lateral head wall in both decapods, pulling at a more advantageous angle than in *Anaspides* (figures 7, 9B and 13*d*) owing to the presence of the anterior apodeme. The muscle in the crab (the external adductor of Pearson) is very large and pulls from a tendinous flap set at a sharp angle to the tip of the apodeme, so providing plenty of surface far from the hinge for the origin of muscles 1 and 2. In the crayfish a forward extension of muscle 2, corresponding with the separate adductor 1 of the crab, passes forwards to the front wall of the head (figures 13*b* to *d*). Muscles 1 and 2 in the crab are now the principal adductors, superseding muscle 4. The more ventral part of the transverse muscle 5*a* is present in the crayfish, but inserts on to the head endophragmal skeleton, no transverse tendon being present; muscle 5*c* is absent. The crab also lacks muscle 5*c* and muscle 5*a* is much reduced as shown by Snodgrass (1950); the antero-ventral hinge allows little space for muscles pulling on its postero-ventral side, so large a proportion of the mandible being a narrow skeletal lever. Muscle 5*a* is not shown in figure 13 (see Snodgrass 1950, fig. 16*B* IV).

Promotor (abductor) muscles 3 and 6 are present in both decapods but 5*b* is absent. Muscle 3 leaves the anterior margin of the mandible close to the dorsal articulation in the crayfish and from a long thin apodeme similarly situated in the crab (figures 13*a*, *b*) and passes directly upwards to the head wall (cf. figure 7 and 9C). Muscle 6 leaves the anterior apodeme in both and passes inwards and backwards to the endophragmal skeleton (figures 13*a–c*) as the 'abductor major' of Schmidt and the 'internal abductor' of Pearson. In *Anaspides* the homologous muscle 6 inserts upon tendinous endoskeleton (figures 7, 9C). In the crab muscle 6 is much more bulky than muscle 3 and forms the principal antagonist of muscles 1 and 2.

13. CONCLUSIONS CONCERNING THE CRAYFISH *ASTACUS FLUVIATILIS* (*POTAMOBIUS ASTACUS* L.) AND CRAB *CARCINUS MAENAS* (L.)

Thus a common basis for the unlike mandibular mechanisms of *Ligia* and crab can be recognized in the skeleto-musculature and movements in spite of great differences in the shapes of the heads and mandibles, and both mechanisms are derivatives of the mysid-*Anaspides* type.* Antagonistic muscles swing the transversely biting mandibles about a

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* The claim that decapod mandibular muscles 1, 2 and 3 represent the 'single dorsal promotor, or anterior rotator' muscle of *Anaspides* (Snodgrass 1952) will not be discussed further, since the homologues of these decapod muscles are clearly recognizable in *Anaspides* where they possess antagonistic functions. The decapod adductor muscles 1 and 2 correspond with a single muscle 2 in *Anaspides*, but these muscles are not always separate from one another in decapods.

differently placed hinge in both *Ligia* and crab, but these are muscles 4 and 3 in the former and principally muscles 1–2 and 6 in the latter.

The reduction of the transverse muscles 5*a*, 5*b* and 5*c* and elimination of the tranverse mandibular tendon in the crayfish is probably correlated with the same factors already noted for *Ligia* (p. 19), although the gape is not so wide as in animals possessing a wide labrum (figures 10*b*, 12*a*, 13*e*, 28). The closed and open positions of the crab mandibles are shown in figures 13*d* and *e*, from the anterior and ventral aspects respectively. The greater reduction of the transverse mandibular muscles in the crab than the crayfish is correlated with the formation of a lever from the combined upper mandible and anterior apodeme whose length is several times the distance between the anterior articulation and the cutting edge. An extensive displacement of the tip of the apodeme results in a lesser but stronger displacement of the biting cusps and leaves less space for muscle 5*a* as seen in the crayfish. Large movements of the tip of the anterior apodeme can only be promoted by long muscles, note the great length of muscles 1 and 2 in the crab compared with the size of the gnathal lobe, made possible by the wide carapace (figures 13*c*, *d*). Long muscles 1, 2 and 6 are easily housed in the wide cephalothorax.

The mandibular mechanisms of *Ligia* and crab are two examples of many divergent evolutions within the Malacostraca. A mandible which in effect is a rod which see-saws about a middle articulation, as in the crab, is very rare in arthropods. Such a device is present in the Chilopoda although the details are very different, the middle fulcrum being the chilopod transverse muscle and tendon (§ 31 (ii)).

The suggestion has been made that the bite of a crab is less efficient than that of a pterygote insect. This conclusion seems to be questionable, although no comparative figures have been obtained of the biting forces which can be exerted by these animals. The mandibular cuticle of large crabs is much marked and worn and the bite is very effective for cutting and holding. The mandibular adductors of *Ligia* and the locust are about as large as the deep and dome-shaped head capsules will allow, and these muscles pull on apodemes situated on the same side of the articulation as the effective bite. The long lever of the crab, situated on the opposite side of the articulation to that of the biting cusps, is mechanically a much more advantageous arrangement. The bulk of mandibular muscle in the crab is relatively less than that of *Ligia* and the locust, and the head space in the crab could easily accommodate more muscle. The amount present is presumably suitable for the crab's needs and the lever system makes possible this economy in muscle.

14. THE FEEDING MECHANISM OF THE CHELICERATA

The Chelicerata share with the Crustacea the utilization of pairs of biting or chewing mesially directed coxal lobes or gnathobases, but the Chelicerata differ from the Crustacea in that their biting is done primarily by direct adductor-abductor movements in the transverse plane and not by an antero-posterior roll or a derivative thereof (see above).

In *Limulus** both locomotory and feeding movements are carried out by prosomal limbs 2 to 5, and fairly soft but large food, such as worms and molluscs, can be shredded and entirely eaten with rapidity. The Arachnida, on the contrary, are fluid feeders, chewing their prey with the coxae of the pedipalps for long periods, and the distal parts of these

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* See footnote † p. 31.

limbs are not usually locomotory. However, the coxal feeding movements of the Xiphosura and Arachnida are essentially similar.

The scorpion's feeding mechanism has recently been described by Alexander (1958) and it will be convenient to refer briefly to this animal before considering the anatomy and movements of *Limulus*.

The prey of the scorpion, consisting of other arthropods, is caught by the chelae of the pedipalps, with which it is crunched several times, and brought up to the alternately grasping chelicerae. These tear pieces off the prey and pull them towards the preoral cavity. The coxae of the scorpion's pedipalps form the side walls of a preoral cavity situated between the labrum above and the endites of walking legs 1 and 2 below. The pedipalp coxae carry out rhythmical small sideways-medial movements which enlarge and reduce the size of the preoral cavity into which food has been pushed by the chelicerae. The endites of walking legs 1 and 2 assist by their slight movements. Digestive juice from the mouth is poured over the food and alternately sucked back. Chewing may be exercised for as long as three hours, interrupted at intervals by the rejection of a hard, indigestible and compact mass in which every segment of the legs and antennae of the prey is crushed or split open. The alternate grasping by chelicerae, which place the food between transversely chewing gnathobases of more posterior limbs, exactly resemble part of the feeding mechanism of *Limulus*.

(i) *Exoskeleton of* Tachypleus tridentatus *Leach**

The skeleto-musculature of *Limulus* has been described by Benham (in Lankester, Benham & Beck 1885), Patten & Redenbaugh (1899, 1900) etc., but the mode of action of the system does not appear to have been ascertained from living animals, and the views of Snodgrass (1952) concerning the mode of action of the limbs are not confirmed.

The endosternite, correctly described by Lankester (1881) as an enlargement and interlacing of the tendons of certain muscles, represents the segmental transverse tendons typical of all arthropods (§ 4 (ii)). These tendons on the prosomal segments are enlarged, as is frequent in arthropod heads, and fused together (blue in figures 14 to 16; cf. figures 3C–D, 5*e*, *f*, 9C, E, 21, 24, 32, 44, 53, 57 and 63). The substantial form of the endosternite is associated with the strong digging and feeding movements of the closely set prosomal limbs set in so flexible a body wall (see below).

The coxae of the prosomal legs 5 and 6 are seen in anterior view in figures 14*a* and 15 and a sagittal half of the prosoma (figure 16) shows the relationship of the parts. The coxae of legs 2 to 6 are remarkable for their enormous size compared with the body proper, excluding the carapace. Terrestrial and fast moving arthropods usually do not possess such large legs. Each coxa extends up the pleuron from the lateral edges of the flexible prosomal sternite as shown, the coxa being narrow antero-posteriorly (figures 16*a*, 17*a*, *b*). The coxae of legs 6 are set approximately transversely to the body while the dorsal ends of those in front fan forwards as shown by the dotted lines on figure 16*a* (also figure 67, plate 1). A maximum amount of space is thereby gained for the carapace insertions of extrinsic coxal muscles 25 to 29 (see below), while successive gnathobases can be brought very close together (figures 16, 18*e*).

* See footnote † p. 31.

The spines on the anterior and mesial edges of the gnathobases are directed towards the middle line as shown by figure 67, plate 1, those from the second coxa lying across the gnathobase of the third leg (see p. 35). The gnathobases of legs 2 to 4 are closely set and sloped, but a gap can be left between the gnathobases of legs 5 and 6 as shown in figure 16*a*. This gap can be closed, the gnathobases of leg 6 being drawn forward as in figure 17*b*. The gnathobases of leg 6 curve closely round the anterior side of the chilaria in all leg positions (figure 18; also figures 68, 69, plate 1). These gnathobases are the most jaw-like of all and bear heavy cusps which in large specimens appear to be much worn and flattened, an appearance seen also on the mandibles of very large crabs and elderly Anomura long past a moult. Some particularly strong spines are borne by the gnathobases of legs 5 (figures 14*b*, c and figures 68, 69, plate 1) and anteriorly the spines are more slender. The paired gnathobases can meet each other in the middle line more closely than in figures 14 and 15 and they can swing out as in figure 67, plate 1. The position of the coxa of left leg 3 in this photograph shows the limit of abduction, see also figure 18*a*, where the black spot marks the ventral mesial corner of the gnathobase at the edge of the median 'food basin', on adduction of the coxa this point reaches the middle line. The sternite roofs this food basin.

The gnathobases of legs 3 to 5 each possess a movable transversely flattened endite directed towards the mouth which bears spines on its mesial edge and anterior face (figures 14, 16). The endite is tightly hinged to the coxa along its straight posterior margin, but anteriorly the endite is set in ample arthrodial membrane linking it with the stiff coxal cuticle (figures 14*b*, *c*). The hard parts of the hinge are so arranged as to prohibit

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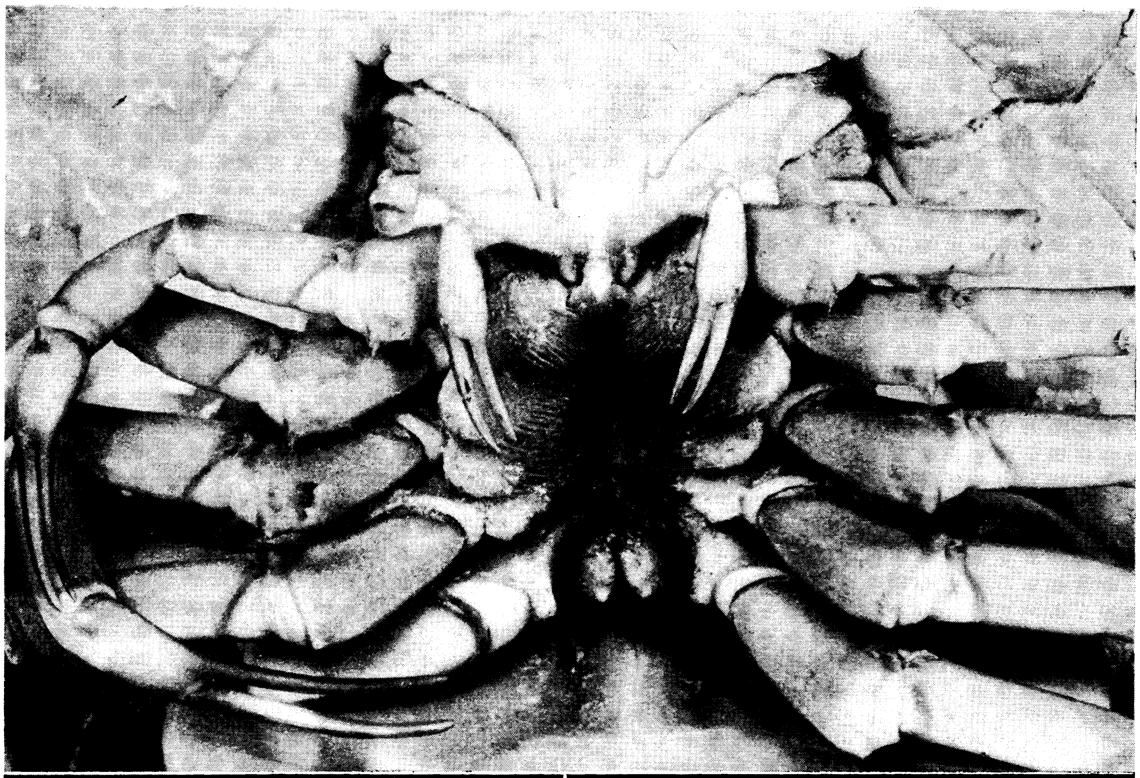
Description of plate 1

Figure 67. Ventral view of a dead *Limulus rotundicauda* Latr. with its gnathobases in a position of abduction, exposing the food basin, roofed by the sternite, in the middle line between the chilaria and labrum (see figure 18). The animal's left 3rd coxa shows the most lateral position reached during feeding; and the overlap of the spines of the gnathobase of leg 2 on the succeeding gnathobases is shown. The furrows at the dorsal ends of the coxae of legs 2 and 3 are visible anterior to the telopodite of leg 2.

Figures 68, 69. Ventral views of *Limulus polyphemus* L. walking on the glass bottom of a tank. The distal parts of the legs bearing the pincers are much foreshortened, and the 'knee' extends upwards towards the carapace. The chelicerae are turned backwards and have open pincers. The legs were moving in irregular metachronal rhythm. In both photographs the gnathobases of legs 2 almost meet in the middle line, anterior to them lies the labrum, and the sternite and mouth entrance is exposed behind them. On adduction the gnathobases of legs 3 to 5 meet ventral to the sternite.

Figure 68. Legs 2, 3, 5 and 6 on the animal's right side are executing the propulsive backstroke. Legs 5 and 6 are in the backstroke of pace '*n*', legs 4 have just completed this pace and have left the ground, and legs 2 and 3 are starting the backstroke of pace '$n+1$'. The cusped gnathobase of legs 6 are seen close round the chilaria and the strongly sclerotized spines of the gnathobases of legs 5 almost meet in the middle line.

Figure 69. Ventral view as for figure 68. The strongly sclerotized spines of gnathobases of legs 5 are here slightly abducted, leg 5 being at the beginning of the backstroke. Legs 2 are off the ground and starting their forward swing.



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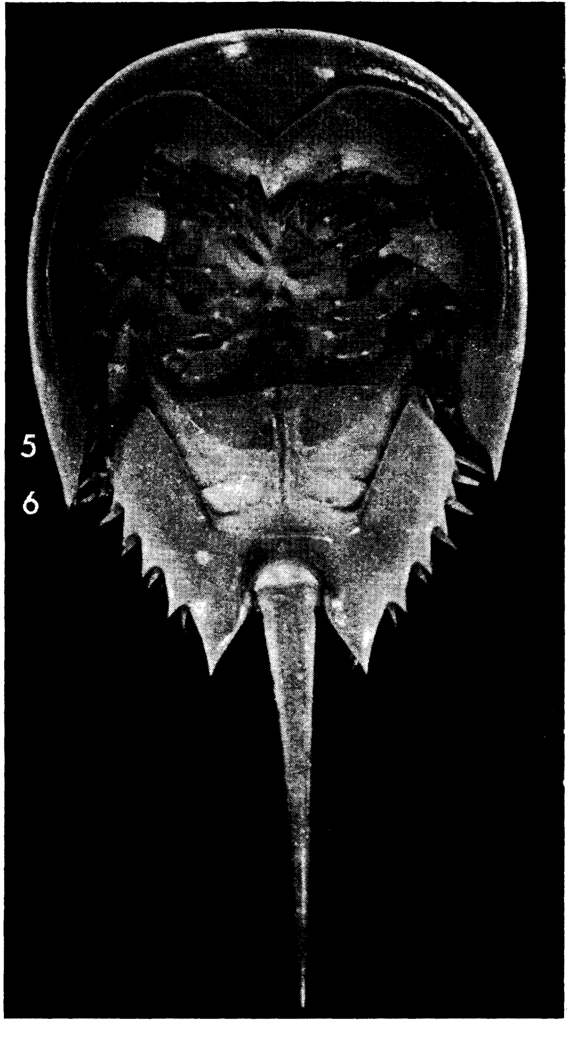

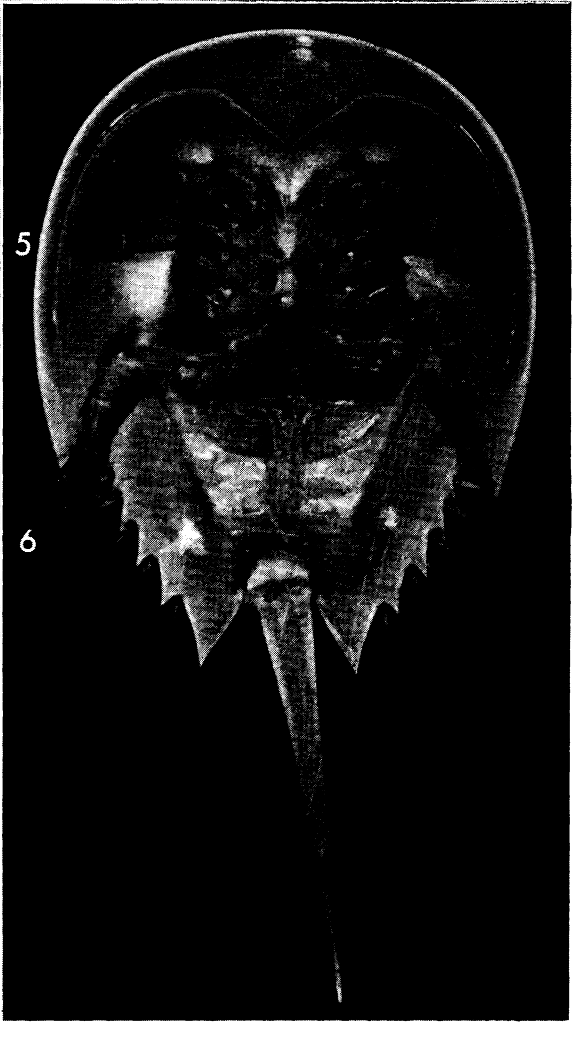

any flexure of the endite on the coxa in a posterior direction, but free anterior flexure of the endite can take place (figure 16*b*). A muscle extends from the most lateral part of the base of the endite to the posterior rim of the coxa below muscle 42 (figure 14*a*, *c*). When the endite is passively flapped forwards this muscle can pull it back into line with the rest of the gnathobase.* The presence of a large nerve passing into the endite (figure 14*a*) indicates an abundance of sensory nerve endings, probably concerned with taste and mechanical pressure.

Dorsally each coxa articulates with the stem of a Y-shaped pleurite situated at the edge of the leathery pleural wall which merges into the stiffer cuticle under the carapace fold (figures 17*a*, 18*b*). In front and behind this articulation the coxa bears anterior and posterior flanges from which abductor muscles 26 and 25 arise, the posterior flange being long, dorsally directed and sinking into a pocket of the pleural arthrodial membrane ('dorsal flange' in figures 14, 15, 17). The arms of successive pleurites unite with one another more or less, thus maintaining the dorsal spacing and stability of the coxae, which are ventrally so free.

The dorsal parts of the coxae of legs 2 to 5 bend sharply outwards to reach their articulations, which are thus as lateral as possible, and here internal cuticular ridges below external grooves pass from the articulation across the coxa to unite with its thickened margins as shown in figures 17*a*, *b*, and figure 67, plate 1. The bend in the coxa itself and the mouldings on the cuticle appear to be simple devices which support and strengthen the coxal cuticle where its surface area is smallest, bracing the coxa against the deformatory pull of adductor and abductor movements about the small pleuro-coxal articulation. A coxa with a flat pleural face would bend or buckle more easily. On leg 6 the basic plan of the ridges is the same. The regions marked X on coxa 5 and 6 in figures 15 and 17*a*, *b*, are comparable and the flabellum arises from this area on coxa 6. This coxa is much wider than those preceding it, so providing a greater internal surface for the insertions of intrinsic leg muscles appropriate for the digging activities of this limb. The ventral half of the cuticular ridge delimiting the area X on leg 6 in figures 17*a*, *b*, lies parallel to the lateral margin of the coxa above the flabellum (figure 15), and has been hailed as an obvious suture between a precoxa and coxa (see p. 38).

(ii) *The muscles and basic movements of the prosomal coxae of* Tachypleus tridentatus *Leach and* Limulus polyphemus *L.*†

The walking and burrowing movements of prosomal limbs 2 to 5 entail a promotor and remotor swing of the coxa on the body as in Crustacea and many Myriapoda. The muscles causing this swing insert on the carapace and endosternite. The former are neatly arranged in a manner avoiding mutual interference by the musculature of one leg and the next, although the limbs are so closely spaced. Remotor muscle 29 pulls on the arthrodial

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* The absence of a muscular antagonist to this endite muscle does not mean that cuticular elasticity is responsible for the reverse movement. Arthrodial membrane links the endite with the gnathobase, and the stiff cuticle at the hinge limits the passive movement to a certain range (see p. 34).

† Four species of recent Xiphosura are recognized, only one of which bears the generic name *Limulus* (Waterman 1958). The general similarity between these species suggests that the feeding and locomotory mechanisms are substantially similar. Only *Limulus polyphemus* L. has been studied alive and the anatomical work has been done largely upon *Tachypleus tridentatus* Leach.

membrane close to the posterior margin of the coxa and inserts dorsally on the carapace as in figure 14*a*. The promotor muscle 27 pulling from the anterior margin of the coxa inserts on a fibrous flange from the cuticle of the lateral groove, and is well away from muscle 29 of the preceding limb (figures 14*a*, 17*b*, *c*). Muscles 41*a* and 41*p* (figures 14*a*, 17*b*) from the anterior and posterior coxal margins to the endosternite contribute to this movement (see also below).

Adductor and abductor movements of the coxa in the transverse plane are effected by different muscles although simultaneous contraction of muscles 41*a* and 41*p* (figure 14*a*) presumably assists adduction. The musculature of legs 2 to 5 is similar and that of leg 5 is figured. The principal adductor muscles are 42 and 43, arising from the most ventral parts of the posterior and anterior margins respectively of the coxa and inserting on the ventral side of the endosternite. Owing to the lateral position of the coxal articulation on the pleurite, muscles 42 and 43 also levate the gnathobase and bring the movable endites just into the mouth opening. Muscle 28 appears to be mainly a levator, useful also as a stabilizer during adduction. This muscle passes from the upper part of the posterior coxal margin to the dorsal cuticle of the lateral groove (figure 14*a*) and is very large on the coxa of the heavy 6th leg (figure 15).

The principal abductor is muscle 25 pulling on the dorsal flange above the pleuro-coxal articulation. It is a thick muscle attached to a large area of the carapace to the side of the lateral groove, the series of similar muscles from limbs 2 to 6 forming close-set insertions. Small shortening of this muscle situated close to the articulation will pull the dorsal flange towards the middle line a little, and this will result in considerable abduction of the ventral parts of the coxa far removed from the fulcrum. A poor mechanical advantage for abductor muscles is frequent in arthropod jaws (cf. the abductor muscles of *Ligia* and locust and mandibular muscle 2 of *Scutigerella*; figures 10, 12*a*, 28 and 57*a*). Muscle 25 is aided by the more slender muscle 26 from the shorter postero-dorsal corner of the coxa which passes ventral to muscle 25 and inserts on the fibrous flange from the lateral groove (figures 14*a*, 17*b*, *c*). Mechanical interference between muscles 25 and 26 is thus neatly avoided.

It is probable that the pleurites themselves are pulled inwards a little by abductor muscles 25 and 26. The under side of the carapace fold is only rigid round its margins and a little way from them. The area shown by coarse strippling in figure 18*b* is flexible and allows some movement. Lateral flexibility under the carapace is absent in most Malacostraca, and one would expect rigidity to have been developed in this position in *Limulus* had there been some mechanical advantage in it. This flexibility of the leathery cuticle permits the whole coxa to pivot about the endosternite a little, thus enhancing the range of adductor and abductor effects at the gnathobase. The dorsal coxal muscle shown in figure 15, left-hand side, may assist the restoration of the outward movement of the coxal articulation; this muscle is absent on the less heavy anterior coxae. Such pivoting about a wide transverse mandibular tendon is marked in the mandible of *Campodea* (§22 (iv)).

The great width of the endosternite of *Limulus* results in short extrinsic muscles passing to it from the coxal margins, and these muscles lie at a considerable angle to each other in the horizontal plane, thereby most easily causing the promotor-remotor rocking of the coxa (muscles 41 *a* and 41 *p*, leg 5, and 44 *a* and 44 *p*, leg 6, on figures 14 *a*, 15 respectively, and 17 *b*). The same is true for the mandibles of *Chirocephalus*, *Anaspides*, *Petrobius* and *Campodea* (figures 2 *d*, 9 E, 24 H, 46 A, B).

The large coxae of leg 6 differ from those preceding them in possessing more bulky extrinsic musculature. Muscles 25, 26, 29 are similarly numbered on legs 5 and 6 in figures 14 *a* and 15, and muscles 44 *a*, 44 *p*, 45 and 46 from leg 6 are homologous with muscles 41 *a*, 41 *p*, 42 and 43 from leg 5. Two additional muscles are present, 47 and 60 from the most ventral part of the anterior and posterior margins respectively, which pass forwards to insert on the ventral side of the endosternite (figures 15, 17 *b*). Contraction of these two pairs of muscles pulls the gnathobases of legs 6 forwards and up to the gnathobases of legs 5, so closing the gap shown in figure 16, a movement used in feeding (see below). Probably muscle 29, which here passes backwards to the posterior margin of the carapace instead of upwards to the dorsal face (figures 14 *a*, 15, 17 *b*), acts as an antagonist to muscles 47 and 60, but during normal locomotion the gnathobases of leg 6 are not pulled forward at all.

(iii) *Walking and burrowing of* Limulus polyphemus *L.*

The record of the activities of *Limulus* given by Lockwood (1870) can now be amplified. Like the Diplopoda, *Limulus* walks slowly and burrows strongly to shallow depths by head-on shoving, using 'bottom gear' gaits (Manton 1952, 1954) which provide the greatest pushing force from the available legs. As is well known, the 6th and longest legs are the main digging organs and possess strong scale-like spines which fan out, so increasing the resistance to the substratum in which the animal is burrowing (figures 15, 18). Each pair of prosomal legs 2 to 5 is used in similar phase, and the short duration of the forward stroke compared with the backward stroke (often of the order of 2:8) enables 4 or 5 pairs of legs to be in the propulsive phase at any one moment. The phase difference between successive legs is small, of the order of 0·2+ to 0·1−, as is necessary for long legs situated close behind one another (figures 68, 69, plate 1 and Manton 1954). When walking fast in a bright light the relative duration of the forward to the backward stroke is (5·0:5·0) to (5·5:4·5) with a phase difference of about 0·16 between successive legs. The backstroke of the branchial limbs and genital operculum also gives a propulsive thrust, against the water, following on the backstroke of prosomal legs 6.* During walking, and presumably during burrowing also, the legs are kept under cover of the carapace except for the end of the backstroke of leg 6, see the fields of movement of the legs shown in figure 18 *c*. In the burrowing iuliform diplopods the legs are also covered by the flanks (Manton 1954). The fields of movement of legs 2 to 4 overlap greatly, thus permitting little change of gait, but that of leg 6 is almost clear of leg 5, and thus considerable freedom for variation in the digging movements by these legs is possible without causing interference with the other legs moving in metachronal rhythm (figure 18 *c*). The fields of movement of the legs of *Scutigera* and *Ligia* similarly overlap and stereotyped gaits result, compared with the lack of overlap and the variety of gaits in *Leander*, *Galeodes* and *Forficula* (Manton 1952,

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* The phase differences between legs 2 to 4 is usually greater than those between legs 5 and 6. The propulsive thrust of legs 5, 6 and of the opisthosomal limbs occurs almost simultaneously and gives a spurt to the walking and a strong heave to the digging movements.

text-figs. 2 and 3, and below). Strong flexure of the opisthosoma on the prosoma by the very strong flexor muscles (see legend to figure 16), and similar flexure of the spine, forces the head shield down into the substratum. The antagonistic retractor dorsalis, which merely straightens the body for surface walking, etc., is small.

(iv) *Feeding of* Limulus polyphemus *L.*

The chelicerae and prosomal legs 2 to 5 bear strong terminal pincers which can all reach the food basin between the chilaria, labrum and gnathobases (figure 18, and figure 67, plate 1). Food is found in the substratum by the pincers during burrowing. Soft food, such as a worm or a nudibranch, is manipulated by prosomal limbs 1 to 5 and by the chilaria, the gnathobases of coxae 3 to 5 forming a shredding and ingestion unit. Hard food, such as a lamellibranch, is subjected to a preliminary 'nut-cracking' treatment by the combined action of the 6th coxae, the chilaria and sometimes the genital operculum also, before being passed to the shredding gnathobases of legs 3 to 5.

Soft food is put deep into the food basin by any of the pincers. The grasping chelicerae, usually working alternately as in scorpion, are very active in putting the food between the chewing gnathobases behind coxae 2, where each pair moves in similar phase at a frequency of about 0·3 s. The promotor-remotor swing of the coxae seen in walking is replaced by adductor and abductor movements of equal duration (figures 18*d*, *e*). The phase difference between successive pairs of gnathobases during feeding is increased to 0·5 and successive legs thus move in opposite phase, an impossible rhythm for the walking promotor-remotor swing, but which is a usual relationship between the biting movements of mandibles and maxillae 1 in Isopoda and also in the more primitive Pterygota. By this means food is partly shredded and pushed forwards in the food basin.

Promotion of the genital operculum and contraction of muscles 47 and 60 and of the strong trunk flexor muscles have a telescoping effect upon the ventral surface of the prosoma, packing successive coxae close together (figures 18*d*, *e*), so preventing lateral escape of food from the food basin during chewing. A longitudinal spread of the coxae is necessary for the locomotory promotor-remotor swing. The difference in the lengths of the lines (*a*) and (*e*) in figure 18*i* shows the range of contraction and expansion; the pre-oral cuticle is rigid, and the postoral shortening during feeding produces a ventral surface 60 % of the length used when walking.

Owing to the lateral position of the pleuro-coxal articulation, adduction of the gnathobase also gives considerable levation to the movable endites of coxae 3 to 5. Their spineless posterior faces are pressed against the sternite, their long terminal spines enter the mouth opening (figure 16*a*), and the strong armature of the mesial edges and anterior surfaces pushes food forwards, upwards and into the mouth. On abduction the endites are brought into line with their gnathobases by the endite muscle (see above and figures 14*c*, 16*a*, *b*), and they are then ready to push and shred the next 'mouth full'. Levation of the endosternite, by contraction of its suspensory muscles from the carapace, facilitates close adduction and levation of the gnathobasic endites, so helping the ingestion of food. A lowering of the endosternite, caused by relaxation of its suspensory muscles while tension is maintained by the muscles between the coxae and the endosternite, facilitates wide gnathobasic abduction and the preliminary seizing of food.

The gnathobase of leg 2 curls closely round the side of the labrum, preventing anterior escape of food, and has no free endite. The most mesial spines of this gnathobase are directed upwards and backwards, across the free endites of the succeeding limbs (figure 67, plate 1, and not well shown in figure 16*a*). The large phase difference between successive legs during feeding results in the prey being held by some gnathobases and shredded and pushed forwards by others, while food sticking to the most mesial setae, particularly on the free endites, is scraped off by the upward and backwardly directed setae of the gnathobase of leg 2, leaving the food in the middle line where it will be pushed into the mouth by the next adductions of legs 3 to 5.

When the food mass is large, the gnathobases of legs 4 and 5 are most active, their strong spines shredding out a strand of tissue which is drawn forwards and passed into the mouth. Long objects are orientated and gripped by the chilaria, whose spinous antero-mesial margins can meet together (figures 68, 69, plate 1). The chilaria hold the food, swing forwards and pass it directly to the shredding gnathobases in front, by-passing the inert 6th coxae whose mesial dorso-ventral shortness facilitates this transfer. The chilaria also press food forwards into the food basin (figures 18*d–g*). A molluscan crystalline style, three times the length of the food basin, was gripped by the chilaria, passed forwards to coxae 5, shredded and swallowed with rapidity. Chilarial musculature, described by Patten & Redenbaugh (1899, text-fig. 14 and pls. VII and VIII), is suitable for creating these movements, muscle 7*c* is a strong promotor, muscle 7*a* a transverse adductor, muscles 7*e* and 7*f* are remotor-abductors, and muscle 7*d* is a remotor-adductor.

Hard food such as a lamellibranch, is gripped between the chilaria, and at times is pressed forward or held in position by promotion of the genital operculum, a position readily assumed during feeding when the genital operculum can lie up to 90° on the opithosoma. The strong cusped gnathobases of the 6th prosomal legs bite together, cracking or cutting the prey, the chilaria then assuming a vertical position (figure 18*g*). The gnathobasic armature of leg 6 is asymmetrical, as are the cusps on all mandibles. The food so gripped is moved forwards, together with the gnathobases of legs 6, towards the shredding limbs in front by muscles 47 and 60, and sometimes in a very asymmetrical manner, one or other gnathobase of legs 6 pushing the food forward (see left leg 6 in figure 18*a*). That this cracking up of hard food is very effective is shown by Turner, Ayers & Wheeler (1948) who record a *Limulus* $3\frac{1}{16}$ in. wide clearing a sand tray containing 100 $\frac{1}{2}$-in. clams within 72 h. Only one clam remained and the others were ground so that few shell fragments did not pass a sieve of 0·078 in. mesh. In this way well-populated clam beds can be depleted by *Limulus*. The more important food organisms appear to be *Nereis*, *Cerebratulus*, *Gemma*, *Macoma*, *Ensis* and *Mya* (Shuster 1950).

The opening of the mouth is controlled in part by a large muscle* extending from its posterior margin back to the transverse ‘endoskeletal connective’ (figure 16*a*), the ‘occipital ring’ of Patten & Redenbaugh (1900). This muscle may also control the shape and volume of the anterior part of the food basin and may, with the pair of lateral sternite muscles from the coxae of legs 5 (figure 14*a*), control the shape of the flexible sternite also.

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* This is probably a muscle but perhaps may be composed of some other type of fibril. Patten & Redenbaugh (1900) figure it as a muscle, but in my material it looks macroscopically different from the other muscles.

In a few minutes sufficient food can be swallowed to fill the proventriculus. After that the animal may walk about, still holding the remains of the food mass between the gnathobases. Abductor movements are then absent and the coxae carry out the normal promotor-remotor swing but maintain adductor tension.

Schlottke (1935) denies Lockwood's (1870) conclusion that 'die Nahrung durch die Gliedmassen sehr fein zerkleinert würde'. Schlottke fed *Limulus* on pieces of fish, and later found sizeable pieces of flesh in the proventriculus. However, when *Limulus* is fed on *Mya*, much too tough and large to be swallowed whole, the gnathobases shred persistently, producing narrow strands of tissue and small pieces which can be swallowed. Schlottke is correct in stating that comminution of food takes place in the gizzard, a short section of the foregut situated beyond the capacious proventriculus and communicating by a valve with the mid-gut (figure 16). The gizzard is longitudinally furrowed, and provided with 'in Reihen stehenden kräftigen, scharfen Chitinhöcker' (Schlottke 1935), but sand grains, quartz crystals, etc., were firmly lodged in the grooves in the specimens here examined so that the chitinous processes and the much larger mineral particles all can be brought together at the axis of the gizzard, the whole forming an effective organ of trituration allowing only fine material to pass on to the mid-gut. The rasping of one gnathobase across its fellow, as described by Lockwood (1870) in an animal held against the glass side of a tank, has not been observed in *Limulus* feeding freely on a glass bottomed tank or when held on its back, a position in which the animals will readily eat.

15. Conclusions concerning Chelicerata

The feeding mechanism of *Limulus* is unique among present-day arthropods, and is well suited to the burrowing life. Unlike most arthropods the strongest and most jaw-like pair of gnathobases lies at the posterior end of the series and not close to the mouth. The feeding mechanism of *Limulus* differs greatly from those of Crustacea which utilize a series of limbs (Notostraca, Cladocera, Chonchostraca, etc.). There is some resemblance to decapod feeding in that the cusped gnathobases of legs 6 of *Limulus* functionally resemble chelipeds, and the shredding gnathobases of legs 3 to 5 of *Limulus* resemble the maxillipeds of a decapod which often shred food which is held by the mandibles (Borradaile 1922). Such chelicerate and crustacean resemblances are clearly convergent, all the details being different. No crustacean shows a telescopic flexible surface bearing the principal limbs as in *Limulus*, and in Crustacea limb movements occur distal to static insertions formed by inflexible trunk cuticle. And no arthropod feeding mechanism shows such an approach to radial symmetry about a central prosomal mouth as shown by *Limulus*.

The biting mechanism

The skeleto-muscular system of the prosomal limbs of *Limulus* is suited to produce the observable movements, and the suggestion (Snodgrass 1952) that abductor muscles are absent and that cuticular elasticity is responsible for abductor movements is unfounded. There is no sclerotized cuticle situated between the coxa and body which could produce such a force.

The transverse chewing action of the gnathobases of *Limulus*, suited to large-food feeding, and of Arachnida, suited to fluid feeding, are essentially similar, but crustacean and chelicerate gnathobases are moved in a fundamentally different manner. Transverse biting in Crustacea is an end-point acquired secondarily from a promotor-remotor roll more than once in their evolution, but not from an exploitation of the small direct adductor-abductor movements seen in the mandible of *Chirocephalus*, promoted by muscles 5*d*, 5*e* and 6 without a lever (figure 3D). The direct transverse biting of the *Limulus* gnathobase appears to be primitive, and to indicate a wide phylogenetic gap between the Chelicerata and Crustacea, a conclusion in keeping with other points of similarity and difference between these two great groups (§§ 33 (i), (ii)).

Body form

Many structural features of *Limulus* can now be seen to be of functional significance, and the most conspicuous, as well as small morphological details, are correlated with feeding and locomotory habits. The form of the head shield, its ventral bracing ridges (figure 68, plate 1), and the relation of limb size and movement to the carapace shape, are as exact in suiting burrowing requirements as is the morphology of a iuliform diplopod (Manton 1954, 1961 *b*). The great influence which the burrowing habit has exercised upon the evolution of certain classes and orders of arthropods has recently been pointed out (Manton 1961 *a*). The limulid body form and feeding mechanism must have evolved early in association with shallow burrowing into the substratum and feeding there upon soft invertebrates. So successful have been these habits that they have persisted to the present time, but the niche is severely limited, and potential radiations from it need an ability to negotiate either large hard food or suspension feeding, unless the animal is to become an entirely scavenging bottom liver.

It is clear that the dorso-lateral grooves along the prosomal carapace and the dorsal crest of *Limulus* provide rigidity, bracing the cuticle against the pull of the promotor, remotor and abductor muscles from exceptionally large coxae, just as does the cervical groove of the anostracan and syncaridan head, the marginal and frontal lines of *Ligia*, etc. Reconstructions of trilobites, such as those of *Olenoides* by Størmer (1939), show a wider sternal expanse than on the *Limulus* prosoma, and fairly wide coxal bases from legs which are, as in *Limulus*, very large compared with the sectional area of the body proper. The two dorsal grooves of the carapace, which divide the trilobite body into the three longitudinal lobes, bear somewhat the same relationship to the coxae as do the less deep grooves of *Limulus*. The musculature extending between the coxae and the carapace of *Limulus* is simple, and such muscles, without the particular refinements seen in *Limulus*, might have been present in trilobites. The longitudinal grooves on the dorsal cuticle might have served the same purpose in the two. The tergite of each free short segment of a trilobite such as *Olenoides* would be very weak if it formed a simple arch from the mid-dorsal line to the edge of the pleural fold. The resemblance in body lobation between the trilobite larva and adult of *Limulus* and the trilobites may have a common functional basis. Whether the apodeme shown in Størmer's (1951) reconstructions carried extrinsic leg muscles is unknown, but trunk muscles are more likely to have been served by such structures.

Limb structure

In attempting to determine whether or not there is a basic uniformity of leg construction among fossil and living Arthropoda it has been suggested that the free endites of legs 3 to 5 of *Limulus*, together with the ridged part of the coxa supporting the pleuro-coxal articulation of legs 2 to 5 and bearing an exite (flabellum) on leg 6, indicate the remains of a once free precoxal segment. This conclusion is accepted by Fage (1949) and others. Størmer (1951) has reviewed the discussions on this subject, and they all lack an adequate functional consideration of limb structure. This is largely due to the shortage of suitable information concerning the correlations between structure and use of the limbs of living arthropods.

The present study shows that the presence of free endites by *Limulus* and the form of the dorsal part of the coxa are both directly connected with function. Since the endites push food into the mouth, any supposition that they once existed all along the body on free precoxal segments must imply some other function for the more posterior endites which could never reach the mouth. It seems more logical to regard the endites as having arisen just where they are, by the formation of a crescent of arthrodial membrane at their bases. The legs of scorpions show how easily an arachnid can 'carve out' a section of leg cuticle by the formation of a slot of arthrodial membrane round it when circumstances demand (see Manton 1958*b*, text-fig. 5B area '*d*' on the trochanter). The form of the dorsal part of the *Limulus* coxa is clearly suited to meet certain stresses and strains due to the proximity of the pleuro-coxal articulation and a need for a firm base for the flabellum on coxa 6, and its ridges may not represent sutures between units once free any more than the majority of 'sutures' on the heads of insects (Strenger 1952) and the ridges and folds of the head of *Ligia* (see above), which cannot be regarded as being anything more than local specializations serving functional needs.

Whether or not a free precoxal segment ever existed, there is no denying the similarity between the legs of Trilobita and Merostomata stressed by Strømer (1951), which suggests that the former may be the prototypes of the appendages of the Chelicerata. Trilobite reconstructions, however, do not show a movable proximal endite, and trilobite coxae near the mouth slope forwards ventrally, whereas those of *Limulus* slope in the opposite direction, the proximal mesial parts being farthest forward (figure 16). Thus it seems probable that the free endites of *Limulus* may have been evolved within the Merostomata alone, and only in the proximity of the mouth. Another example of the presence of gnathal lobes near the mouth alone is the Devonian *Cheloniellon*, 105 mm long, where well-developed gnathobases are present on the four legs behind the antennae but not further along the trunk.

16. Feeding mechanisms of terrestrial Arthropoda

The embryonic development of the mandibles of myriapods and hexapods shows that the adult jaw is formed from a whole limb rudiment and not from the base alone, as in crustacean mandibles and the prosomal limbs of *Limulus* and arachnids. Terminal cusps on the mandibles of myriapods and hexapods represent the tips of the limbs and not the tips of a basal endite or gnathobase as in Crustacea.

Glandular secretions are usually of greater importance in terrestrial classes than in most aquatic arthropods. Labral glands are particularly well developed in the Branchiopoda and assist the feeding mechanism (Cannon 1933, 1935) but generally the Crustacea do not produce copious fluids which lubricate the mouth parts, help transport food, carry out external digestion, provide grooming fluids, etc., and these functions are reflected in head morphology of terrestrial types. A median projection from the ventral head wall forms the hypopharynx, so typical of hexapods and myriapods, situated between the labium and mandibles. Among Crustacea it is the terrestrial or aerial feeding isopods in which a comparable structure is present, but here both maxilla 1 and 2 adduct in front of it. The superficial similarity between this median lobe of *Ligia* and the woodlice on the one hand and the hexapods and Symphyla on the other, in position, in the abundance of glandular tissue, in the paucity of intrinsic muscles, and the presence of a few extrinsic muscles is clearly a case of convergence, under somewhat similar environmental conditions. Among the least specialized of hexapods and myriapods there are many examples of hydraulic efficiency around a well defined preoral cavity, particularly in the least advanced forms. The aquatic habits of Crustacea do not lead to these developments.

Among terrestrial arthropods it is certain Thysanura which show an apparent resemblance to the Isopoda in head structure. It is the Thysanura also which show how a parting of two lines of head evolution has occurred within the Apterygota (see below), and it is necessary to consider the Thysanura with reference to the Pterygota and myriapod classes. But in order to arrive at an understanding of the mandibular mechanisms of all these animals it has been necessary also to consider to some extent the form and functions of the first maxilla and hypopharynx, etc.

The considerations which follow concerning the structure, functions and evolution of organs occurring in the myriapod and hexapod classes refer, unless otherwise qualified, to the less specialized representatives of these classes. Extreme specialization leads to modification or even loss of certain muscles, mouth parts or tentorium.

17. The mandibular movements and the feeding mechanism of *Petrobius brevistylis* Carpenter

Both *Petrobius* and *Ligia* run about swiftly above tide level and are omnivorous in habits. In both the head is short antero-posteriorly (figures 10*a* and 19*a*, *b*), one pair of long antennae is present, and the mouth parts project well below the head capsule (figures 11, 12*a*, 20, 21), their tips forming the small end of a cone which is applied to the surface of food. These general similarities are presumably due to convergence, since a maxillipedal segment is incorporated into the head of *Ligia* but not of *Petrobius*, and the former still retains a very short antennule (figure 11).

The mandible of *Petrobius* is long and narrow. It bears a molar lobe just below the mouth and a long distal spike, slightly serrated near the tip where the two mandibles can be approximated (figures 19*c*, 20, 21). Proximally the mandible ends in a small highly sclerotized ball which articulates with a shallow socket, also thick and sclerotized, in the otherwise thin cuticle below the small pleural fold (figures 19*b*, 21B, 4*a*). The socket is secured by unstriated fibrils to the dorsal head wall. Two horizontal flanges of strengthening cuticle lie across the dorsal narrow part of the mandible. Snodgrass (1950, 1951, etc.) has stressed the importance of the lack of a second mandibular articulation in an antero-ventral position, but if one were present it would make little difference to the mandibular movement. What is important is the position of an axis of swing of the mandible situated between the dorsal ball and socket, marked by a cross, and the black spot in figures 19*b* to *f*. This axis lies near the anterior margin of the mandible, and just behind is the laterally expanded part of the transverse mandibular tendon (cf. *Chirocephalus* and *Anaspides*, figures 3, 5*e*, *f*, 8 and 9 with 19, 20 and 21). Since the mandible is so narrow, the range of movement of its lateral face is smaller than in the above-named Crustacea. The ends of the promotor and remotor swing are shown in figures 19*c*, *d*, the former being directly comparable in aspect with figure 19*b* above it. The arrows show the direction of roll of the posterior margin and the solid line indicates the transverse part of the mandibular tendon. The remotor swing brings the molar areas together and approximates the distal spikes, but there is little or no biting or gripping; the promotor movement separates the mandibles. There is no large backward roll of the lateral part of the mandible, so that it occupies a quite different place on the 'cheeks', as in *Chirocephalus* (figures 1*a*, *b*).

The mandible of *Petrobius* is hardly visible in lateral aspect, being confined between the forwardly directed lobe of maxilla stipes, the base of maxilla 1 palp, the galea and the clypeo-labrum (figures 19*a*, *b*, 21, 23, 24). The drawings in the literature showing side views of the head of *Petrobius* with all the limbs set well apart could not provide a working basis for the feeding mechanism. The mandible rotates in a slot, the lateral mandibular margins alternately approaching the sagittal plane (see figures 23, 24H, J, muscle 5 being a promotor and muscles 6 and 7 being remotors). The distal spike of the mandible rotates in an almost enclosed slot between the labrum, galea and superlingua (figure 23F), the extreme tip only being free to scrape food surfaces.

The long median hypopharynx is separated from long, paired, superlinguae by a deep cleft through which runs the lacinia of maxilla 1 (figure 20). The large segmental organs of the labial segment are salivary in function and discharge behind the hypopharynx (figures 20, 23F). Their coiled ducts and end sacs lie dorso-laterally above and within the pleural folds (figures 19*b*, 21B, 22). The thin lateral edge of the labium can be held close against maxilla 1, both on the stiff part of the stipes and against its ample posterior arthrodial membrane, and the lateral distal parts of the labium overlap the lacinia and hinder edge of the galea (figures 19*a*, *b*, 23, 24).

During feeding salivary juice is poured over the surface of the food from behind the hypopharynx. The lateral walls of the feeding cone (labrum, galea, lacinia and labium) fit together well and enclose the elaborate and strong tips of the laciniae which, with the mandibular spikes alternately scratch, scrape and hold the food, stirring salivary juice into the abrasion. The long and narrow oesophagus is provided with adequate circular and longitudinal muscles capable of providing a suctorial peristalsis. Large-food feeders possess a wider oesophagus (cf. figures 5*e*, *f*, *g* with 20). Suction draws fluid and finely divided food up a food channel, situated between the labrum, superlinguae and hypopharynx (figure 23F), which leads into the narrow section of the preoral cavity lodging the molar lobes (figure 20). Comminution of food particles either by rubbing or squeezing together of the finely serrated molar surfaces follows, according to whether the movements of the mandibles occur in exactly the same or slightly alternate phase. The fine mass then enters the mouth, close behind which are large dilator muscles. The mesial projection of the molar surfaces on long lobes enables the hydraulic efficiency of the median food channel between labrum, superlinguae and hypopharynx to be maintained during movement of the distal mandibular spikes. It has not been possible to record the frequency of the mandibular movements, but it is probable that the movements of small amplitude can be carried out rapidly, much more rapidly than most crustacean mandibular movements.

The only major feature in common between the mandibular movements of *Petrobius* and certain Crustacea lies in the utilization of an anterior axis of rotation. The movements otherwise differ, and it is the Anostraca and less specialized Malacostraca and not the Isopoda which show a resemblance in the rolling movement. In other respects the morphology of the mandible, the associated endoskelton and muscles show considerable differences (see below and § 33 (iii)).

(i) *Endoskeletal basis of the feeding movements of* Petrobius brevistylis *Carpenter*

It is necessary to consider the musculature and endoskeleton of *Petrobius* more exactly than has hitherto been done because this is needed for an understanding of the observable movements and of the relationship of the morphology to that of other hexapods.

Endoskeletal apodemes

The paired anterior and posterior tentorial apodemes* are shown in red in the figures. Each anterior tentorial apodeme arises from a wide cuticular depression between the mandible and clypeo-labrum (figures 20, 21A, 24H) and passes inwards and backwards. The two form flat hollow plates, just separate from one another in the middle line (figure 21). Their inner anterior faces bear antennal muscles and their outer faces bear mandibular muscles. A blind ventral lobe on either side ends in the transverse tendon complex (see below and figure 20). Paired dorsal lobes carry a fan of muscles, E1, which insert over the posterior tentorial apodemes. A hollow dorsal suspensory process is attached by muscles to the dorsal head wall on either side (figures 20, 24K), and a muscle links the dorsal lobe with the preocular apodeme (figure 20, unlabelled).

The posterior tentorial apodeme does not arise from a pit in the extreme posterior angle of the cranial wall (Snodgrass 1951). It arises from a very long dorso-ventral intucking in the maxilla 1–labium intersegment extending from a point below the pleural fold to a point near the divergence of the free portions of maxilla 1 and labium; both are marked on figure 19*b* and the whole opening is shown by dotted lines in figure 20. The horizontal section in figure 24J also shows the external opening. The apodemes pass inwards and slightly forwards and unite in the middle line. The bridge so formed is not a narrow postero-dorsal bar as often figured. The cuticle dorsally is thickest and is shaped so that it appears to have considerable antero-posterior thickness when viewed from in front or behind. In sagittal section the whole transverse bridge is Y-shaped. The arms of the Y are short, bearing muscle E 3 to the prothorax at the head-thorax articulation (figure 20),

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* Snodgrass has stated (1951) that the Thysanura lack a tentorium but that they possess the elements which compose the insect tentorium. These elements here will be termed the anterior and posterior tentorial apodemes because they correspond exactly with the component apodemes of the pterygote tentorium (§§ 19 (i), 20).

and form the transverse structure seen in the transverse sections (figures 22D, E). The stem of the Y is less long than the exterior tentorial opening and is curved ventrally. On either side a ventral lobe extends forwards and supports the median tendinous base of maxillary muscles VI and VII, endoskeletal muscle 4 lying between the apodemes and the median tendon (figures 20, 22E, 24H). The anterior face of the posterior tentorial apodeme bears the endoskeletal muscles E 1 and E 2 from the anterior tentorial apodeme and the posterior face bears the ventral longitudinal muscles from the trunk (figure 20). Muscle E 2 is drawn in two sectors, only one of which is labelled, and E 2 is the more bulky of the two muscles (figures 22D, E). Muscles E 1 and E 2 must be antagonists to some extent, and certainly control the relative positions of anterior and posterior tentorial apodemes (see also § 20).

Paired preocular and postocular apodemes lie more dorsally in the head, the latter passing in from the postocular groove (figures 20, 21A). These apodemes bear mandibular and maxilla 1 muscles and sectors of the dorsal longitudinal muscle.

These head apodemes of *Petrobius* bear no close resemblance to those of any crustacean head considered here. The anterior tentorial apodeme is entirely absent in these Crustacea. The posterior tentorial apodeme resembles the paired head apodemes of *Ligia* in that it takes its origin from the maxilla 1–2 intersegment and supports maxilla 1 muscles, but in all other respects the differences are striking. A superficial set of cuticular ribs, such as those forming the 'maxillo-sternal framework' of *Ligia* (Jackson 1926, and p. 24 above), is not present in *Petrobius*, although certain cuticular thickenings exist as in most arthropods. The most conspicuous of these is a dorso-ventral sclerite supporting the anterior angle between labium and head, shown in the horizontal sections in figures 23G, 24H).

Endoskeletal transverse tendons

Well-developed transverse mandibular and maxillary tendons are present (figure 24H) which carry the transverse muscles to these limbs. The two tendons are united by a web of connective tissue fibrils in the sagittal plane, shown diagrammatically in figure 20, and the fibrillar complex extends posteriorly between maxillary muscles VI (figure 24H). The ventral lobes of the anterior tentorial apodemes end blindly within the maxillary tendon (figure 22C, D). A pair of short muscles ties the mandibular tendon to the ventral inner faces of the anterior tentorial apodemes above it, unlabelled on figures 20, 21.

In the presence of transverse mandibular and maxilla 1 tendons *Petrobius* resembles the more primitive Malacostraca, but the details of the tendons and of their connexions are entirely different in the two, and no such tendons are present in the Isopoda.

(ii) *Musculature and movements of the mandible of* Petrobius brevistylis *Carpenter*

Mandibular muscles are labelled by Arabic, and maxilla 1 muscles by Roman, numerals in the figures. The anterior margin of the mandible is strengthened by a fold of stiff cuticle as shown in figures 21A and 24J, and carries a number of promotor muscles: muscles 1, 2 and 3 pass upwards to insert respectively on the head wall just above the pleural fold, on the head wall just above and in front of the postocular apodeme and on to the postocular apodeme itself (figures 19*b*, 21A, 24J). Muscles 4 and 5 pass inwards and a little downwards to the outer face of the anterior tentorial apodeme as shown in figures 21A, 24J.

The posterior mandibular margin is strengthened by an inwardly directed thickened ridge (figures 21B, 24J) and it bears remotor muscles 6 and 7, the former passing obliquely and the latter transversely to the outer face of the anterior tentorial apodeme behind muscles 4 and 5 (figures 21, 24H, J). A hollow, rod-like apodeme leaves the posterior mandibular margin just above the molar lobe and passes dorsally, bearing remotor muscle 11, which inserts on the dorsal head wall, interdigitating with its fellow from the opposite side (figure 21B).

The cavity of the mandible is filled with a fan of muscles, 8, 9 and 10 shown in figure 21, all inserting on the transverse segmental tendon, a separate tendinous section passing ventro-laterally to support muscle 10. Simultaneous contraction of all these so-called adductor muscles must produce adduction, but alternate contraction of muscles 9 and 10 could cause slight rocking of the whole mandible about the transverse tendon. Muscle 10 must tend to levate the molar processes and relaxation of muscles 4, 7 and 9 must allow the whole dorsal ball and socket articulation to move outwards a little since the articulation is set in very flexible cuticle of the pleural fold. The different slopes of muscles 4 and 5 and of muscles 6 and 7 so that they pull in different directions probably would not be present did they not serve some function, which appears to be a very slight adductor-abductor rocking movement about the transverse tendon. A much more important rocking movement occurs about the tendon in the horizontal plane caused by the promotor and remotor fibres marked in figure 24H, the latter being much the stronger.

It is clear that the mandibular musculature is suited to produce the observed movements. Moreover, the great differences between the mandibular musculature of *Petrobius* and of Crustacea with the rolling type of mandible emphasizes the specialities of *Petrobius*. The rapid scratching action of the distal mandibular spikes, doubtless capable of much minor variation in detail, and brought about by a mandible rolling within a socket, needs (i) a freely twisting dorsal mandibular articulation, (ii) strong promotor as well as remotor muscles pulling on the anterior and posterior margins of the mandible, and (iii) a wide transverse mandibular tendon which will give divergent slopes to the muscles fanning from it in a dorso-ventral as well as a horizontal direction.

The promotor muscles 1, 2, 3, 4 and 5 provide much greater strength than would be required of muscles which perform only the recovery swing of the mandible (cf. promotor muscle 3 of *Chirocephalus* and *Hemimysis*, promotor muscles 3 and 6 of *Anaspides*, the single abductor of the locust (figures 3, 7, 9 and 28) and the maxilla 1 muscles XI and XIII of *Petrobius* which are antagonistic to ten bulky effector muscles; see next section). Therefore the scratching mandibular spike of *Petrobius* is probably effective on both the promotor and remotor movement. Muscles 6 and 7 are a little more bulky than muscles 4 and 5, and, with the strong muscle 11, provide a remotor roll which must be stronger than the promotor roll, doubtless of service for grinding by the molar lobes. Among Crustacea it is possible that the stylet-like mandibles of certain parasitic Copepoda scratch effectively in more than one direction, and the Branchiopoda can roll the mandibles across each other on the promotor as well as the remotor roll. Whether or not the nick which lies in *Petrobius* on the inner face of the mandibular cuticle below the molar lobe (figure 21) houses some sensory or proprioceptive device, which is useful in the scratching movement, is not known.

Endoskeletal movements which may promote a slight protractor piercing action by the mandibles are considered in § 20.

The absence of direct transverse muscles comparable with 5*c* of *Chirocephalus* and *Anaspides* is doubtless due to the difference in the type of rolling movement, the lateral part of the mandible of *Petrobius* not being carried far back on the remotor swing.

Both the Malacostraca and *Petrobius* utilize a posterior mandibular apodeme, adductor in function, and they both use the head wall for the insertions of promotor muscles. The former feature is of frequent occurrence in arthropods including Onychophora, but the apodeme does not appear to be always homologous (pp. 74, 105). The latter feature is of general occurrence in all classes of arthropods, including the prosomal limbs of *Limulus*. It is unlikely that these two resemblances between *Petrobius* and Crustacea are anything more than convergent (§ 33 (iii)).

(iii) *Musculature and movements of maxilla* 1 *of* Petrobius brevistylis *Carpenter*

Proximally the cardo bears a strong postero-dorsal point of articulation with the cranium, below the hinder part of the pleural fold and just anterior to the intucking of the posterior tentorial apodeme. Distally a long antero-posterior hinge unites cardo and stipes (figures 19*b*, 22). The cranial articulation allows a variety of small movements while the cardo-stipes hinge permits considerable adductor-abductor movements of the stipes. The lacinia tip is complex, the shaft is strongly constructed and lies in the cleft between the superlingua and hypopharynx. The lacinia is hinged to the stipes laterally; mesially a long stout lacinial apodeme, flattened in the transverse plane, projects into the stipes, anterior to muscle X (figures 22, 23F, G, 24H, J). This apodeme can be retracted, so adducting the lacinia. The apodeme is a very strong replacement of the tendons of flexor muscles situated in this position in the distal segments of a walking leg.

The maxilla 1 muscles are shown in anterior view in transverse sections at progressively more posterior levels in figures 22C, D, E.

Promotion of the cardo and stipes is caused by muscle XII, arising from arthrodial membrane near the anterior margin of the stipes (but directly from the cardo in *Ctenolepisma* and Pterygota), and inserting on to the inner end of the postocular apodeme (figures, 19*b*, 21A, 24K). The distal origin of this muscle in *Petrobius* is probably correlated with the great length of the mouth parts compared with the biting Thysanura (Lepismatidae) and Pterygota.

Very strong rectractor-adductor movements of the lacinia are effected by (i) muscles arising from the lacinia apodeme: muscle I passes to the cavity of the stipes (figures 22C, 24H, J); muscles III and IV pass to the lateral head wall between the origin of the pleural fold and the postocular apodeme (figures 19*b*, 21A, 22C, 24J); and muscle V passes to the posterior edge of the anterior tentorial apodeme (figures 22C, 24J); by (ii) muscles pulling on the stipes: muscles VI to IX form a series arising both from the posterior margin of the stipes and the arthrodial membrane behind it (figure 22E), muscle VI passes forwards to the ventral lobe of the anterior tentorial apodeme, muscle VII is very thick and joins its fellow by a median sheet of connective tissue fibrils connected to the transverse maxilla 1 tendon, muscle VIII inserts on the ventral lobe of the posterior tentorial apodeme, and muscle IX passes to the dorsal part of the posterior tentorial bridge (figures 20, 22D, E, 23G, 24H, J, K); and by (iii) muscle X from the cavity of the stipes to the transverse maxilla tendon (figures 22D, 24H).

The antagonistic muscles causing protraction and abduction of the lacinia are indirect and arise from either side of the cardo-stipes hinge, they are: the very large muscle XI from the cardo to the posterior edge of the anterior tentorial apodeme (figures 22C, 24K); and muscle XIII from the proximal edge of the stipes to the transverse maxilla 1 tendon. Protraction (depression) of the cardo-stipes hinge not only protracts the stipes but causes abduction of its distal part by the hinge being pulled down and towards the middle line. Protraction of the stipes stretches muscles III, IV, V, VI, VII, VIII, IX and XII, and, if tension is momentarily maintained by muscles V, muscle I will also be stretched. It is possible that small movements of the highly scletorized distal armature of the lacinia also takes place, but no muscles are involved and elasticity of such sclerotized cuticle can be expected to account for recovery movements.

That only two muscles give the protraction-abduction movement while ten contribute to the strong retractor-adductor movement of the lacinia indicates that the latter alone is the effective stroke and that the lacinia scrapes and lifts towards the middle line and not away from it (unlike the mandible; see above). Such a movement is also indicated by the distal armature of the lacinia which is directed towards the middle line.

18. Conclusions concerning the mandibular mechanism of *Petrobius brevistylis* Carpenter

Petrobius cannot bite, it is expert at scraping food material with the tips of the mandibles and laciniae, the food surface being copiously lubricated with saliva from the labial segmental organs. Hydraulic efficiency of the labrum, superlinguae, galea, hypopharynx and labium permit finely divided and fluid food to be sucked up, ground by the molar lobes and swallowed.

There is little in common between the mandible of *Petrobius*, which rotates in a slot, and the rocking mandibles of the more primitive Crustacea, other than the utilization of an axis of rotation lying along the mandible and the presence of transverse segmental tendons. The former represents the basic coxal movement of an ambulatory limb (p. 16, §7 (i), (ii)) and the latter is a usual potentiality of all arthropodan segments. The details of the endoskeleton, exoskeleton and muscles and the principles of the whole feeding mechanism present fundamental differences from the Crustacea (§ 33 (iii)).

The details of the maxilla 1 skeleto-musculature and movements is of interest because, with the mandibles, they form part of a combined feeding mechanism, and this type of maxilla, or its clear derivative, is of frequent occurrence among land arthropods (see below). Entirely different maxillules characterize Crustacea.

There seems to be little justification for exactly equating the crustacean paragnaths with superlinguae of hexapods and Symphyla (Snodgrass 1951). The functions of these organs are not the same. Superlinguae could not serve their purpose in *Petrobius* and others in the absence of a hypopharynx, and paragnaths do not and could not carry out their normal functions in the majority of Crustacea if a median lobe lay between them. Paragnaths may fuse under particular circumstances, as in suctorial parasites with stylet-like mouth parts. There is no embryological justification in Crustacea for supposing that paragnaths belong exclusively to the mandibular segment. Paragnaths and the hypopharyngeal complex of hexapods are likely to have been independently evolved, as has the median hypopharynx-like lobe of isopods feeding on land.

It will be shown below how mandibular movements and a feeding mechanism of the *Petrobius* type, but at a less perfected evolutionary stage, could be further advanced in either of two ways: (i) by the acquisition of a biting ability sufficient to deal with hard food in quantity (*Ctenolepisma*, Pterygota), or (ii) by the evolution of entognathy permitting great freedom of mandibular movement (Collembola, Diplura). Particular specializations of *Petrobius* which may have been lacking at an ancestral stage are: the long mouth parts; the abundance of muscles utilizing the margins of the mandible; the great bulk of the maxilla 1 muscles arising not only from the stipes but from the post-stipial arthrodial membrane; the origin of muscle XII from arthrodial membrane; the well-developed inter-tentorial muscles, which contribute to the fine control of the mandibular and maxillary movements (p. 42); and the hydraulic efficiency of the oral cone.

19. GENERAL CONSIDERATIONS CONCERNING THE MANDIBULAR MECHANISMS OF *CTENOLEPISMA CILIATA* (DUFOUR) AND *LOCUSTA MIGRATORIA* L. AND THEIR FUNCTIONAL EVOLUTION

Ctenolepisma, as is well known, can live indefinitely upon dry grain which is strongly bitten into by hinged mandibles which adduct and abduct in the transverse plane. The head is relatively wider and longer and the mouth parts dorso-ventrally shorter than in *Petrobius* (cf. figures 19*b*, 21, 22 with 25*a*, 26, 27). The hypopharynx of *Ctenolepisma* lacks superlinguae and there is no hydraulic efficiency around the preoral space. It is not surprising, therefore, to find a very much smaller labial segmental organ than in *Petrobius*. In *Ctenolepisma* the duct forms a single loop from the end sac within the labium up to the posterior remains of the pleural fold and down to the median exit duct (figure 27D; cf. figures 19*b*, 21, 22).

The mandible of *Ctenolepisma* is freely exposed laterally and it could not abduct in the transverse plane if it were boxed in as in *Petrobius*. The axis of swing between the dorsal articulation, marked by a cross, and the black spot in figure 25*a* differs from that of *Petrobius* in the backward shift of the dorsal articulation, in the formation of an anterior articulation near the black spot and in the conversion of the small pre-axial part of the mandible into the long hinge. There is no fundamental difference between the mandibles of *Petrobius* and *Ctenolepisma*. The hinge provides rigidity and a wider gape suitable for biting hard food. The shape of the mandible harmonizes with the hinge position. No molar area is present, and no grinding is practised. The distal parts of the mandible bear strongly opposable cusps, not all in the same plane, which interlock with one another on adduction. A pleural fold does not overhang the mandible as in *Petrobius*, if present such a fold might be a hindrance. The homologue of this fold is reduced to the postero-lateral corner of the head, marked 'pleural fold (*h*)' on figure 25*a* and 27D (cf. figures 19*b*), where it still lodges part of the small segmental organ. Chaudonneret (1950) calls it the hypostoma.

As in the Isopoda, these changes convert the rolling type of mandible into a biting one. *Thermobia* shows a more horizontal axis of movement than *Ctenolepisma* and a striking convergence with the head of *Ligia* (figures 25*c*, 10*a*). The primitive pterygote *Leptophlebia* (Ephemeroptera, larva) repeats the general form of the *Ctenolepisma* mandible, but lacks an anterior articulation (Snodgrass 1950). In most pterygotes the mandible has both dorsal and anterior articulations, and in the locust and others the morphologically dorsal articulation is more ventral in position than the anterior articulation (figure 25*d*), so that the hinge line slopes downwards in the posterior direction. The length of the mesial biting armature of the locust mandible is much greater relative both to whole mandible and to the head than it is in *Ctenolepisma* (cf. figures 26 with 28, 30).

The functional significance of the several positions of the mandibular hinge line is not far to seek. The *Ctenolepisma–Thermobia* position allows direct abductor and adductor muscles to pull on the morphological anterior and posterior margins of the mandible from the dorso-lateral parts of the head wall roughly as in *Ligia* (see below), and figures 25*a*, *c* show abductor muscles 1 and 2 plus 3 and adductor muscle 11. These muscles take precedence over the rest, and the dissolution of the transverse mandibular tendon allows the wider gape, as in *Ligia*. A ventral view of the head of *Ctenolepisma* (figure 25*b*) shows the labrum occupying about one-third of the width of the head, and no mandible abducts the cusps farther than the lateral part of the labrum. But the pterygotes have a much wider labrum (figure 28) and their gape can be greater than those of the biting Thysanura. Figure 25*d* shows that the locust possesses a very long mandibular adductor apodeme and long adductor muscles relative to the size of the mandible, and the apodeme lies at right angles to the hinge and occupies the longest available head space. A thick adductor composed of many fibres set along a great expanse or length of apodeme will most easily give large and strong mandibular movements, and the application of the pull at right angles to the hinge line is a mechanically more advantageous arrangement than the oblique pull of *Thermobia* and *Ctenolepisma*. Thus the position of the hinge line of the mandible and the width of the labrum of the pterygotes are correlated with the ability to operate a very long cutting edge very strongly and through a wide angle.

Petrobius, *Ctenolepisma*, *Thermobia*, *Leptophlebia* and the locust form a series in which the exoskeletal shapes of the head and mandible can be correlated with progressive development of biting ability. Snodgrass (1950, 1951) considers that the mandibles of Lepismatidae and Pterygota have become doubly articulated independently and by different means. He states that the anterior articulation of the former 'is by means of a small knob on the ventrally inflected anterior angle of the gena' while in the Pterygota the articulation is with the clypeus. Yet Chaudonneret (1950) figures the articulation in *Thermobia* from several angles and says that the cranial condyle is 'porté par l'angle latéro-dorsal du clypeus, au niveau de l'invagination antérieure du tentorium' and for the beetle *Atomaria* Evans (1961) says 'the subgena bears a condyle which articulates with the dorso-lateral base of the mandible'. It seems that less equivocal evidence is required for the justification of the claim by Snodgrass, although the presence of only one condyle in the Ephemeroptera supports his general conclusion.

The facts mentioned above and below should not be taken to indicate that these thysanurans and pterygotes represent a phylogenetic series. All that is suggested is that these animals show a series of conditions which roughly indicate how the very effective biting mandibles of hexapods may have been evolved. This does not imply that the mandibular mechanisms of *Petrobius*, *Ctenolepisma* and *Thermobia* are inferior or less effective for their purposes than that of the locust. The efficient filter feeding of *Chirocephalus* and *Paranaspides* is not inferior to the very different feeding mechanisms of *Ligia* or a crab. The morphology and movements of all these animals are doubtless eminently suited to their several types of food and ways of life. Were it not so geological time would have allowed evolutionary perfections to have taken place. But the evolution of a biting mandibular mechanism with the strength of that of the locust type clearly paved the way for the pterygote adaptive radiation.

The Thysanura indicate that their evolution of stronger biting mandibles probably took place at the expense of hydraulic efficiency of the mouth parts, and that a reduction in salivary juice production and in size of labial segmental organs, together with the disappearance of superlinguae, have accompanied the formation of biting mandibles.* Paired labial segmental organs (derived from coelomic end sacs and mesodermal ducts) are absent in pterygotes, but whether this represents an end term to the thysanuran tendency is uncertain. Pterygote salivary glands of quite different morphology open behind the hypopharynx in much the same position as do the labial glands in Thysanura but with elaborations (figure 29; cf. figure 20). The salivary glands of pterygotes have shown greater potentialities than the labial segmental organs. It is possible that the presence of labial glands in the Thysanura and of salivary glands in the Pterygota indicates a parallel evolution of the two groups, perhaps supporting the suggestion of Snodgrass mentioned above, but for quite different reasons. On the other hand, the small and simple hypopharynx of *Ctenolepisma* would not do for the locust (cf. figures 26 with 28, 29), where the long cusp row of the mandible requires a long tongue. The wide labrum and large cusp area of the locust indicate a need for salivary juice far exceeding that of *Ctenolepisma*. If the ancestors of pterygotes had so reduced their labial segmental organs at a *Ctenolepisma*-like stage, and had utilized to the full the cranial space vacated by these glands for the enlargement of mandibular adductor muscles (see figure 25), it would not be surprising to find that an entirely new type of salivary gland had been evolved to meet the newer need.

The morphological basis for the above suggestion, which is provided by the details of the endoskeleton and musculature in addition to the features just noted, can now be considered, and a summary of further conclusions is given in § 21.

(i) *The head endoskeleton of* Ctenolepisma ciliata (*Dufour*) *and* Locusta migratoria *L.*

The endoskeleton and musculature of *Ctenolepisma*, *Thermobia* and the locust are clearly derivatives of the *Petrobius* type. The tentorial apodemes of *Ctenolepisma* are less expanded, bear no large flat lobes and are shorter dorso-ventrally than in *Petrobius*. The short mandible of *Ctenolepisma* has no need for large tentorial areas bearing insertions of a long series of muscles from the anterior and posterior mandibular margins, so important for the rolling movement. The rigidity of the anterior tentorial apodemes is increased as is fitting for the stronger biting movements. The anterior tentorial apodemes unite trans-

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* Snodgrass (1950) has noted that superlinguae are present in ephemeropteran larvae but not in other Pterygota.

versely and extend upwards and backwards as a thin median plate overlying the posterior tentorial bridge (figures 26, 27; cf. 20 to 22). The two plates are joined by very short muscles representing E1 and E2 of *Petrobius*. Were the head of *Petrobius* dorso-ventrally flattened, including the tentorial apodemes, an overlap of the posterior by the anterior tentorial apodemes would result (figure 20); and the muscles between them would be reduced to a thin sheet as in *Ctenolepisma*. In *Thermobia* the muscles are absent and the apodemes are fused. The cavities of the tentorial apodemes, so conspicuous in *Petrobius*, are difficult to see in sections of *Ctenolepisma* and they are very small in *Thermobia* (Chaudonneret 1950, fig. 13). These changes doubtless add strength to the apodemes.

The position of external origin of the anterior tentorial apodeme in *Ctenolepisma* is similar to that of *Petrobius*, although less funnel-shaped (figures 19*b*, 24H, 25*a* to *c*, 26A). The position in pterygotes is usually much the same, and Snodgrass (1951) has shown that sometimes it lies lateral to the mandible (larva of Odonata). In the locust great anterior tentorial strength is achieved by double bars linked with a thinner flange (marked 'anterior process' and 'lateral bar' in figures 28, 29) which unite with the cuticle of the epistomial suture, no open pit or cavity remaining. A dorsal suspensory process and muscle is present in *Ctenolepisma* as in *Petrobius*, and the antennal muscles insert over the posterior part of the dorsal face of the anterior tentorium (figure 27), the same morphological site as in *Petrobius*. In the locust the antennal muscles cover the 'dorsal arm' of the anterior tentorium (figure 29) which probably represents the suspensory arm of *Ctenolepisma*; the great rigidity of the anterior epistomal connexion in the locust making dorsal suspensory muscles unnecessary.

The posterior tentorial apodeme of *Ctenolepisma* is very solid and its external origin lies just below the reduced pleural fold (hypostoma). The cranial articulation of maxilla 1 is stronger than in *Petrobius*, a condyle projecting into a furrow on the cardo (figure 27D). Chaudonneret (1950) describes the position of the condyle in *Thermobia* as 'porté par la face inféro-ventrale de crâne, juste en avant de l'orifice de l'invagination métatentoriale'. The junction of the pterygote maxilla with the head capsule, close to its union with the posterior tentorial arm, is directly comparable. The posterior tentorial opening in *Ctenolepisma* represents the dorsal end of the slit-like origin of the apodeme in *Petrobius*. The suggestion of Chaudonneret (1950) that the posterior tentorial opening in *Thermobia* lies at the maxilla 1–labial intersegment is amply confirmed by the condition in *Petrobius*. The posterior tentorial bridge in *Ctenolepisma* is not deep in the sagittal plane; if it were deep as in *Petrobius* there would be insufficient length for labial muscles. Fusion of the anterior and posterior tentorial bridges in *Thermobia* gives this thysanuran a horizontal tentorial plate which resembles in essentials the pterygote tentorium, as noted by Snodgrass. The plate of the locust is shown cut sagittally in figure 29, the posterior arms passing backwards and outwards to unite widely with the cranium (figure 28). (For further consideration see § 20.)

(ii) *The musculature of the mandible of* Ctenolepisma ciliata (*Dufour*) *and* Locusta migratoria *L.*

The three cranial promotor muscles arising from the anterior mandibular margin in *Petrobius* are represented in *Ctenolepisma* by two abductors and in the locust by one. In

Ctenolepisma muscle 1* leaves the antero-dorsal end of the pre-axial margin and a muscle representory 2 plus 3 of *Petrobius* pulls of an apodeme from the postero-dorsal part of the margin (figure 19*b*, 21A, 25*a*, 26A). The tentorial promotor muscles 4 and 5 are small in *Ctenolepisma*, where the abducting mandible does no outside work (cf. *Petrobius*), muscle 4 arises just posterior to muscle 2 plus 3, and muscle 5 arises about half way between muscles 1 and 2 plus 3. These tentorial muscles are abductor in function resembling muscle 6 of the Malacostraca (cf. figure 9C). In the locust only one large cranial abductor is present corresponding with muscles 1 to 3.

The principal adductor muscle of *Ctenolepisma* is an enlarged muscle 11 from a stout apodeme arising on the posterior mandibular margin near the distal cusps (figures 21B, 26B, and see Chaudonneret (1950) text-fig. 50 *adcm*, the corresponding apodeme and muscle of *Thermobia*). The adductor is composed of many sectors, fanning forwards as far as the dorsal tentorial suspension (figure 26A) and backwards to the limit of the cranium, one large sector inserting upon the post-occipital flange and shown by dotted lines on figure 26B.* The tentorial muscles 6 and 7 which leave the posterior mandibular margin in *Petrobius* gain length in *Ctenolepisma* by arising from the face of the mandible behind the transverse muscles 8, 9 and 10. The narrower and more dorso-ventral course of this muscle in *Ctenolepisma* suits its adductor function, in contrast to the assistance this muscle renders to the backward roll in *Petrobius*. The locust possesses only muscle 11 which is enlarged further (see below).

The muscles attached to the transverse mandibular tendon of *Petrobius* are recognizable in *Ctenolepisma* where they insert mainly upon the anterior tentorial apodemes, the transverse tendon being absent. Muscles 8 and 9 form a fan inserting over the outer face of the anterior tentorial apodemes and are adductor in function. Muscle 10, the most ventral part of the series in *Petrobius*, where it has its own tendon, inserts in *Ctenolepisma* mainly on the inner face of the anterior tentorial apodeme, and the most ventral fibres of all (10*a*) insert on the lateral ends of a transverse sclerite across the base of the hypopharynx (figure 26A). Unless adductor muscle 8 undergoes great length changes in *Ctenolepisma* it must limit the gape of the mandible, and the narrow labrum indicates that the range of mandibular movements is less than it is in typical pterygotes. In one of the more primitive pterygotes (*Leptophlebia*) and in the cockroach Snodgrass (1950) has shown that two muscles leave the inner face of the mandible, the larger V. 2, inserting on the ventral face of the anterior tentorial arm and the smaller, V. 1, on the suspensory arm of the hypo-

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* The interpretation of the functions of the muscles of *Ctenolepisma* given here corresponds with that given by Chaudonneret (1950) for *Thermobia* with two exceptions. I do not think that muscle 1 arising from the pre-axial border of the hinge (Chaudonneret's muscle *adcl*) can be other than abductor in function. No adductor muscles have been found on any mandible working at such a poor mechanical advantage, and abductor muscles are habitually found in this position in other arthropods. I do not think that the posterior sector of muscle 11, which inserts on the post-occipital flange, and the other small muscles which do likewise (Chaudonneret's muscles *abcmd*, *abcm*, and *abcpm*), can do other than add to the pull exerted by the main body of muscle 11 on the mandibular apodeme. No arthropod has been found in which antagonistic muscles are inserted on to the posterior mandibular apodeme.

The correspondence between the muscles numbered here for *Ctenolepisma* and those of *Thermobia* lettered by Chaudonneret is as follows: Muscle 1 = *adcl*; muscle 2 plus 3 = *abca*; muscle 4 = *abtp*; muscle 5 = *abtl*; muscle 6 plus 7 = *adt′*; muscles 8 to 10 = *adt*; muscle 11 = *adcm*, *abcmd*, *abcpm* and *abcm*; the mandibular-hypopharynx muscle = *adh*.

pharynx. These two muscles are clearly the homologues of muscle 10 and its neighbour 10*a* which runs to the hypopharyngeal sclerite in *Ctenolepisma*, but not of muscles 8 and 9, the greater part of the transverse muscles. In the locust muscles V. 1 and V. 2 are absent and the mandible is empty of muscles, as is almost so in the crab. In both the elimination of muscles from the mandibular cavity enables a strongly biting mandible to be moved through a wide angle in the transverse plane, but the details of the evolutionary processes towards this end are quite different in the two. In the locust, the upper section of the hypopharyngeal suspensory sclerite sends one arm to the oesophagus, and the other bends outwards and downwards to become continuous with the mesial mandibular cuticle just anterior to the base of the mandibular apodeme (figures 28 to 30). This union supersedes muscle 10*a* (V. 1) and is clearly a strengthening device associated with the wide mandibular movements of the locust, which are made possible by the absence of muscles 4 to 10 as seen in the Thysanura.

The locust possesses a large and divided mandibular apodeme homologous with the posterior apodeme of the Thysanura. It arises from the mesial corner of the mandible, now triangular in dorsal aspect (figure 30). The two apodemal flanges support a mass of lateral and postero-dorsal muscle fibres (figures 28, 29). An outward bulge of the mandible lateral to the hinge line gives the single abductor muscle small but sufficient mechanical advantage. The abductor, inserting on the lower part of the gena, does not compete with the adductor for head space (figures 25*d*, 28 to 30).

The anterior articulation of the locust mandible is much stronger than the morphologically dorsal articulation, as in the crab. The anterior articulations in both animals lie approximately in line with the biting cusps, a position mechanically suiting the strongly biting action and representing an end-term refinement evolved in parallel manner by two unrelated groups. The more primitive types of mandible in hexapods and in Crustacea possess either a dorsal articulation alone or a dorsal and a less strong anterior articulation.

(iii) *The musculature of maxilla* 1 *of* Ctenolepisma ciliata (*Dufour*) *and* Locusta migratoria *L.*

The general morphology of maxilla 1 of Thysanura, and of Pterygota such as Orthoptera and Odonata, is very similar, and such a maxilla is not found outside the pterygote and apterygote groups, nor even in the Symphyla (§ 27 (iii)). A detailed study has not been made of the movements, but the general manner of usage is indicated by the morphology. Snodgrass (1928, 1952, etc.) described the maxillary muscles of *Periplaneta*, Strenger (1952) has described those of the orthopteran *Saga serrata* and of *Aeschna cyanea* and Albrecht has done the same for the migratory locust (1953). The muscle numbers used by Strenger and Albrecht will be prefixed by S. and A, respectively, below.

Maxilla 1 muscles of *Ctenolepisma*, *Thermobia* and the Pterygota lack a transverse tendon, and the homologues of muscles inserting on this tendon in *Petrobius* are attached instead to the anterior tentorial apodemes or to the tentorium. These muscles are more dorso-ventral in slope than they are in *Petrobius*, thereby effecting adduction and levation of the lacinia more easily. The bulk of maxilla 1 musculature, as in *Petrobius*, produces the adductor-retractor movement of the lacinia and a similar antagonistic muscle or muscles depresses and protracts the cardo-stipes hinge, thereby stretching the adductor-retractor muscles in a manner similar to that described above for *Petrobius*.*

A promotor to the cardo is present in *Ctenolepisma*, *Thermobia* and the more generalized Pterygota, arising from a knob situated distal to the cardo-cranial articulation, and inserting on the cranium. Muscle XII in *Ctenolepisma* in two sectors (figure 27C) resembles that of *Thermobia* (Chaudonneret, 1950 *rl* and *rm*), and the pterygote homologues are muscle S. 6 in *Saga* and *Aeschna*, A. 10 in the locust and muscle 3 in *Periplaneta* (Snodgrass1952).

Retractor-adductor movements of the lacinia, affected in *Petrobius* by muscle-groups i to iii (p. 44), are little changed. Muscles of group i pull on the lacinia. In *Ctenolepisma* muscles III and IV arise from the lacinia apodeme (figure 27C), muscle S. 9, in one or two sectors, arises in *Saga* and *Aeschna* from the base of the lacinia, muscle 32 in *Periplaneta* (Snodgrass 1952) is similar, and muscles A. 13*a* and A. 13*b* in the locust (figure 29) arise from the tendon at the mesial corner of stipes and lacinia. These muscles insert upon the head wall except in the locust where they pass to the under side of the large tentorium. Muscles I and V of *Petrobius* from the lacinia apodeme are represented in *Ctenolepisma* by muscle I, in *Saga* and *Aeschna* by muscle S. 10 and in *Periplaneta* by muscle 41 (Snodgrass 1952). Muscles corresponding with groups ii and iii of *Petrobius* arise from the stipes; muscles VI and X of *Ctenolepisma* insert on the anterior tentorial plate (figure 27C) and muscles VII and VIII of *Ctenolepisma* insert on to the posterior tentorial plate (figure 27D). In *Thermobia* Chaudonneret (1950) figures two muscles, *ata*. 1 and *ata*. 2 corresponding with muscle X. In *Saga* and *Aeschna* muscle S. 8, in more than one sector, inserts on the tentorium, and muscles A. 12 in the locust and muscles 34*a*, *b* and *c*(Snodgrass 1952) in *Periplaneta* are similar.

The antagonists to the above retractor-adductor muscle groups appear to be the protractor-depressors to the cardo arising either from the distal part of the cardo or from the cardo-stipes hinge. These are muscles XI and XIII in *Petrobius* (see above), which are represented by muscles XI (not clearly divisible) in *Ctenolepisma*, by muscle S. 7 in *Saga*, by muscle S. 7 arising from both sides of the hinge in *Aeschna*, by muscle 33 (Snodgrass 1952) in *Periplaneta* and by muscle A. 11*a* in the locust. In addition, a flexor to the galea is present in all these animals.†

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* I cannot agree with Chaudonneret (1950) in considering that there are no antagonists to the stipes muscles inserting on the tentorium of *Thermobia*. There are no direct antagonists, but a strong protractor-depressor movement of the cardo-stipes hinge by his protractor of the cardo, *prc* (corresponding with muscle XI in *Ctenolepisma*), must effect the recovery movement.

† A further investigation of the mechanism of movement of the pterygote maxilla 1 is beyond the present purpose, but some differences between the above suggestions and those of others may be noted. Popham (1959, 1961) states that the maxillae of the cockroach (and of *Forficula*) move 'downwards and outwards by haemocoelic fluid pressure, there being no muscles capable of performing these movements'. Snodgrass (1952) on the other hand says that his muscles 33 and 34 in the cockroach from the tentorium to the cardo and stipes, respectively, are both protractor in function although his figures show the muscles to lie at an angle to one another. He states that the stipes muscle 34 is protractor in function because the lacinia slides against the hypopharynx. I would agree with Popham in considering that fluid pressure may assist recovery and protractor movements of mouth parts and hypopharynx in a manner comparable to the full extension of certain arthropod limbs when off the ground (Manton 1958*a*, *b*), but Popham gives no due consideration to the functions of muscles or to Snodgrass's work. I agree with Snodgrass in considering that the cardo-tentorial muscle of the cockroach must protract the distal parts of the maxilla, but the stipes tentorial muscles in three sectors (34*a* to *c*) appear to be situated so as to give a strong retractor-adductor pull on the stipes and not protraction. The view that both muscles 33 and 34 in the cockroach are primitively adductor in function (Snodgrass 1928, 1935, 1952, etc.) is referred to in § 33 (i).

This detailed similarity in the form of maxilla 1 in Thysanura and the more primitive Pterygota is striking indeed without reference to further details, a similarity that has been pointed out by Snodgrass.

20. MOVEMENTS AND EVOLUTION OF THE HEAD ENDOSKELETON OF THYSANURA AND PTERYGOTA

Little or no movements of head apodemes or tendinous endoskeleton take place when they are united to the body wall by cuticular or fibrous struts as in *Anaspides*, *Ligia* and the locust (figures 8, 11, 29). Since it would be physiologically wasteful for muscles to be employed in situations where simple rigidity is needed, the presence of an abundance of endoskeletal muscles in *Petrobius* (figures 20, 22, etc.) suggests that some movement of the endoskeletal units does take place here. The amplitude must be small because of the four tentorial unions with the surface cuticle. Muscles E. 1 and E. 3 may tend to raise the posterior tentorial apodemes while muscles E. 2 and E. 4 may lower them, while the dorsal suspensory muscles must tend to raise the anterior tentorial apodemes and the muscles from the mandibular tendon to these apodemes may lower them.

The grinding roll of molar areas is often performed by mandibles momentarily moving a little out of phase with one another, while transversely biting mandibles largely work in exactly similar phase (*Ctenolepisma* and locust), as do the maxillae 1 of these animals and of *Petrobius*. It is probably significant that the anterior tentorial apodemes associated with the independently moving mandibles of *Petrobius* are independent while they are fused in *Ctenolepisma*, and the posterior tentorial apodemes are fused in both. It is probable that slight protractor and retractor movements in *Petrobius* result in piercing by the tip of the mandibles, food being held by the laciniae. No protractor or retractor movements are possible to hinged mandibles biting in the transverse plane (*Ligia*, *Ctenolepisma* and locust), and endoskeletal muscles are here almost or entirely absent. In *Thermobia* a fusion of anterior and posterior tentorial plates eliminates the very small connecting muscles present in *Ctenolepisma*. The dorsal suspensory muscles present in the Thysanura are redundant in the Pterygota where the anterior and posterior tentorial unions with the head capsule are so massive (figures 28, 29). Disappearance of such muscles leaves their apodemal processes available for the pterygote antennal muscles. By contrast, the Collembola and Diplura possess more marked mandibular protractor-retractor movements than the *Thysanura* and there is greater elaboration of the endoskeletal system (§ 22 (i), (v)).

Thus the fusion of the four tentorial apodemes into a massive immobile structure in the Pterygota represents an end term to an evolutionary series showing perfection of strong biting by hinged mandibules working in the transverse plane, while mobility of tentorial apodemes is associated with freely protrusible mandibles. It is also possible that endoskeletal muscles may be of service in an elastic capacity for storage of energy when mandibular movements are rapid (§ 22 (v)).

21. CONCLUSIONS CONCERNING THE MANDIBULAR MECHANISMS OF *CTENOLEPISMA CILIATA* (DUFOUR) AND *LOCUSTA MIGRATORIA* L.

There is striking functional and morphological continuity in the structure of the mandible, maxilla 1, tentorial apodemes and their musculature in the series of thysanuran and pterygote hexapods here considered. The simplicity of the locust mandible appears to be as far removed from a basic type as is that of *Ligia* with reference to the more primitive Crustacea. The general course of evolution appears to have been the same within the Peracarida and Thysanura-Pterygota, and correlated with similar functional assets, namely the usefulness of strong biting, but the details in the two groups of animals are very different and phylogenetically distinct, as is the decapod series culminating in the crab. All three series start with a primitive rolling type of mandible with or without feeble powers of biting, but it is suggested here that these rolling mandibles have been convergently acquired in Crustacea and in the hexapod groups.

Snodgrass (1928) referred to the same three animals, *Petrobius*, *Ctenolepisma* and the locust in considering the derivation of the pterygote mandible. The similarity in general conclusion and the differences in the basic evidence and argument are considered in § 33.

22. General considerations concerning the evolution and functional significance of entognathy

The feeding mechanism of *Petrobius* is essentially a scratching one, and the hydraulic principles on which it depends have been considered in §§ 17 to 18. From an archi-*Petrobius* condition evolution appears to have proceeded in two directions (i) towards transversely biting mandibles of the Thysanura and Pterygota, suited to cut into large food masses, which is accompanied by a loss of the *Petrobius* type of hydraulic efficiency (§§ 19 to 21), and (ii) towards protusible mandibles of the entognathous Apterygota capable of piercing and/or cutting and grinding minute objects by a rotatory movement, which is accompanied by another type of hydraulic efficiency (see *Tomocerus* (Collembola) and *Campodea* (Diplura) below).

These two types of evolutionary change have taken place independently many times within the Arthropoda. Transversely biting mandibles have been evolved by the Decapoda and Isopoda (§§ 10 to 13) besides the Pterygota (§§ 19 to 21) and it is probable that protrusible mandibles and entognathy have also arisen independently several times (see below). Stylet-like mandibles which pierce food surfaces turn up in the adaptive radiations of many groups, for example the parasitic Copepoda and Isopoda, Hemiptera and Diptera, Colobognatha among the Diplopoda and the Protura, etc. In many of these a lowering of the head and telescoping of the ensheathing structures result in piercing. A mandible which is protrusible relative to the head must have a very mobile attachment such as is impossible when the head capsule and mandibles must together produce a united front to the outside world. Entognathy permits the formation of freely moving protrusible mandibles operating within an enclosed space, from which tongue-like structures can also be protruded, for example the labrum of the Onychophora and the hypopharynx of the Collembola.

Development of entognathy

The prothoracic tergite of *Petrobius* projects forwards on either side as far as the antennae, closely covering the mouth parts (figure 19*a*). Underneath it lies the head pleural fold. These two structures contribute to the smooth external surface, protective in running about in rough and tight places. The pleural folds probably also contributing to the hydraulic efficiency of the mouth parts which distally fit together so neatly. Pleural folds are absent from heads possessing hinged mandibles.

Hydraulic efficiency around scratching mouth parts, useful in sucking up fluid and finely divided food, could be obtained in a terrestrial archi-trignathan arthropod by the elongation of a pleural fold and its fusion with the labrum and labium. The mandibles and maxillae 1, so enclosed in a gnathal pouch, must then carry out their scratching activities within a confined space well lubricated with salivary juice. Suction by a long and narrow oesophagus could take in finely divided food. The head capsule would be entire, as in Collembola and Diplura, well suiting a life within woodland litter, etc., and no protective flanges from the prothorax would be needed. The mandibles and maxillae within the gnathal pouch could become mobile and loosely articulated with the head. The external face of the mandible could become available for the origin of additional muscles.

The embryonic development of Collembola shows that their entognathy is in fact developed in this manner. A pair of lateral folds in the embryo of *Anurida* (Folsom 1900) grows round the mandibles and maxillae (figure 31*e* to *g*) fusing with the labrum and labium. Whether these folds are called pleural or oral is immaterial. An essentially similar entognathy is present in the Onychophora where the embryology is also similar. Paired oral folds arise lateral to the jaw rudiments (figure 31*c*, *d*) and grow right round the labrum, fusing in front of it and behind the jaws, so forming the round lip of the adult.*

The pleural fold of *Petrobius* (figure 22) overhangs the cranial articulation of maxilla 1 cardo and the dorsal end of the posterior tentorial opening, the former being very close to the latter. A downgrowth of such a pleural fold would bring both these structures within a gnathal pouch. Figure 22 shows that there is no clear demarcation between the thick cuticle of the posterior tentorial apodeme and that of the under face of the posterior part of the pleural fold; figure 34 and 45 show the posterior tentorial apodemes† (fulcrum) of *Tomocerus* and *Campodea* lying at the base of the gnathal pouch as a surface sclerotization and bearing the union with the cardo in an essentially similar manner. Moreover, the long external origin of the posterior tentorial apodeme in *Petrobius* (figures19*b*,20), situated between the labium and maxilla 1, would lie, after the elongation of the pleural folds and their fusion with the labium, at the junction of the posterior edge of the maxilla and the wall of the gnathal pouch (labium,) just as occurs in *Tomocerus* and *Campodea* (figures 34, 37, 45, 46A). Elongation of the pleural folds would also permit the coils of the labial segmental organ to spread postero-ventrally in the head as seen in *Tomocerus* and *Campodea* (cf. figures 19*b*, 21, 22, with 32 to 34, 37 to 40, 44, 46D).

The stylet-like mandibles of mosquitoes are supported distally by the labium as they pierce. It has been shown in § 17 how each mandible of *Petrobius* rotates in an almost

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* Paclt (1956) supports the statement by Denis (1949) that hexapod entognathy develops, not from a sinking of mouth parts into the head, as claimed by Snodgrass (1938), but by the covering growth of an oral fold, a conclusion in agreement with the present work. The further suggestion by Denis (1949) that the pleural (oral) fold is derived from subcoxal epipodites appears to be without any supporting evidence and to be most unlikely. A pleural head fold overhanging the base of rolling type I mandibles is of frequent occurrence in Arthropoda (see figures 7 and 19*b* of *Anaspides* and *Petrobius*), and there is no reason to suppose that this fold appertains to the coxa when the base of the fold is so clearly dorsal to the articulation of the mandible and the embryonic origin in entognathous animals is from the head and not from limb rudiments.

† The justification for the identification of the posterior tentorial apodemes is considered on p. 58.

enclosed slot. *Tomocerus* shows a parallel development of supporting and restricting skeleton which holds the distal parts of the mandibles. Figure 20 shows the fronto-clypeal sclerite of *Petrobius* at the base of the long clypeo-labrum. The much larger, but similarly situated sclerite of *Tomocerus* at the base of the short labrum (figures 35, 32, 36A), forms a stout hoop laterally enclosing the mandibles but not the maxillae 1. This sclerite, together with the surface sclerotizations described below as the boss, branches ii and iii of the anterior tentorial apodeme and the bearing of the superlingua (figure 36B to D), together guide the mandibular mobility into movements which are largely rotator and counter-rotator. The much shorter preoral cavity of *Campodea* contains no particular bearings for mandibular movement, but the smallness of the animal combined with the confined space between the free margins of the gnathal pouch and the hypopharynx (figures 44, 45 near direction line 'pleural fold') suggests that skeletal support may be mechanically unnecessary.

The type of hypopharynx and superlingua seen in *Petrobius* could readily undergo alterations in shape to give those seen in *Tomocerus* and *Campodea*, and maxilla 1 and the endoskeleton in these three animals show marked resemblances (see below).

Entognathous feeding

When resting the round lip of *Peripatus* closes completely over the preoral cavity. When feeding the lip is widened and clamped down on to the prey. The protrusible jaws slice antero-posteriorly into flesh or cuticle from the enclosed preoral space, the pair working in opposite phase. The round lip retains copious salivary juice from the huge segmental organs of the oral papilla segment, the ducts discharging just within the posterior margin of the lip (figure 31*a*, *b*). Sizeable pieces of flesh are pulled in and swallowed, or salivary juice is poured into the lesion, fluid material being sucked back into the oesophagus until an empty cuticle is all that is left of the prey. The labrum acts as a mobile anterior 'tongue' (Manton 1937), much as in the crab.

In *Tomocerus* and *Campodea* the external opening of the gnathal pouch is small. Copious salivary juice is produced from labial segmental organs lodged in similar posterior parts of the head in both animals (figures 32 to 34, 37 to 40, 44, 46). In *Tomocerus* the pair of salivary ducts discharges into a median posterior diverticulum of the preoral cavity (figures 35, 37E); the juice can then flow either to the posterior side of the hypopharynx and so to the food surface, or directly out through a median gap in the labium (figures 35, 36D), according to the pressure maintained by the two halves of the labium at this point. In *Campodea* the paired salivary ducts open ventrally into a salivary groove (figures 45, 46, 47) which continues between the two halves of the labium. Salivary juice passing along this groove (arrows on figure 47), reaches the posterior side of the hypopharynx and so to the food surface. Further glands on the inner surface of the oral folds discharge into the gnathal pouch in both animals; some of the large ductless gland cells of *Tomocerus* are shown in figure 37E, H.

Macnamara (1924), Poole (1959) and others have shown that vegetarian Collembola, such as *Tomocerus*, feed largely upon fungal hyphae, spores, pollen and such small objects. As in *Petrobius*, the tips of the mandibles of *Tomocerus* can scratch the food surface, but they can also reach out and grasp and carry food back without disturbing the hydraulic efficiency of the oral cone formed by the labrum, the lateral margins of the gnathal pouch and the labium (cf. Onychophora). The hypopharynx can also be protruded a little and is mechanically useful, being free from some of its hydraulic functions seen in *Petrobius*, now taken over by the structures forming the margins of the gnathal pouch. The tips of the protrusible mandibles can cut small objects by a rotatory-counter rotatory movement about the long axis (similar to the promotor-remotor movements described for *Petrobius*), the remotor (rotatory) movement bringing the short distal series of interdigitating cusps together in the middle line. This is a different method of cutting from that seen in *Ctenolepisma* and the locust (p. 46) suiting large food objects, and such biting by wide transverse movements and long cutting margins is impossible to entognathous apterygotes. In *Tomocerus* and some other but not all Collembola, a molar area lies proximal to the cutting cusps (figures 35, 42); the rolling rotatory movement, as in *Petrobius*, effects trituration between the molar areas, which bear large cusps along the hinder edge in both animals. In *Campodea* the distal mandibular cusps curve towards each other more sharply than in *Tomocerus*, and are well suited for seizing and retracting food into the preoral space. A movable tooth, the prostheca, is present (adducted by muscle *b* from a long tendon; figure 44).

While the amplitudes of movement, apart from protraction and retraction, of the distal parts of the mandibles of *Tomocerus* and of *Campodea* are small, being restricted by the surrounding parts, it is probable that at times the rotatory (remotor) movement may be rapid. The transversely cutting 'shears' of a pterygote, working from a strong hinge, can cut effectively and with a minimum of muscular effort when movements are slow. But the cutting of a hedge by a sickle is effective only when movements are rapid. In *Tomocerus* the rotatory movements of the pair of mandibles, which lack all firm articulations, must be able to nip off fungal hyphae etc. the more effectively when their movements are rapidly performed. The mechanism is only suitable for operating a short cutting edge.

The Chilopoda possess quite another type of entognathy in which a freely moving mandible is used quite differently from those of Collembola, Diplura and Onychophora (§§ 30, 31).

(i) *The head endoskeleton of* Tomocerus longicornis (*Müller*) *and* Campodea staphylinus *West*

There must be a few anatomical systems about which such conflicting statements have been made, without adequate knowledge of the facts, as those concerning the head endoskeleton of the myriapod and apterygote groups. Actually in all these classes paired apodemes and transverse segmental tendons are present which are directly comparable with those already considered for the Thysanura. In addition there is a system of skeletal membranes in *Tomocerus*. The findings of Hoffmann (1905, 1908) on the skeleto-musculature of *Tomocerus* have been confirmed. His comment (1905) that the tentorium 'ist ein recht schwer zu beschreibendes Gebilde' has made figures 32 to 41 necessary here.

Anterior tentorial apodeme

Tomocerus possesses a pair of apodemes, the 'anterior tentorial arms' of Denis (1928) and Hoffman (1905, 1908), which resemble in all essentials the anterior tentorial apodemes of *Petrobius* with which they appear to be homologous. They arise in *Tomocerus* as hollow intuckings of the surface cuticle lateral to the mouth and mesial to the mandibles, which, when allowance is made for the presence of the gnathal pouch, the freedom of the mandible and large size of the superlingua, is seen to be the same morphological position as in *Petrobius*. Just distal to the point of invagination an elaborate cuticular boss forms a bearing against which the smooth cuticle of the mandible slides and rotates (figures 33, 35, 36D, 42). The hollow apodeme, invested by thick epithelium as noted by Hoffmann (1905), passes inwards to end blindly below the transverse mandibular tendon to which the apodeme is attached. The apodeme carries many muscles, as in *Petrobius*.

A slender solid branch i leaves the apodeme in a forward and distal direction, dividing to end on the surface cuticle ventro-lateral to the base of the antenna and on to the oesophageal wall; the branch stains pink with Mallory's triple strain (figures 33T, 36D, 37E to G). No muscles insert on branch i, which is presumably suspensory and stabilizing in function (cf. dorsal suspensory arm of the anterior tentorial apodeme of *Petrobius*; figure 20).

From the boss near the external origin of the anterior tentorial apodeme two arms extend distally, mainly as surface sclerotizations (figure 33U, branches ii and iii). Branch ii sinks into the hypopharyngeal tissue at level C, figure 36, after leaving the mandibular boss shown in level D; it reappears on the surface at level B, sending an arm towards the mouth to the side of the middle line, which bears a spine row, and this arm passes distally along the superlingua, ending in a fold of cuticle (figure 35, 36A). Branch iii leaves the boss and remains in the surface cuticle although partly folded from it, fading out antero-dorsal to the mandible (figure 36C, B).

In *Campodea* there is no corresponding apodeme, and probably no functional need for one. The preoral cavity is here very small and the transverse mandibular tendon much closer to the hypopharynx and preoral space than in *Tomocerus* (figures 33, 35, 44, 47).

Posterior tentorial apodeme

Paired posterior tentorial apodemes of *Petrobius* have their clear homologues in *Tomocerus* and *Campodea* in the 'sternum', 'sternal arms' or 'fulcrum' of Snodgrass (1950, 1960, etc.) and Tuxen (1959). It has been shown above how the position of the surface sclerite of *Tomocerus* in the angle between maxilla 1 arthrodial membrane and the gnathal pouch wall (i.e. the labium; figures 34, 35), corresponds with the external opening of the posterior tentorial apodeme of *Petrobius* (p. 55). Reference to figures 19*b* and 20 shows that the external opening of the posterior tentorial apodeme in *Petrobius* is undeniably lateral or pleural in position. No sternum can lie here or form any part of the intucked apodeme or of its external margin. The sclerite in *Tomocerus* and *Campodea* in an exactly comparable position cannot be 'sternal' as claimed by Snodgrass (1960, etc.) or be properly described as a 'sternal arm'. It is true that a boiled head viewed from the hinder face shows the sclerite somewhat parallel to that side of the head (cf. figure 35) but this is no evidence of a sternal position.

The form and position of the collembolan and dipluran apodeme can be apprehended properly only from sections (figures 36 to 39, 46) and reconstructions. If a series is followed from the front of the head of *Tomocerus* backwards, levels A to M are marked on figures 32, 33, 35 to 39, the following points may be seen, and for ease of reference two crosses mark the superlinguae, one marks the lateral flange of the hypopharynx, and heavy black indicates thick highly sclerotized exocuticle and endocuticle. At level D the base of the superlingua merges into the junction of maxilla 1 and head, and the gulley below, in which runs the lacinia, is open. At level E maxilla 1 is united below to the basal angle of the hypopharynx (single cross) leaving a tentorial sclerotization which is V-shaped in cross-section, and between the single and double crosses lies the now enclosed space leading into the maxilla 1 apodeme (see also figure 34). The surface sclerite (marked posterior tentorial apodeme) passes backwards, carrying maxilla 1 muscles (as in *Petrobius*, see below, and level H), and at the base of the gnathal pouch the sclerite sinks into the head (levels J and K). The sclerite appears to be solid at these levels but is clearly hollow farther back at M and N, and it ends blindly (figures 34, 35, 39N). The pair of apodemes are united by a narrow muscle just short of the blind ends (unlabelled muscle in figure 39M and marked 'transverse endoskeletal muscle' in figures 34, 35). A cuticular branch from the hollow apodeme turns sharply outwards and runs along the surface of the hinder wall of the gnathal cavity (marked 'transverse process' in figure 34). Here it carries the maxillary cardo by a short link of arthrodial membrane (figures 34, 39M), and the end of the process is tied to the lateral head wall by fibrils extending right through the pleural fold. A transverse union through the base of the hypopharynx links the anterior ends of the pair of tentorial apodemes and is continuous with the complex hypopharyngeal cuticular thickenings (figures 34, 36B to D).

Each hollow apodeme with its two surface extensions, the one alongside the maxilla and the other across the base of the gnathal pouch, resemble the posterior tentorial apodeme of *Petrobius* in essentials, the actual intucking from the surface cuticle being restricted to a point corresponding with the postero-dorsal end of the *Petrobius* intucking, and the transverse union between the pair being an antero-ventral bar instead of a wider proximal union. Since the head of *Petrobius* is strongly hypognathous and that of *Tomocerus* prognathous it is perhaps remarkable to find such close similarity in the posterior tentorial apodemes in spite of the further changes due to the presence of the gnathal pouch.

In *Campodea* the posterior tentorial apodeme is much as in *Tomocerus*, the internal part spreading as two surface sclerotizations along the angle between the maxilla and labium and across the basal surface of the gnathal pouch (figures 45, 46A to D). The latter fades out in the thin cuticle lining the gnathal pouch and is not linked with the lateral head wall as in *Tomocerus*, a difference possibly connected with small size. The internal apodeme appears solid (cf. figures 46C, D with 38, 39L, M). The pair of apodemes are linked posteriorly by a large but very thin sheet of connective tissue, staining blue with Mallory, while the apodemes stain red ('endoskeletal plate' in figures 45, 46C to D, 47). Distally the surface arms of the posterior tentorial apodemes unite across the base of the hypopharynx, as in *Tomocerus* (cf. figures 44, 47 with 34, 35), and branch sclerotizations support the hypopharynx. *Tomocerus* also shows sclerotizations of the hypopharynx linked to the posterior tentorial apodeme (figure 36C, D), the details differing in the two animals.

The linkage of the posterior tentorial apodemes with the hypopharynx is probably associated with the feeding movements and protrusibility of the hypopharynx. A distal extension of the ventral end of the external opening of the posterior tentorial apodeme of *Petrobius* (figure 20), so as to reach the base of the hypopharynx, would be an easy morphogenetic change and would produce the collembolan and dipluran conditions (figures 35, 47).

The ventral longitudinal muscle and a sector of the dorsal longitudinal muscle insert on the inner end of the posterior tentorial apodeme in *Campodea* (figure 47), much as does the ventral longitudinal muscle complex of *Petrobius* (figures 20), but in *Tomocerus* only one sector of the ventral longitudinal muscle inserts on the posterior tentorial apodeme (figures 39M, N and drawn but unlabelled in figure 35), the greater part inserting on to a complex of the segmental tendon system (figure 35). The insertion of the labial and maxilla 1 muscles on to the posterior tentorial apodemes of *Tomocerus* and *Campodea* are similar (figures 34, 35, 45, 47; see also the labial muscles of *Ctenolepisma* in figure 27D).

Thus the anatomy, connexions and associated muscles of the posterior tentorial apodeme of a collembolan and a dipluran substantiate the homology of these apodemes with the similarly named structures of the Thysanura and with the posterior part of the pterygote tentorium. There is no need to use the terms fulcrum, sternal arm, or any other distinctive designation. Movements of the endoskeleton are considered in § 22 (v).

Transverse segmental tendons of Tomocerus

Both the transverse mandibular and maxilla 1 tendons are present, the former situated distal to the latter, and they link respectively transverse mandibular and maxilla 1 muscles. The form of these tendons has not hitherto been appreciated or distinguished from the tentorial apodemes. Both tendons form square plates (figures 32, 35, 37H and 38K). They are united laterally by longitudinal connectives which extend beyond the maxilla 1 plate to join with the internal ends of the posterior tentorial apodemes and posterior endoskeletal plate (figure 33).

The mandibular tendon lies over the terminations of the anterior tentorial apodemes and from the distal upturned edges of the tendon the following paired extensions arise:

(1) *The inner dorsal arm* (so called by Hoffmann (1905, 1908) corresponding with the trabecula of Denis (1928)) passes forwards, upwards and towards the middle line, the pair uniting to form the main support for the median junction of some antennal muscles (figures 32, 35, 36D, 37E, F). The inner dorsal arm stains pink, like branch i of the anterior tentorial apodeme, and not blue with Mallory's stain as does the median part of the tendon. Several small branches anchor the median tendinous junction of the inner dorsal arm to the surface cuticle, one is shown in figure 32R.

(2) *The outer dorsal arm* (Hoffmann) branches laterally from the inner dorsal arm, it passes forwards, lateral to the circumoesophageal commissure, and outwards to end on the lateral head wall in front of the eye and beside the posterior edge of the antennal base (figures 32R, 37G and 37H). This branch carries no muscles.

(3) *The dorsal suspensory arm* passes directly upwards and bears the dorsal suspensory muscle to the head wall (the muscle but not the skeletal arm is labelled in figures 32, 35 and 37I).

(4) *The ventral suspensory arm* passes directly downwards bearing the ventral suspensory muscles to the head wall, and a branch carries the middle and lower sectors of the ventral longitudinal muscles from the trunk (figures 33, 35, 37I).

(5) *The anterior dorsal arm* from the anterior corner of the mandibular tendon passes upwards and forwards, the arm is short and bears antennal muscles (figures 32S, 33T and 37G).

Paired longitudinal connectives

These are formed of connective tissue fibres staining blue with Mallory's stain, they resemble those of *Anaspides*, etc. (figure 8) in principle, but are much more elaborate in detail. These connectives in *Tomocerus* arise from the mandibular tendon at its postero-lateral corners (just behind the level of figure 37I). Each passes backwards as a dorso-ventrally expanded plate, curved as shown by figure 38J and labelled also in 32R. A cross and a triangle mark the middle and upper ends of this sheet in figures 38J, K. A little behind, where the connective unites with maxilla 1 tendon, the manner of doing so is shown by the marked points. Both faces of these connectives are clothed with muscles which have been partly cut away in figure 33. Behind the maxilla 1 tendon each longitudinal connective divides between the parts marked by a cross and a triangle (figure 39L). The outer upper section (marked by a cross) passes obliquely outwards and backwards to the blind end of the posterior tentorial apodeme with which it is linked by the flange shown in figures 39M, N passing between the cross and the hollow apodeme. The connective marked by the cross ends posteriorly by union with the U-shaped posterior endoskeletal plate (figures 39O, 40P). The inner fork of each longitudinal connective, marked by a triangle, continues directly backwards to end by union with the posterior endoskeletal plate on either side of the middle line (figures 32R, 33T, 35, where the inner fork of the longitudinal connective between the maxilla 1 tendon and the endoskeletal plate is shown but not labelled, also 39O, 40P).

The posterior endoskeletal plate

This is a transverse U-shaped cuticle-like membrane situated as shown by figures 32, 33, 35 and 40P. Laterally the plate is suspended by fibrils from the dorsal head wall. Thinner skeletal membranes pass from the plate dorso-ventrally round the segmental organ, both mesially and anteriorly to end on the head wall (unmarked in figure 40P and 'skeletal membrane' in figure 32S). An oblique endoskeletal muscle extends from the outer lateral face of the plate to the posterior tentorial apodeme (labelled in figures 33T, 35, 39N, O and 40P). The function of this plate is obscure, it may have something to do with controlling the pressure on the segmental organ as well as anchoring the posterior tentorial apodemes.

Transverse segmental tendons and posterior plate of Campodea

In this animal the head segmental tendons are much simpler than in *Tomocerus*. The transverse mandibular tendon is a flat bar (figure 44, 46A, B) lying far forward in the head and not opposite the posterior part of the mandible as in *Tomocerus* (cf. figure 44 with 32, 33). What appears to be the maxilla 1 tendon lies immediately behind and is united laterally with the mandibular tendon (figure 44). There are no paired longitudinal connectives. Reference has already been made to the sheet of connective tissue linking the posterior tentorial apodemes ('endoskeletal plate' in figures 45, 46C, D), paired fibrils leave the posterior part of this plate and unite with a median ventral cuticular intucking (figures 45, 47). Anteriorly this plate lies close behind the transverse mandibular and maxilla 1 tendons, and bears antennal muscles dorsally and labial and tentorial muscles ventrally (figure 47). The posterior tentorial apodemes rise in the head to meet the posterior part of the plate. The homology and function of this plate is uncertain, other than providing muscle insertions and anchorage for the tentorial apodemes. The plate floors the head space occupied by bulky mandibular and maxillary muscles much as does the posterior endoskeletal plate of *Tomocerus*, but the plate in *Tomocerus* appears to be a stout membrane and not a fibrillar layer. The plates in both *Tomocerus* and *Campodea* are connected by oblique muscles with the posterior tentorial apodemes (unlabelled muscles from the anterior end of the plate in figure 47; cf. figure 35 'oblique endoskeletal muscle'). It is probable that the presence of these plates in the collembolan and dipluran are correlated in some manner with entognathy and the protrusibility of the hypopharynx.

No useful purpose will be served by considering further the enormous differences between the present account of the endoskeletal systems of a collembolan and a dipluran and the statements which have preceded it (Borner 1921; Denis, 1928; Snodgrass 1928, 1932, 1935, 1951, 1960; Tuxen 1959, etc.).

(ii) *The musculature and movements of the mandibles of* Tomocerus longicornis (*Müller*)

The mandibles and their muscles in *Tomocerus plumbeus* were first described with accuracy by Hoffmann (1908) who correctly stressed the rotatory movement of these limbs. Most of these muscles appear to be homologous with those of *Petrobius*; a summarizing comparative table is given at the bottom of figure 21. Reconstructions show the musculature at progressive levels in figures 32 and 33, sections are given in figures 36 to 40 and a functional diagram in figure 42.

As is well known the mandible of *Tomocerus* is very free within the gnathal pouch, being suspended from its lateral wall by a fold of thin flexible cuticle, representing the folded base of the limb (figures 32S, 33U, 37H, I; see Denis (1928) for derivation, there is no rod as claimed by Snodgrass (1950)). Ample arthrodial membrane passes from the margins of the mandibular cavity to: the inner surface of the gnathal pouch, to the upper flexible face of maxilla 1 and to the superlingua. At the proximal postero-ventral corner this membrane is stiffened (origin of muscle 6 in figure 37I) forming a 'chitinzapfen' which provides 'ein hinteren Dreh- und Articulationspunkt für das Organ ab' (Hoffmann 1908). It bears muscles 3, 4, 5 and 6, inserting on the cranium, which rotate the posterior border of the mandible mesially and upwards (clockwise as seen in figure 37I). This 'Zapfen' represents the posterior mandibular apodeme of *Petrobius* and is not an articulation; muscles 3 to 6 of *Tomocerus* (figure 32S) correspond with adductor muscle 11 in all its sectors of *Petrobius* and *Ctenolepisma*. Figure 37H shows muscle 9 from the antero-dorsal edge of the mandible pulling in the opposite direction. Muscles 3 to 6 and the others which rotate the mandible in this same direction will be referred to as 'rotator' muscles; they cause the grinding between the molar areas and the distal cutting, and the 'counter-rotator' muscles such as muscles 7 and 9 (figure 37E, H) perform the recovery rock, separating the cutting cusps. The mandible is well provided with bearings: the anterior tentorial boss, branch iii of the anterior tentorial apodeme, the bearing of the superlingua (figure 36B to D) and the frontal sclerite (see above) all support and restrict its movement to one of rotation and counter-rotation. They lie distally, as near as possible to the cutting and grinding parts.

The isolated mandible shows an oblique dorso-lateral ridge on the outer face (figure 42*a*), but in the normal position within the head this ridge is longitudinal to the head (figures 42*b*, 32S, 36D) and bears large muscles 1 and 2 which fan upwards, outwards and downwards to the head wall. They are strongly rotator in function; see arrow in figure 36D. They could not be present but for entognathy, and have no counterparts in *Petrobius*. The slope of the ridge is appropriate to its function.

The mandibular boss on the anterior tentorial apodeme lies at the upper level of the mandible. Not only does the mandible rotate against this boss, but the boss limits the upward movement slightly, so that rotation by muscles 1 and 2, etc., forces the mesial molar areas of the mandible well together in the middle line. Hoffmann (1908) figures a hump in *T. plumbeus* which he thought articulated with the boss. In *T. longicornis* a hump lies as shown in figure 36D; it does not form an articulation, but it is possible that it serves as a stop preventing excessive counter-rotation.

The rotator movement is combined with a retractor-adductor one since muscles 3 and 4 also retract. The counter-rotator movement is in effect a protractor-abductor one, but, as already seen, the range of adductor-abductor movement is very small.

The counter-rotator muscles are 7 and 8 arising from the morphological anterior border of the mandible and inserting on the anterior tentorial apodeme (corresponding with muscles 4 and 5 of *Petrobius*). These muscles must also tend to protract the mandible, but if they pull in unison with muscles 9, 10, 11 and 12, also arising from the anterior border (figure 32S), they all must counter-rotate the mandible, while muscles 11 and 12 contracting alone must cause retraction. Muscles 9 to 12 correspond with muscles 1 to 3 in *Petrobius*.

Muscles 6 and 7 of *Petrobius*, arising from the proximal part of the posterior margin of the mandible, and from the posterior part of the mandibular concavity in *Ctenolepisma*, are represented in *Tomocerus* by muscle 17 arising from a position corresponding with that of *Ctenolepisma* (figures 33, and 37I) but inserting on the longitudinal tendinous connective between the mandibular and maxillary tendons and on to the posterior corner of the mandibular tendon. The anterior tentorial apodeme in *Tomocerus* is too distal in position to be serviceable for muscle 17. Muscle 17 must be a rotator, corresponding with its homologues in the Thysanura (remotor in *Petrobius* and adductor in *Ctenolepisma*).

Muscles 13, 15 and 16 arise from the concavity of the mandible (figures 33, 35, 37H) and correspond respectively with muscles 9, 10 and 8 of *Petrobius*. Muscle 13 is oblique, as shown in figure 33T, and inserts on the transverse mandibular tendon, spreading forwards on to the anterior tentorial apodeme. Muscle 13, like muscle 9 of *Petrobius*, can cause promotion and abduction of the distal tip of the mandible. Muscles 15 and 16 unite with their fellows from the opposite mandible and lie below the transverse mandibular tendon, loosely tied to it by connective tissue fibres in the middle line. Since these muscles join the proximal ends of the mandibles their contraction can only cause abduction of the tips. It is probable that length changes in muscles 15 and 16 are small and that their main function is stabilizing the mandibles which are otherwise so free, as does muscle 32 of the Chilopoda (p. 90). Muscle 14 is very small, passing from the concavity of the mandible up to the postero-ventral face of the mandibular tendon, as shown by the dotted line in figure 33U; the muscle is cut away from the level of figure 37E. It is apparently levator in function.

The movements and musculature of the mandible are summarized in figure 42. *Tomocerus* contrasts with all arthropods so far considered in the possession of well developed mandibular protractor muscles 7, 8 and 13 (cf. muscle 9 of *Petrobius*, figure 21) which are countered by retractors 3, 4, 11 and 12. This movement is made possible by entognathy.

The disposition of the muscles of *Tomocerus* shows a remarkable similarity to those of *Petrobius*. The bulkiness of the counter-rotator muscles pulling on the anterior margin suggests that outside work can be done by the tips of the mandibles during counter-rotation as well as during rotation, as is suggested for *Petrobius*. Mandibular muscles of other arthropods which cause recovery movements only have been seen to be much less bulky in comparison with the effector muscles, be they remotor, rotator or adductor in function (cf. muscles 3 and 4 of *Chirocephalus* and *Anaspides*, and the promotor compared with the remotor components of the transverse muscles inserting upon the transverse mandibular tendons of Crustacea, *Petrobius* and *Campodea*; figures 2*d*, 3, 7, 9E, 21, 24H 46B). The planes in which the mandibular muscles lie indicate how very varied may be the movements caused by different combinations of muscles. The great length of many of the muscles, such as 4 to 6 which cross over to the other side of the head, combined with the small range of movement (a restriction imposed by the skeleton, see above), indicates that many movements are effected with a small degree of muscular shortening, and the nearer the approach to isometric contraction the more efficiently will the muscle work.

The design of slowly contracting musculature which gives strong movements of arthropod ambulatory limbs differs from that providing rapid but weaker movements (see limb musculature of Diplopoda and Chilopoda (Manton 1958*a*, 1964). It is probable that the mandibular movements of *Tomocerus*, which are difficult to observe, are small, varied and rapid. The many long mandibular muscles appear to be suited to provide such movements with physiological and mechanical efficiency.

The histology of the mandibular muscles of *Tomocerus* differs markedly from those of other arthropods and from the trunk musculature. Snodgrass (1960) states that no other arthropod has so many mandibular muscles. It is not the large number of muscles, but the large size and small number of muscle fibres which is remarkable. Single fibres composed of a central core of fibrils surrounded by an irregular billowing mass of nucleated cytoplasm (figure 35, muscles 4 to 6 and 15 to 16 and figure 37, muscles 1, 2, 6, 8 and 9, etc., and maxilla 1 muscles) can be counted with ease, and each has been called a muscle (i.e. muscles 1 to 17). Hoffmann (1908) has drawn attention to the existence of twin muscles, i.e. two fibres situated side by side. By ordinary description twin muscles 9 and 10, 11 and 12, and 15 and 16, might be regarded as three and not six muscles. The separate muscle fibres composing the muscles of the mandibles of other arthropods are uncountably large in number. Separate fibres have sometimes been drawn in the figures here (as in figures 3, 26), but usually the fibres are too numerous for this and conventional fibres are marked on the drawings. The trunk and limb muscles of *Tomocerus* do not show the large cytoplasmic investment of the contractile elements found in the muscles of maxilla 1 and mandible. Perhaps some physiologist will study the properties of the mouth part muscles and determine whether their histology has anything to do with rapidity or other peculiarity of action.

(iii) *Distinctive characteristics of the entognathy of* Campodea staphylinus *West and the movements and musculature of its mandibles*

The entognathy of *Campodea* differs from that of *Tomocerus* in the following respects.

(1) The mandible is very long, sinking into the base of the head instead of reaching about half way (figures 33, 44). Maxilla 1 is entirely covered antero-dorsally by the mandible, and thus muscles III and IV have no access to the roof of the cranium and insert instead upon an exoskeletal fold crossing the postero-dorsal margin of the head (figures 44, 45, 47).

(2) The small size of the preoral cavity and the absence of anterior tentorial apodemes necessitates a distal position for the transverse mandibular tendon, which carries muscles apparently homologous with those inserting upon the anterior tentorial apodemes of *Tomocerus*.

(3) The transverse mandibular tendon is wide in *Campodea*, much as in *Chirocephalus* and *Anaspides* and not narrow as in *Tomocerus* (figures, 3, 9, 33, 44), and its function differs in the two apterygotes. In *Campodea* the mandible rocks in the horizontal plane about the wide transverse tendon, as in primitive Crustacea, in *Petrobius* and in the prosomal limbs of *Limulus*. The muscles inserting on the tendon and causing this promotor-remotor swing (marked by brackets in figure 46B) are directly comparable with those of *Chirocephalus* and *Paranaspides* (figures 2*d*, 9E, muscles 5*b*, 5*a*), *Limulus* (figure 14, muscles 41*a*, 41*p*) and *Petrobius* (figure 24H, marked muscles on either side of 8). The transverse mandibular tendon of *Tomocerus* does not form an axis of mandibular movement and it does not carry rotator or counter-rotator muscles. The narrow tendon, proximal in position, here carries long transverse mandibular muscles which appear to be mainly stabilizing in function, as in Chilopoda (p. 90).

(4) The protractility of the mandibles, which appears to be such an important feature of entognathy, is accomplished quite differently in *Campodea* and in *Tomocerus* (see below).

The mandibular muscles of *Campodea* have been imperfectly described, the bulkiest of them being omitted from the account by Tuxen (1959). As in *Tomocerus*, the basic plan of the mandibular muscles of *Petrobius* can be recognized in *Campodea*, and it has been possible to use the same numbering of muscles in figures 44 to 47 as for *Tomocerus*. The differences in musculature of *Tomocerus* and *Campodea* relate to the difference in function of the transverse mandibular tendon, muscles arising from the concavity of the mandible converging on to the tendon in *Campodea* but diverging in *Tomocerus* (muscles 13 to 17); to the difference in the protractor mechanism; and to the presence of a prostheca. Tuxen's lettering of the muscles is included in brackets below. The muscles will be considered in functional groups, as summarized for *Tomocerus* in figure 42.

The *rotator* (*remotor*) *movements* are caused (i) by muscles pulling on the outer face of the mandible: muscles 1 and 2 (Tuxen *d* and *c*) arise over the much incurled margin of the mandible, and insert on the antero-dorsal face of the cranium as shown (figures 44, 46A). Their contraction has the same effect upon the mandible as that of muscles 1 and 2 in *Tomocerus* which fan outwards and downwards from a more laterally placed origin. (ii) By muscles pulling on the posterior margin of the mandible essentially as in *Tomocerus*:

muscles 3 and 4 comprise about 6 strands arising from the arthrodial membrane on the posterior mandibular border as shown in figures 44, 46C and 47. They pass posteroventral to muscles 5 and 6 and insert upon the hinder wall of the cranium near the middle line. Muscles 5 and 6 arise proximal to muscles 3 and 4 (figures 44, 46C). Muscle 6, with about 4 strands, inserts on the cranium behind muscle 9 on either side of the median septum, while muscle 5 finds cranial space between muscles 6 and 11 as shown, passing steeply upwards from the mandible. (iii) By muscles arising from the concavity of the mandible posterior to the transverse tendon, marked remotor on figure 46B. The most posterior of these, Tuxen's muscle *h*, and so marked in figures 44 and 46, inserts half way along the tendon, thereby gaining leverage in opposition to that of muscles 7 and 8.

Counter-rotator (*promotor*) *movements* are caused (i) by muscles pulling on the anterior mandibular margin (figures 44 and 46): muscles 9 and 11 (Tuxen *e* and *i*) insert on the cranium just lateral to the anterior end of the median septum, and on to the exoskeletal fold, respectively, and correspond with twin muscles, 9, 10 and 11, 12 of *Tomocerus.* Muscles 7 and 8 (Tuxen *f*, right side of figure 44, 46B) insert upon the base of the branch of the transverse mandibular tendon bearing the dorsal suspensory muscle; the emargination of the mandible at the origin of muscles 7 and 8 (cf. figures 46A, B) enables these muscles to be long and to exert greater leverage than they would do if the mandibular edge was incurled all along. These muscles are not protractor as are their homologues in *Tomocerus* which insert on the anterior tentorial apodeme. (ii) By muscles arising from the concavity of the mandible and anterior to the transverse tendon, marked 'promotor' in figure 46B.

Retractor movements are caused by the few short fibres from the mandibular concavity passing to the distal side of the transverse tendon (figure 44, left side); by muscle 3 and 4 (see above); and to some extent by muscle *b* pulling on the long tendon from the prostheca.

Protractor movements are caused by Tuxen's muscle *g* (figure 44, left side) and the fibres alongside it on the proximal side of the transverse tendon.*

Such protractor fibres are not found outside the entognathous groups. This dipluran condition could have arisen by elaboration of muscle fibres 9 of the *Petrobius* type (figure 21). In the collembolan it is muscles 7, 8 and 13 which provide the strong protractor movements and only muscle 13 is somewhat comparable with the muscles from the mandibular concavity to the tendon in *Campodea.* If a functional advantage of entognathy lies in the facilitation of protractile mandibles, as is here suggested, the provision of the protractile force from different muscles in Collembola and Diplura suggests a parallel and independent evolution of entognathy in these groups.

The similarities between the mandibular musculature of *Tomocerus* and of *Campodea* reside in the very full use of the mandibular margins for the origin of rotator and counter-

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* Tuxen (1959) has compared the mandibular muscles of the collembolan *Onychiurus armatus* with the dipluran *Campodea plusiochaeta*, yet his account of the anatomy of both animals is too superficial to be used for such a purpose for which accurate knowledge of the origins and insertions of all muscles are needed, together with a detailed knowledge of the endoskeleton. Such data can only be obtained from serial sections, as the comparison with Tuxen's figures and those presented here shows. (See also footnote to p. 68). No useful purpose will be served by further consideration of the differences between Tuxen's suggested resemblances and homologies and those put forward here.

rotator muscles, whose insertions are also comparable (muscles 3 to 12, figures 32, 44), and in the possession of muscles 1 and 2 from the outer surface of the mandible. The former appears to be a simple evolutionary advancement from an archi-*Petrobius* type of ancestor and the latter is a feature made possible by entognathy; such muscles are found also in the Chilopoda (muscles 25 and 26, § 31 (ii)). Since muscles 1 and 2 pass predominantly upwards (anteriorly) in *Campodea* and outwards and downwards (posteriorly) in *Tomocerus* they may well have evolved independently. The differences in the entognathy and mandibular mechanisms of *Tomocerus* and *Campodea* suggest that the one could not easily be transformed into the other without a direct reversal of previous evolutionary progress, but both might readily have been evolved for an archi-*Petrobius*-like state.

(iv) *The musculature and movements of maxilla* 1 *of* Tomocerus longicornis (*Müller*) *and of* Campodea staphylinus *West*

While the purpose of the present work is a study of mandibular mechanisms, it is useful to point out certain similarities and differences between the maxilla 1 of some of the animals considered.

Maxilla 1 of *Petrobius*, *Tomocerus* and *Campodea* are remarkably similar in general form, musculature and movements. A large apodeme controls the lacinia in *Petrobius* and *Tomocerus* while the stout base of the lacinia serves the same purpose in *Campodea* (figures 22, 33, 34, 45). The muscles which are probably homologous in these three animals bear similar Roman numerals. The differences some muscles show in their attachments at one or other end suggest modifications of the same basic set-up which are no greater than the modifications of muscle insertions which have been found in a recent survey of the musculature within a single class (the Diplopoda (Manton 1961 *b*)).

Muscle I is similar in all (Tuxen *f* in *Campodea*). Muscle II from the lacinia apodeme to the cardo is absent in *Petrobius*. Muscles III and IV are similar in all three animals but insert of necessity on the back of the cranium in *Campodea* (p. 65). Muscle V to the anterior tentorial apodeme in *Petrobius* and to the transverse tendon in *Campodea* is absent in *Tomocerus*. Muscles VI, VII, VIII and IX from the stipes insert on the posterior tentorial apodeme and transverse maxilla 1 tendon in *Petrobius*, and on to the posterior tentorial apodeme of *Tomocerus* and *Campodea*, the four muscles being more or less merged in *Campodea*. These muscles usually appear to contribute to the adductor-retractor movement of the distal maxilla 1 armature, although the different directions in which these muscles pull in *Petrobius* and *Tomocerus* are probably associated with functional differences. Muscles VIII and IX in *Tomocerus* appear to be protractors. Muscle X, the principal transverse muscle associated with the transverse maxilla 1 tendon, arises from the stipes in *Petrobius* and is adductor in function. In *Tomocerus* and *Campodea* the muscle arises from the cardo, it is largely stabilizing in function in *Tomocerus* and protractor in *Campodea*. Muscle XI from the cardo is a principle protractor in all three animals, inserting on the anterior tentorial apodeme in *Petrobius*, on to the transverse maxilla 1 tendon in *Tomocerus* (figures 33, 38K) and on to the posterior tentorial apodeme in *Campodea* (figures 45, 46C). Muscle XII, a protractor in *Petrobius* and *Ctenolepisma*, appears to be largely retractor in *Tomocerus* (see pp. 44 and 52), but there is no space for such a muscle in *Campodea* and here muscles VI to IX must retract as well as cause adduction, as do muscles VI and VII in *Petrobius* and *Tomocerus*.* Movements of the complex units of the distal maxilla 1 armature of *Petrobius* and *Tomocerus* occur but are not directly controlled by muscles. Cuticular elasticity of the highly sclerotized parts probably accounts for recovery movements. A summary of the muscles and movements of maxilla 1 of *Tomocerus* is given in figure 43.

(v) *The musculature and movements of the head endoskeleton of* Tomocerus longicornis (*Müller*) *and of* Campodea staphylinus *West*

In § 20 attention has been drawn to the slight movements of the head endoskeleton of *Petrobius* caused by muscles E1 to E4. In *Tomocerus* the provision for movements of this kind are more elaborate and consist of: (i) The paired dorsal and ventral suspensory muscles from the transverse mandibular tendon (figures 35, 37H, I). (ii) The paired posterior dorso-ventral suspensory muscle which unites in part with the blind end of the posterior tentorial apodeme (figures 32, 35, 39M to O). Both of these paired suspensory muscles are attached to the postero-ventral head cuticle directly by fibrils, but antero-dorsally they possess cuticle-like rods situated between the striated muscle fibres and the unstriated fibrils inserting upon the surface cuticle (figures 37H, I, 39M, N, and 41). The rods are simple in *T. longicornis*, but branched in *Orchesella villosa* and they stain as does the endocuticle. They are probably elaborations of the basement membrane. They are also reminiscent of the elastic units of 'resilin' situated between the flight muscles and wings of insects, which have been shown to be of great importance in elastic storage of energy during the rapid movements of the flight muscles (Weis-Fogh 1959). (iii) The transverse muscle uniting the internal ends of the posterior tentorial apodemes (figures 34, 35, 39M). (iv) The paired oblique endoskeletal muscle extending from the internal ends of the posterior tentorial apodemes to the outer face of the posterior endoskeletal plate (figures 33, 35, 39N, O, 40P). (v) The paired fans of muscle from the internal ends of the posterior tentorial apodemes passing to the transverse maxilla 1 tendon (figure 33).

Movements created by these muscles must be small because both tentorial apodemes are anchored to the surface cuticle and the longitudinal connectives of the tendon system are doubly linked with the posterior endoskeletal plate and with the tentorial apodemes. The former are united to the surface cuticle by fibrils which do not appear to be muscular.

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* Tuxen (1959) described the maxilla 1 muscles of *Campodea plusiochaeta* but he cut no sections and could see no segmental tendons, although he supposes such structures (an 'endosternite') to be present. He could not ascertain the insertion of many muscles and the morphology portrayed is partly inaccurate. The correspondence between Tuxen's muscles, marked by letters in his account, and those marked by Roman numerals here (figures 45 to 47) is as follows: *a* = III or perhaps IV; only one of these muscles was seen in *C. plusiochaeta*; *b* = II but this muscle, in two sections, arises entirely on the cardo and not from 'the corner between the stipes and cardo'; *c* = XI but it arises from the cardo and does not insert on the 'endosternum'; its insertion is clearly shown by figures 46C and 47; *d* = X but it arises entirely from the cardo; *e* = VI to IX; *f* = I; *g* = ig; *h*, as described by Tuxen could not be identified with certainty in *C. staphylinus*, but a muscle V is present as shown in figure 45 which is presumably not the muscle *h* of Tuxen, although arising in about the same place; muscle *i* to the palp is not shown in figures here. It is probable that the musculature of *C. staphylinus* and *C. plusiochaeta* is much the same, and that the discrepancies noted above are due to examination of muscles by whole mounts without confirmation from sections. Sections and triple staining are essential for such an investigation, accurate knowledge of origins and of insertions being needed for the present consideration of function.

It is possible that the endoskeletal muscle system and the cuticular suspensory units undergo vibrations in association with rapid movements of small amplitude executed by the mandible, hypopharynx and maxilla 1 and they may be of service in an elastic capacity. Heads of arthropods with mandibles which give slow, strong actions have no internal systems capable of undergoing vibratory movements. In the Pterygota with typical biting mandibles the head endoskeleton is rigid, possessing no muscles of its own; and in the Diplopoda, where slow movements of the head endoskeleton form an integral part of the biting mechanism (§ 25 (i)), the endoskeletal muscles are very massive and not long and thin, and they lack elastic units.

The head endoskeleton of *Tomocerus* being linked with the dorsal and ventral longitudinal muscular systems of the trunk may be retractable as a whole by these muscles. Such a movement must pull back the hypopharynx and the mouth parts within the gnathal pouch. Protraction of the endoskeletal system is caused by less obvious means. Deformations imposed upon the suspensory muscles can be restored by their contraction, and contraction of endoskeletal muscles must tend to protract the posterior tentorial apodemes with respect to the tendon system, but an adequate muscular basis of protraction does not appear to be present. It is possible that a hydrostatic one is operative, as in the extension of ambulatory limbs of myriapods and cirri of barnacles (Manton 1958*a*, *b*; Cannon 1947). The subject deserves further study.*

In *Campodea* the endoskeletal muscles are fewer: (i) Paired dorsal suspensory muscles pull on long processes from the transverse mandibular tendon (figures 44, 46A, B). (ii) A more median small pair of inner dorsal suspensory muscles passes from the transverse mandibular tendon to the cranial roof, as shown in figures 44, 47. (iii) A pair of dorsal suspensory muscles from the inner ends of the posterior tentorial apodemes passes directly upwards to the cranium without intervention of an elastic-like unit (figures 44, 46C, 47). It is probable that these endoskeletal muscles serve the same general purposes as those of *Tomocerus*, and that their lesser development is related either to smaller frequencies of mandibular movements or to the smaller size of the animal.

23. Conclusions concerning the entognathous Apterygota

Many statements which have been made, in the absence of accurate information concerning head anatomy and movements of Thysanura and entognathous Apterygota (Snodgrass and others), must now be rejected. Some of these are: (i) The homology of so-called sternal brachia of Malacostraca (which in any case are not characteristic of the whole group) with the posterior tentorial apodeme of the Collembola and Diplura (pp. 55 and 58). (2) The view that sternal sclerites support maxillae 1 in entognathous Apterygota in contrast to all other arthropods except the Malacostraca (pp. 24, 58). (3) A tentorium of the pterygote type which has its inception in the Thysanura is wholly absent from the entognathous groups (§§ 17 (i), 19 (i) and pp. 55, 58). (4) That the collembolan tentorium has no

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* There is a great readiness in recent work to invoke hydrostatic pressure as the obvious explanation of movements whose cause is not understood. Before taking such a step the full results of such a supposed dislocation of the internal pressure systems with respect of blood circulation should be considered. And the existing bulk of heart musculature together with other muscles supposed to cause a redistribution of fluids should be considered in respect of blood circulation.

correspondence with the myriapod hypopharyngeal apodemes (anterior tentorial apodemes, see pp. 74, 77, 80–81, 83, 88 and 92). (5) That a tripartite metastomal organ of Crustacea composed of a median lobe united with paragnaths is characteristic of Crustacea (p. 22) and, further, is comparable with hypopharynx and superlinguae of many apterygotes. (6) That the head and mouth parts of entognathous apterygotes show little in common with the Thysanura. (7) That the head of Thysanura furnishes no decipherable evidence as to the relation of the Thysanura to other arthropods (see §§ 19 to 23 and p. 54), etc.

More cogent statements can now be made. The head structure of Collembola and Diplura, including the pleural folds, hypopharynx, superlinguae, mandibles, maxillae 1, tentorial apodemes, musculature and movements, are clearly derivatives of the *Petrobius* type as is the head structure of *Ctenolepisma* and the Pterygota. The latter illustrate the evolution of strong transversely biting mandibles with very long cusp rows which are capable of cutting into large objects. The Collembola and Diplura represent an opposite evolutionary trend, towards protrusible mandibles which grasp and cut relatively small objects by a rotatory movement, using very short cusp rows, or they pierce food surfaces.

The development of a gnathal pouch (entognathy) by enlargement of a pleural fold, such as present in *Petrobius*, has permitted the evolution of the proximal freedom conferring protrusibility to the mandibles, and has emancipated the hypopharynx and superlinguae from a predominantly hydrostatic function (now taken over by the gnathal pouch), permitting these structures to be large, protrusible and mechanically useful in feeding. The entognathy of the Onychophora is ontogenetically similar to that of the Collembola and has similar functional assets. In Collembola, Diplura and Onychophora a variety of feeding movements can go on without disturbing the hydraulic efficiency of the oral cone when applied to the food. Copious salivary secretions are produced and finely divided and fluid food is sucked up.

The resemblances between Collembola and Diplura concern the general characteristics of entognathy, the very full use of the anterior and posterior mandibular margins for the origin of rotator and counter-rotator muscles and a highly muscular and probably elastic endoskeletal system. All these are derivatives of a *Petrobius*-like condition, mandibular muscles 1 to 3 and 11 of *Petrobius* corresponding with muscles 9 to 12 and 3 to 6 respectively of the Collembola and Diplura.

The different ways in which mandibular protraction is achieved in the Collembola and Diplura, together with the differences in use of the transverse mandibular tendon and the further points listed on p. 65, suggests that entognathy in these two groups has been evolved independently (p. 66). Tuxen (1959, 1960) suggested that the resemblances he observed from his incomplete data indicated a monophyletic derivation of the Collembola, Diplura and Protura which he placed in a class, the 'Entognatha'. The present work does not substantiate a supposed monophyletic derivation of these entognathous apterygotes, although they may have had a common origin in some archi-*Petrobius*-like stock lacking entognathy. No special study of the Protura has been made here, but in them the protractile piercing tendency of the mandibles of many Collembola is carried further. No support is given by the present account for Tuxen's (1959) view that 'the musculature of the mandibles suggests that of myriapodan groups', in fact they exhibit fundamental differences (see §§ 24 to 32). Head structure in entognathous apterygotes cannot be regarded as primitive.

Maxilla 1 in its structure and movements throughout the Thysanura, primitive Pterygota, Collembola and Diplura exhibits a community of basic plan and of detail which is not shared by the Myriapoda. This similarity, together with the demonstration of a basic common plan of mandibular structure and of head endoskeleton, in spite of superimposed divergent lines of evolutionary advancement and specialization, indicates a relatedness among hexapods which is quite independent of the possession of only three pairs of trunk limbs (see further in § 33 (iv)).

Endoskeletal tendinous structures in the head and elsewhere are not necessarily mesodermal when detached in the adult from the surface cuticle as so frequently implied. The anterior and posterior tentorial apodemes and the transverse segmental tendons of the head are present in a basic and simple form in *Petrobius* and are adequately described here for the first time. The loss of the transverse tendons and an acquired rigidity of the tentorial apodemes is correlated with the needs of strong transverse biting, while an increase in endoskeletal mobility, beyond the *Petrobius* condition, by development of more endoskeletal muscles and of units which are probably elastic, is associated with the needs of entognathous feeding.

24. GENERAL CONSIDERATIONS CONCERNING THE MANDIBLES OF THE MYRIAPODA

As in the apterygote and pterygote insects the mandible of the myriapod classes is formed by a whole limb, but it is composed of two segments in Symphala, three in the Diplopoda, five articulated scutes are present in scolopendomorph Chilopoda and in the Pauropoda the mandible is unjointed. The Diplopoda and Symphyla respectively bite entirely and largely in the transverse plane, the mandibular segmentation enabling this to be done with ease. Transversely biting mandibles which are not segmented cannot occupy the whole dorso-ventral head length as in Diplopoda (cf. figure 49 with 10*a*, 13 and 25). The usual abductor difficulty (p. 9) has had to be resolved, and in Diplopoda, Symphyla and Chilopoda skeletal elements outside the mandibles serve this purpose to varying extents.

It is probable that transverse biting in Diplopoda and in Symphyla has been evolved directly from adductor-abductor (depressor-extensor) movements such as seen in trunk limb telopodites, and not via a rolling type of mandible as for transversely biting Crustacea and insects. Undifferentiated anterior pairs of trunk limbs are used to grip a food mass in *Anapsides* and *Scolopendra*, the same limbs being locomotory at other times. In the carnivorous and scavenging diplopod *Callipus* the three anterior pairs of trunk limbs are used for holding food and not for walking; these limbs are short and stout and bear gripping spines (figure 48). A limb of this general type could readily become a segmented mandible, with its base spread up the side of the head permitting a large attachment by adductor and other muscles, provided some suitable abductor mechanism were simultaneously evolved. The distal segments of the trunk limbs of diplopods, and of many other arthropods, are extended indirectly by proximal depressor muscles acting during the propulsive backstroke, and when off the ground by blood pressure alone. No arthropodan mandibles have been found whose anatomy and connexions suggest that hydrostatic pressure is a major agent causing either abduction or any other type of recovery stroke. It is probable that the utilization of an extra-mandibular abductor mechanism has permitted the evolution of transverse biting directly from telopodite gripping in Diplopoda and Symphyla. This type of movement is facilitated by a segmented limb while the rolling type of movement, seen in *Petrobius*, would be hindered by segmentation. It is probable that the mandibles of Chilopoda have been derived from a type not unlike those of ancestral Diplopoda and Symphyla.

25. COMPONENTS OF THE FEEDING MECHANISM OF THE SPIROSTREPTOMORPH DIPLOPOD *PORATOPHILUS PUNCTATUS* ATTEMS

As is well known, the diplopod mandible is attached to the head by a long, strong hinge permitting small adductor and abductor movements. The hinge lies alongside the external pseudoccipital process in Iuliformia and Spirostreptomorpha (figures 49, 53 U, V) but is set in the cranium in Spiroboloidea, as shown for *Chirsastus fasciatus* in Manton (1961, text-fig. 32). The short cardo is hinged distally (W, X) to a longer stipes much of which is covered by the collum. A stout gnathal lobe is hinged (Y, Z) to the stipes and capable of opening out widely. The transversely expanded labrum indicates the use of a wide gape, as in the locust (figures 51 and 28 in contrast to 25*b*). Figure 52 shows the position of mandibular adduction, the labrum being removed; the abduction position is seen on the right side of figure 53. Ample arthrodial membrane links the anterior and posterior margins of the cardo and stipes (figures 49, 53) to the labrum and gnathochilarium. The gnathal lobe lies freely in a very large preoral cavity, floored by the hypopharynx from which flexible cuticle continues to the distal anterior margin of the gnathochilarium behind and below the gnathal lobes (figures 49, 50).

The mesial face of the gnathal lobe bears distal cusps on a fixed 'incisor process' and a movable tooth row; many small rows of spines are set in flexible cuticle and a large molar area (figures 50, 52) is present, as in some other herbivores and omnivores (*Tomocerus*, *Petrobius*, *Anaspides*, etc.). The gnathal armature is asymmetrical, as is usual in arthropods, and the whole shows convergence with the basic armature of the mandible of peracaridan Crustacea. The molar areas point towards the mouth. Within the Diplopoda there is great range in detail of gnathal lobe armature, correlated no doubt with the nature of the food. The cuticle-lined pharynx, which is capable of sucking much food at once into the wide pharyngeal lumen, bears strong dilator muscles inserting on the cranium, the median cranial septum, the post-occipital flange and the posterior process of the anterior tentorial apodeme. The soft oesophagus leaves the pharynx behind the head. *Petrobius* and the entognathous apterygotes considered above contrast in possessing a long and narrow oesophagus suited to smaller quantities of fine or fluid food (figures 20, 35, 47).

The details of the hypopharynx vary in different species, but two essential features are: a furrowed median portion capable of lateral expansion and often bearing a thick cuticular scute, and paired lateral cuticular scutes lying over the endoskeleton (see below) and opposite the gnathal lobe armature. The proximal end of each lateral plate lies against the proximal mesial shoulder of the gnathal lobe, marked by the arrow on the right side of figure 53.

Feeding movements. Diplopods feed largely upon decaying vegetation, decaying wood, humus, etc. The labrum is fixed but the epipharynx is movable. Opening of the preoral cavity is accompanied by a lowering of the free end of the gnathochilarium, the gnathal lobes of the mandibles swing wide open, like doors, and salivary juice is discharged over the food surface. Strong biting follows, the distal cusps of the gnathal lobes lifting food into the preoral space (figures 50, 53) and crushing it between the large opposed mesial faces; the epipharyngeal and hypopharyngeal surfaces, close fitting against the mandible, prevent escape of particles, and the gnathochilarium is simultaneously raised. Since the food value of humus and decaying vegetable matter is low, large quantities must be eaten, and the very large mesial faces of the gnathal lobes relative to the size of the head, the very strong construction of the mandibular segments and their joints, the bulky adductor musculature giving strong crushing movements and the wide pharynx are all correlated with this food requirement. The rigidity of the labrum on the head and the strong form of the mandibles is in part correlated with the needs of burrowing by head on pushing (Manton, 1954, 1961 *b*).

(i) *The musculature and the adductor mechanism of the mandibles of the diplopod* Poratophilus punctatus *Attems*

The mandibular muscles of the spirostreptomorph *Plusioporus Salvadorii* Silvestri were described by Silvestri (1903). The morphology resembles that of *Poratophilus* and the present account is largely in agreement with Silvestri as to form and function, with the important exception of the abductor mechanism. Silvestri's naming and lettering of the muscles is followed as far as is practicable.

The entire musculature, composed of both intrinsic and extrinsic muscles arising on the mandibular segments, contributes to the adductor biting movement, in contrast to all other arthropodan classes. Since the cranial attachment of the mandible is a firm hinge, no rotatory or rocking movements are possible, and very few muscles utilize the mandibular margins for their origin (cf. *Chirocephalus*, *Anaspides*, *Petrobius*, *Tomocerus* and *Campodea*). Only muscle *k* arises from the mandibular margin, leaving the middle of the anterior edge of the stipes and inserting on the postoccipital flange (figures 52, 53). Silvestri (1903) regarded this muscle as an abductor, but the nature of the hinges and position of the muscle precludes this. The muscle appears to be a levator, relieving the strain on the cranial hinge by holding the mandible close against the labrum during adduction. All other muscles except the large adductor from the gnathal lobe tendon arise from the concave faces of the mandibular segments.

A stout transverse mandibular tendon lies at the level of the cardo-stipes hinge. It supports transverse mandibular adductor muscles: *n'* from the cardo; *n* from the stipes as shown (figures 50, 52, 53); and a distal sector of the tendon separates laterally from the rest and carries an adductor from the gnathal lobe, the greater part arising from the proximal anterior face and a smaller part arising more distally (figure 53, 'gnathal lobe tendon').

Large paired retractors of the transverse mandibular tendon fan backwards over the post-occipital flange (figures 50, 53). They appear to be stabilizers without contributing directly to the biting movements. Such muscles are absent in *Cylindroiulus punctatus* Leach, and their presence may be correlated with the large size of *Poratophilus*.

The largest of the adductor muscles, which causes great displacement of the gnathal lobe, arises from a triangular calcified sclerite forming the inner end of a stout flexible tendon pulling from the proximal mesial corner of the gnathal lobe (figures 52, 53). The whole lies anterior to the transverse mandibular tendon, and the muscle inserts widely over the apex of the cranium and the median septum. Muscle 4 in Crustacea and muscle 11 in *Petrobius* arise from rigid apodemes formed by an extension of the posterior margin of the mandible, but the apodemes and muscles lie behind the transverse mandibular tendons. These mandibular adductor apodemes and muscles in Crustacea and *Petrobius* cannot be homologous with the flexible tendon, its terminal calcification and adductor muscle pulling on the gnathal lobe in Diplopoda, although the apodeme of the locust mandibular adductor pulls level with the cusp row as does the tendon of the diplopod (figures 30, 53). This mechanically suitable position has doubtless been convergently acquired.

Two intrinsic muscles arise from the gnathal lobe, muscle *o* inserts on the distal anterior part of the stipes and another muscle inserts on the calcification in the gnathal lobe tendon (see left and right sides of figure 53), and both contribute to gnathal lobe adduction.

(ii) *The head endoskeleton and the mandibular abductor mechanism of the diplopod* Poratophilus punctatus *Attems*

Anterior tentorial apodemes

It will be shown below (and §26) that the so-called tentorium or hypopharyngeal apodemes of a diplopod correspond so closely with the descriptions given above of the anterior tentorial apodemes of the Thysanura and Collembola as to justify using the term anterior tentorial apodemes in Diplopoda also.

Each apodeme passes into the head from a point just lateral to the mouth and well covered by the base of the labrum. This point is not labelled in figures 50 to 52, but from it the posterior process (labelled) extends into the head cavity. This point of origin differs little from that of the anterior tentorial apodeme of *Pterobius*; where a corresponding widening of the labrum would leave the point of origin covered as in the diplopod. In *Tomocerus* the intucking of the anterior tentorial apodeme just behind the boss forming the bearing for mandibular movement is in essentially the same position. Snodgrass (1960) has pointed out how greatly the external position of origin of the anterior tentorial apodeme differs within the Pterygota; these differences are much greater than those existing between *Petrobius*, *Tomocerus* and the diplopods where the origins all lie mesial to the mandibles.

The *posterior process* of the anterior tentorial apodeme passes inwards alongside the pharynx. The posterior process corresponds with the body of the anterior tentorial apodeme in *Petrobius* and with the hollow apodeme lying parallel with and below the oesophagus in *Tomocerus* (figures 50 to 53, 20, 35). In the diplopod the posterior process curls round the gnathal lobe tendon and its sclerite, forming a bearing for their movement (figure 52, right side, the parts are displaced on the left). There is no such bearing in the Apterygota where there is no similar tendon. As in the Apterygota the posterior process bears mandibular muscles, which, as Silvestri suggests, probably move the tentorial apodemes rather than the mandibles. In the diplopods dilator tentorii minor *m'* of Silvestri passes outwards to the cardo, dilator tentorii major *m* passes to the stipes. Muscles 4 to 7 of *Petrobius* and muscles 7, 8 and 13 in *Tomocerus* similarly utilize the anterior tentorial apodeme although their functions are different (figures 21, 33, 52, 53). In the diplopod a large fan of muscles inserts on the post-occipital flange, the retractor tentorii *f* seen in figure 50. The anterior tentorial apodeme in *Petrobius* is linked to the postero-dorsal part of the cranium by the much smaller dorsal suspensory muscle in a roughly similar manner (figure 20). As in *Petrobius* oesophageal dilators are inserted upon the anterior tentorial apodemes.

The ventral longitudinal muscular system inserts upon the posterior tentorial apodemes of *Petrobius*, *Tomocerus* and *Campodea*. In the diplopods *Polyxenus Polymicrodon* and *Brachycybe* the ventral longitudinal muscles insert upon the anterior tentorial apodeme (posterior process), although these muscles do not extend further forward than the sternite of the collum segment in diplopods such as *Poratophilus* with the most specialized heads. The former diplopod condition is believed to be the more primitive (Manton 1961 *b*). No posterior tentorial apodeme is present in any diplopod. Since this apodeme arises from the maxilla 1–2 intersegment and carries muscles largely concerned with adductor movements of maxillae 1, such an apodeme would not be expected to be present in an animal lacking a second post-mandibular pair of divided mouth parts and possessing a gnathochilarium which acts as a plate and not as a strongly opposable pair of gripping limbs. In the absence of a posterior tentorial apodeme it is not surprising to find that the ventral longitudinal musculature inserts upon the posterior process of the anterior tentorial apodeme, nothing else suitable being present.

The anterior tentorial apodeme bears further processes, some entirely or largely internal and others lying in the surface cuticle, as occurs in *Tomocerus*, but the details differ.

A *hypopharyngeal* process passes downwards underneath the lateral cuticular scute of the hypopharynx. The process is jointed, the more distal 'Nebententorium' being loosely articulated with the proximal bar (figures 50 to 52, 54). The hypopharyngeal process is attached to the overlying hypopharyngeal cuticle by cuticular fibrils, as shown by Fechter (1961, text-fig. 6).

A short anterior process passes upwards and outwards from the origin of the posterior process and supports the epipharyngeal corner of the mouth. A small levator muscle inserts on the frontal cuticle (drawn in figures 51, 54), while another levator tentorii muscle *v*, arises just behind from the base of the posterior process.

The *transverse process* is the largest of them all (the paired fulturae of Snodgrass). From the origin of the anterior tentorial apodeme it passes transversely across the angle between the epipharynx and the labrum, set in arthrodial membrane and terminating in the clypeal notch in which it is freely movable (figures 51, 52, 54). From the greater part of the transverse process arises the bulky protractor tentorii *e** muscle which inserts widely over the anterior face of the labrum (figure 51). In the locust the most external parts of the anterior tentorial expansion between the 'anterior process' and the 'lateral bar' (figure 28) lies in a somewhat similar position to the diplopod transverse process, although there is no mobility in the locust tentorium.

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* The letters and designations attached to the muscles shown in figures 50 to 55 are those of Silvestri (1903) as far as the latter are considered to be appropriate. Where there is disagreement between the functional interpretations of Silvestri and the present work, Silvestri's designations are included within commas in the text and are replaced on figures 50 to 55 by non-committal or by more appropriate designations.

The musculature of the gnathochilarium

These muscles need brief consideration in order to understand the mandibular abductor mechanism (figure 50). A levator stipitis gnathochilarium, muscle *s**, inserting on the internal pseudoccipital process, retracts the gnathochilarium and raises the distal end, so closing the external orifice to the preoral cavity. The retractor infrabasilaris ϵ inserting on the tip of the internal pseudoccipital process and the 'depressor basilaris' *t* (a misnamed muscle by Silvestri), must together raise the infrabasilaris while the large 'depressor of the gnathochilarial stipes' *r* (another misnamed muscle by Silvestri) must raise and draw forward the proximal part of the inframaxillaris, tilting the distal part of the gnathochilarium downwards, so opening the preoral cavity. Relaxation of the depressor tentorii muscles *x*, *u* and *z*, which extend from the inframaxillaris and lingual lobe of the gnathochilarium to the tip of the hypopharyngeal process, would facilitate the lowering of the distal part of the gnathochilarium, but contraction of these muscles tends to swing the hypopharyngeal process downwards and forwards, a movement which accompanies the lowering of the gnathochilarium (see below).

Mandibular abduction

If a hole is cut in the cuticle at the top of the cranium, needles can be inserted and the movement possible to the tentorial apodeme can easily be ascertained. The whole apodeme and its processes swing about the clypeal notch. The forward swing, caused in life by the contraction of the very large protractor tentorii *e*, and other muscles, swings the origin of the apodeme beside the mouth forward and slightly downward and outward, so that the posterior process takes up a more anterior position in the head and the hypopharyngeal process moves downwards, forwards and outwards. This movement presses the proximal ends of the paired hypopharyngeal scutes against the proximal shoulder of the gnathal lobes of the mandibles (arrows on the right side of figure 53) and the gnathal lobes swing wide open on their hinges and the cardo and stipes abduct slightly (figure 54). A similar abduction of the gnathal lobes follows a pulling down of the distal part of the gnathochilarium by manipulation, either in a dead specimen or a potash preparation, because the hypopharyngeal processes are linked with the hypopharyngeal cuticle which is also pulled down by the movement of the gnathochilarium.

Figure 55 attempts to show the participation of the muscles of the tentorial apodemes (left side), and of the mandible and gnathochilarium (right side), in causing the opening of the preoral cavity and simultaneous mandibular abduction (upper diagrams), and the closure of the preoral opening and mandibular adduction (lower diagrams). Black indicates tension on a muscle. The circle shows the position of the thrust delivered by the hypopharyngeal process against the gnathal lobe. The change of position of this circle, relative to the fixed edge of the labrum, is not great in the plane of the paper, but the circle also moves laterally, pulled out by the dilator tentorii muscles from the cardo and stipes, and effects the strikingly wide opening of the gnathal lobes. It is assumed for the purpose of the diagrams that the transverse mandibular tendon is stationary and that the retractor from the tendon (absent in small diplopods) is a stabilizer. Probably neither of these suppositions is quite true.

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* The letter *s* was applied to two different muscles by Silvestri (1903) as shown on figure 50.

It is seen from the diagrams that opening of the preoral cavity and abduction of the mandibles, caused by a pulling downward and forward of the anterior tentorial apodemes, is promoted principally by tension of: the protractor tentorii *e*, the 'constrictor tentorii' to the transverse mandibular tendon, the depressors tentorii *x*, *z* and *u* from the gnathochilarium, and muscle *r* from the gnathochilarium to the transverse mandibular tendon.

Closure of the preoral cavity and adduction of the mandibles, caused by a pulling upward and backward of the anterior tentorial apodemes which permits the mandibular adductors to exert their tension, is promoted by tension of: the large retractor tentorii *f*; the two levator tentorii muscles *v*; the levator to the gnathochilarium *s*; the huge adductor from the gnathal lobes; and the transverse adductors from the cardo and stipes to the transverse mandibular tendon, not shown in this aspect.

It is possible that muscles *z*, *x* and *u* between the gnathochilarium and the hypopharyngeal process do not act as suggested above but in an opposite manner. If their contraction assists the distal raising of the gnathochilarium, so closing the preoral cavity, the protractor swing of the anterior tentorial apodeme system must be caused only by the other muscles named above. It will be noted that the two parts of the hypopharyngeal process lie at different angles to one another in the extreme positions of forward and backward swing. Herein lies the functional need for a joint between the 'Nebententorium' and the proximal section. There is no need for the various speculations which have been put forward to account for the 'Nebententorium' (Attems 1926; Verhoeff 1926 to 1932).

Since the anterior tentorial apodemes are not joined together it is possible for the components of the mandibular adductor-abductor mechanism to work slightly out of phase on the two sides of the body. Such small asymmetrical movements could give trituration by the mesial faces of the gnathal lobes. Movements exactly in phase which will bring the armature of the two mandibles squarely together give a crushing effect.

26. Conclusions concerning Diplopoda

All of the mandibular musculature of a typical diplopod such as *Poratophilus punctatus* is utilized in causing strong adduction of a three-jointed mandible in the transverse plane. Abduction is caused by a thrust exerted by the hypopharyngeal processes of the anterior tentorial apodemes upon the gnathal lobes of the mandibles via the lateral hypopharyngeal scutes. Fechter (1961) reaches similar general conclusions for the diplopod *Cylindroiulus teutonicus*.

The so-called hypopharyngeal apodemes or tentorium of a diplopod and the anterior tentorial apodemes described here for Thysanura and Collembola are considered to be homologous because they correspond in: the point of invagination from the surface cuticle; the types of superficial and internal processes which they possess; their positions within the head; and in the sites they provide for the insertion of mandibular muscles. There are no posterior tentorial apodemes in Diplopoda for the reasons given on p. 75.

The great speciality of the diplopod anterior tentorial apodemes concerns their manner of swing about the clypeal notch on either side of the head. The forward and outward swing conveys a thrust to the hypopharyngeal paired scutes which opens the gnathal lobes and abducts the whole mandible, and the backward and inward swing permits the mandibular musculature to cause adduction. The joint between the proximal part of the hypopharyngeal process and the 'Nebententorium' facilitates this swing. In colobognathan diplopods with stylet-like mandibles, which do not adduct in the transverse plane, the anterior tentorial apodeme is differently shaped and there is no clypeal notch.

The musculature of the anterior tentorial apodemes promoting these movements comprises antagonistic components and is much more massive than is the musculature of the tentorial apodemes of the Thysanura and the entognathous apterygotes described here, where the movements serve quite different purposes. In Diplopoda the musculature of the gnathochilarium co-operates with that of the anterior tentorial apodemes in causing a simultaneous opening of the preoral cavity and abduction of the mandibles.

The diplopod gnathal lobe is considered here to be the terminal mandibular segment and not to be equivalent with the whole mandible of Pterygota. The flexible tendon from the gnathal lobe, which carries the principal adductor muscle of the gnathal lobe, is not homologous with the posterior mandibular apodeme and its adductor muscle of Crustacea, Apterygota and Pterygota (see pp. 74, 105). The presence of a transverse mandibular tendon represents the persistence of a primitive feature.

The articulation of the diplopod mandible with the head is further removed from the basic type of coxa-body articulation (figure 5*a* to *c*) than that of any arthropod mandible so far considered. Nothing remains of the mechanism providing a promotor-remotor swing other than the presence perhaps of muscle *k* (figure 52). Only *Limulus*, among the types of mandibles, or their equivalent, considered above, possesses a dorsal articulation (with a pleurite) on prosomal limbs 2 to 6 which permits direct adductor-abductor movements of the gnathobase, but here this movement is alternative to the basic promotor-remotor swing of the coxa-body joint and is operated by entirely different means from that of a diplopod.

It is probable that diplopodan biting in the transverse plane has been evolved directly from a jointed limb employing a prehensile grip by the telopodite in the transverse plane, in contrast to all types of mandibles so far considered which appear to have evolved via a mandible employing the basic promotor-remotor swing of an ambulatory limb. The normal extensor mechanism of a trunk limb telopodite is unsuitable for a mandible (p. 71). Increase in size and strength of an evolving diplopod mandible must have been accompanied by a simultaneous evolution of a new and unique extensor (abductor) mechanism.

27. THE COMPONENTS OF THE FEEDING MECHANISM OF THE SYMPHYLAN *SCUTIGERELLA IMMACULATA* NEWPORT

The symphylan mandibles bite in the transverse plane, but the movement is not a simple one of adduction and abduction, as in the crab, *Ligia*, *Ctenolepisma*, the locust and a diplopod. As in all these animals the problem of how to abduct the mandibles has had to be resolved. The symphylan resolution differs from all others in that it combines the use of outside abductor forces, provided by the movements of the anterior tentorial apodeme and to some extent by maxilla 1, with a partial use of the basic promotor-remotor roll of the mandible.

The general structure of the symphylan head and its development are known from the work of Tiegs (1940, 1945). He was, however, uncertain of the functions of some of the muscles, and he made no special study of the mechanisms or the movements, which are not at all obvious. Further statements by Snodgrass (1950) concerning the absence of transverse inter-mandibular muscles and the absence of the transverse processes of the anterior tentorial apodemes (fulturae) are not substantiated.

Symphyla feed upon the contents of decaying woodland litter and they penetrate deeply into soil rich in decomposing wood fragments, etc. No special head rigidity is required, because Symphyla are adept at twisting and turning so that they can use existing crevices without pushing (cf. Diplopoda).

A side view of the head of *Scutigerella* is shown in figure 56. The two segmented mandible hangs from a single point of articulation with the large lateral cephalic lobes, and behind this point the margin of the cranium (labelled) considerably overhangs maxilla 1 which is longer than the mandible. Arthrodial membrane links the anterior and posterior margins of the basal segment with the lining of the preoral cavity, the cranium and maxilla 1, but the gnathal lobe, as in Diplopoda, is free within the preoral cavity. The mandible can move in many directions on the head since it is not restricted by a longitudinally placed hinge as in the Diplopoda.

The gnathal lobe is obliquely hinged to the basal segment of the mandible. The cusp row of the gnathal lobe projects upwards and inwards into the preoral space over the large and projecting hypopharynx. The mesial cutting edge of the gnathal lobe forms a thin cusped blade (figure 58*a*), in contrast to the Diplopoda (cf. figures 58*a*, 50). A long apodeme projects inwards from the proximal mesial corner of the gnathal lobe and ends in stout tendinous processes within the large adductor muscle 8 (figures 56, 57A, 59E to J).

Maxilla 1 forms a narrow slightly curved plate situated ventrally on the head and open above to the general haemocoel (figures 57C, 59G to J). No joint lies between the parts corresponding with cardo and stipes of pterygote and apterygote insects. The articulation with the head lies distal to the base of the cardo, and is formed by two facets as shown in figure 57C, which allow very free antero-posterior sliding of the maxilla on the head. Distally a stout lacinia is supported by a thick short apodeme and a galea is present. The galea bears an outer concavity of very strong cuticle which is so shaped as to take a knob-like 'lateral' process from the distal outer end of the basal segment of the mandible (figures 56, 57C). The labium forms a floor for the feeding movements, as in many insects, and the gnathochilarium of the Diplopoda does the same. The hypopharynx is expanded into lateral lobes, the superlinguae, which appear to direct the food, co-operating with the narrow blades of the mandibular gnathal lobes. No space for such structures is present in the preoral cavity of a diplopod, and the superlinguae and hypopharynx of *Petrobius* and *Tomocerus* are differently shaped and differently used. Glandular components of the hypopharynx have not been investigated.

A pair of salivary segmental organs is well developed on the maxilla 1 segment, the duct passing through the maxilla on either side (figure 57B, C). The coils of the gland are lodged in the postero-dorsal part of the head, much as are those of the maxilla 2 (labial) segmental organ of Collembola, Diplura and Thysanura. The salivary segmental organ of Diplopoda discharges from the gnathochilarium (figure 50), which appears to correspond with maxilla 1 of the Symphyla. The diplopod glands spread far behind the head into the anterior trunk segments; there is quite insufficient available head space for a gland to supply the large amounts of fluid needed for voracious feeding on material of low food value. Thus the salivary glands of Symphyla and Diplopoda correspond while those of Symphyla and Apterygota do not.

(i) *The endoskeletal system of* Scutigerella immaculata *Newport*

Transverse mandibular and maxilla 1 tendons are present in *Scutigerella* as in *Petrobius*, *Tomocerus*, etc. The so-called hypopharyngeal apodemes of *Scutigerella* appear to be homologous with the anterior tentorial apodemes of Diplopoda and Apterygota (see below).

The transverse mandibular tendon is massive and lies level with the middle of the basal mandibular segment. It carries the transverse mandibular muscles and invests the anterior tentorial apodemes just behind their origins lateral to the mouth (figures 57C, 58, 59H to J). In *Petrobius* the anterior tentorial apodemes pass just above the transverse mandibular tendon, remaining separate from it, but their ventral lobes sink into the maxilla 1 tendon complex (figures 20, 22C, D, 24H).

The transverse maxilla 1 tendon in *Scutigerella* links the transverse maxilla 1 muscles and lies level with the proximal end of the maxilla, far from the mandibular tendon. The maxilla 1 tendon unites the ends of the anterior tentorial apodemes, forming a suboesophageal bridge (figures 57B, 58).

Each *anterior tentorial apodeme* arises on either side of the mouth under the labrum as a hollow intucking, essentially as in the Diplopoda, *Collembola* and *Petrobius* (see p. 74). The apodemes at once become strongly concave ventrally, doubtless a strengthening device (figures 57A, B, 59H to J). A lateral process from the apodeme forms a bearing for the mandibular gnathal lobe apodeme. A similar condition exists in principle in the Diplopoda, and the Collembola possess another type of bearing in the same situation, the mandibular boss on the anterior tentorial apodeme, taking the movement of the unsegmented mandible (cf. figures 59G, H with 50, 52). The hollow anterior tentorial apodeme of *Scutigerella* passes inwards parallel with and just below the oesophagus (figures 57, 58). The pair are linked by the transverse mandibular and maxillary tendons, and beyond the latter the apodemes curl round the oesophagus to the dorsal side where they are linked with one another by connective tissue forming a supra-oesophageal bridge. Both supra- and sub-oesophageal bridges carry insertions of the many antennal muscles and of the longitudinal trunk musculature. The dorsal cuticle of the head is infolded in the middle line (figures 58, 59H to K). Over the supraoesophageal bridge this dorsal infolding becomes very deep and narrow, clothed by its own ectoderm, and forms a suspension for the terminations of the anterior tentorial apodemes (figures 58*a*, 59K). There are no muscle or other fibrils in the dorsal suspension of the anterior tentorial apodemes, as in *Petrobius*, *Ctenolepisma* and Collembola. A mid-dorsal stiffening device is present in Diplopoda and Diplura as a solid flange which forms a brace against deformation by the pull of muscles inserting on the cranium, and is incapable of movement. It is possible that the double infolding of not very thick cuticle in *Scutigerella* is an elastic device capable of deformation (see below). A fine lateral thread anchors the apodeme-maxilla 1 tendon complex to the lateral head wall as shown in figure 57B, C.

This hollow bar-like anterior tentorial apodeme corresponds with the *posterior process* of the diplopod apodeme, with the internal hollow apodeme of *Tomocerus* ending on the mandibular tendon and with the principal part of the anterior tentorial apodeme of *Petrobius*.

Scutigerella possesses no large *hypopharyngeal process* from the anterior tentorial apodeme such as is present in Diplopoda, and there is no mechanical need for one. The corresponding process is probably the blunt antero-ventral lobe on the apodeme near its external origin, seen beside a short hypopharyngeal retractor muscle in figure 58.

Lateral to its point of origin the anterior tentorial apodeme is continued as a surface sclerotization across the base of the preoral cavity much as in Diplopoda, but this *transverse process* in *Scutigerella* fades out into the cuticle and is not set in a clypeal notch, which functionally is not required. The transverse process of *Scutigerella* carries protractor muscles (figures 58*b*, 59F), as in Diplopoda.

The dorsal and ventral longitudinal muscles insert on the anterior tentorial apodemes (figures 57, 58). Only the ventral series do so in some Diplopoda.

Thus there is an essential similarity between the anterior tentorial apodemes of Symphyla, Diplopoda and Apterygota in: the positions of origin from the external cuticle; the position of the main apodeme within the head; the general form of the branches; the mechanical association with the entire mandible (Collembola) or with the gnathal lobe (Diplopoda); the dorsal suspension (absent in Diplopoda because the mobility of the tentorial apodeme about the clypeal notch precludes it); the linkage with the transverse segmental tendons of the head (absent in Diplopoda for the reason just given); and the provision of sites for insertion of muscles from the mandible.

(ii) *The musculature and movements of the anterior tentorial apodemes of* Scutigerella immaculata *Newport*

Movements of the anterior tentorial apodemes of *Scutigerella* are concerned with gnathal lobe abduction, as in Diplopoda. Anteriorly the apodemes are suspended from the dorsal and ventral surfaces of the head by muscles somewhat resembling the dorsal and ventral suspensory muscles of *Tomocerus* (cf. figures 58*b*, 35), but posteriorly the suspension is cuticular. From the transverse process of the apodeme protractor muscles fan upwards and forwards to the cranium, and close behind them a retractor group leaves the base of the tentorial bearing for the gnathal lobe apodeme and fans upwards and backwards (figures 58*b*, 59F, G). These protractors and retractors appear to move the tentorial apodeme within the head, bending the posterior dorsal suspension. It is possible that the presence of sclerotized cuticle only in the dorsal suspension provides an elastic device assisting these movements. Protraction of the apodeme pushes on the gnathal lobe apodeme via the bearing, so abducting the gnathal lobe.

(iii) *Mandibular and maxilla* 1 *muscles and movements of* Scutigerella immaculata *Newport*

The descriptions by Tiegs (1940) of the mandibular and maxillary muscles of *Hanseniella* apply fairly well to *Scutigerella*, but it is necessary to have further information concerning insertions because muscles which arise from opposite edges of a mandible and have antagonistic functions appear very alike when projected on to the plane of one drawing.

It has been shown above how the margins of shoe-shaped mandibles (*Chirocephalus*, *Petrobius*, Collembola, etc.) are used by antagonistic muscles causing a promotor and remotor swing about a dorso-ventral or an oblique axis. Such muscles are not found in the transversely biting diplopod mandibles where adductor muscles only arise from the concavity of the mandible.

Mandibular muscles 4 and 5 of *Scutigerella* arise from the skeletally strengthened posterior margin of the basal segment of the mandible; muscle 4 inserts on the transverse mandibular tendon investing the tentorial apodemes and muscle 5 inserts on the apodeme itself (figures 57B, 59J to H). These muscles must cause a remotor rotation of the basal segment about the cranial articulation. The antagonist is muscle 1 arising from a deep but narrow infolding of the ample arthrodial membrane on the anterior margin of the basal segment; muscle 1 inserts widely over the postero-dorsal part of the cranium (figure 57A, B), its contraction causes promotor rotation of the basal segment.

Muscles 6 and 7 arise from the concave face of the basal segment of the mandible in the middle and distal parts, respectively (figures 56, 57B, 59F to J), and insert on the connective tissue of the transverse mandibular tendon where it invests the anterior tentorial apodeme. Contraction of muscles 6 and 7 must adduct the basal segment, but as the transverse tendon lies at the upper level of the basal segment and not at the middle level (figure 59H to J), the adduction becomes partly a remotor roll. The antagonists of these adductors are muscles 3 and 2 (figures 57B, 59G, J). Muscle 3 arises from an inturned cuticular flange at the joint between the basal segment and the cranium and inserts on the anterior end of the anterior tentorial apodeme. It pulls at a very poor mechanical advantage, close to the articulation, and abducts the basal segment (many examples have been noted above of abductor muscles working at poor mechanical advantages; see *Ligia*, *Ctenolepisma*, locust, *Limulus*, etc.). Muscle 2 arises from a tendon close to origin of muscle 3 and passes posteriorly to insert on the posterior part of the anterior tentorial apodeme where it is tied to its fellow by the transverse maxilla 1 tendon. This tendon strongly supports muscle 2 whose contraction produces abduction of the basal segment of the mandible. Thus the movements caused by the muscles of the basal segment are a combination of adductor-abductor and promotor-remotor movements, the segment moves obliquely about its single dorsal articulation, the stronger movement being the remotor-adductor one.

Another force appears to assist the abductors of the basal mandibular segment and is supplied by maxilla 1 muscles. A series of muscles X arise from the lateral part of the maxilla 1 and pass outwards to the more laterally situated lobe of the cranium (figure 57B, C). Maxilla 1 muscle I from the base of the lacinia also inserts on the lateral cranial margin. Muscles VIII and IX pass from the morphologically anterior and posterior margins of the maxilla respectively and insert on the transverse maxilla 1 tendon and anterior tentorial apodeme as shown in figure 57C. Contraction of muscles VIII and IX must pull the basal end of the maxilla towards the middle line, a movement tending to tip the distal end of the maxilla away from the middle line. Contraction of muscles I and X must strongly abduct the distal part of the maxilla so that the lateral strengthened concavity on the galea pushes against the knob-like lateral process on the distal end of the mandibular basal segment (labelled in figure 56). The intrinsic maxilla 1 muscles III and XI, which appeared to Tiegs as so peculiar in position, brace the slight curvature of the plate-like maxilla against deformatory forces induced by thrusting the mandible into abduction. The antagonistic maxillary muscles are: adductors IV, V and VI and the long retractor II from the lacinia, which passes close below the anterior tentorial apodeme to insert on it near the transverse maxillary tendon, opposing protractor VII from the cardo region to the tentorial apodeme (marked on figure 57C, left side).

Since the gnathal lobe is strongly hinged to the basal segment of the mandible, the remotor-adductor and promotor-abductor movements of the latter are transmitted to the gnathal lobe, whose detailed movements are more complex than those of a diplopod. Adduction of the gnathal lobe on its hinge is effected by the very large muscle 8, arising over the whole of the gnathal lobe apodeme and its tendinous processes and inserting widely over the cranium both dorsally and laterally (figures 56, 57A). As in the Diplopoda there is no direct antagonistic muscle to the gnathal lobe adductor, and protraction of the anterior tentorial apodeme effects the antagonistic movement. The protractor muscles from the transverse process push the tentorial bearing of the gnathal lobe apodeme forwards and this movement automatically abducts the gnathal lobe on the basal segment. Thus the basal segment of the mandible of *Scutigerella* is capable of causing its own effector and recovery movements (unlike the diplopod cardo and stipes which can only adduct) and the gnathal lobe adducts strongly under its own muscles but is dependent upon the tentorial apodeme movements for the recovery movement.

28. CONCLUSIONS CONCERNING SYMPHYLA

The mandibles of the Symphyla have more in common with the Diplopoda than with any other class of Arthropoda. The common plan of mandibular musculature recognizable throughout the Thysanura, Collembola and Diplura is not present in the Symphyla. The two-jointed symphylan mandible bites largely but not entirely in the transverse plane. Food is cut by narrow sharp-cusped blades on the gnathal lobes (cf. the broad biting faces of the gnathal lobes of Diplopoda), and is directed by the large hypopharynx and superlinguae, which differ greatly from the hypopharynx of Diplopoda which is so intimately concerned with the abductor mechanism.

The anterior tentorial apodemes (hypopharyngeal apodemes) of Symphyla correspond in essential details (listed on p. 81) with those of Diplopoda, Thysanura and Collembola with which they are considered to be homologous. Large hypopharyngeal processes are not required by Symphyla since the abductor force is not applied to the gnathal lobe of the mandibles via the hypopharynx. Transverse processes are required and they bear promotor muscles as in Diplopoda, but a clypeal notch is not needed.

An antero-posterior swing of the anterior tentorial apodemes takes place about the postero-dorsal cuticular suspension and not about the clypeal notch, and abducts the mandibular gnathal lobe.

The basal segment of the mandible is united with the cranium by a single mobile articulation allowing free movement (unlike the hinge-joint of the Diplopoda). The musculature of the basal segment causes oblique effector adductor-remotor and recovery abductor-promotor movements. The abductor mechanism of the basal segment is unique, and this segment is not entirely dependent upon extrinsic agents for its recovery movements as are the cardo and stipes of the diplopod mandible. The oblique movements of the basal segment are transmitted to the gnathal lobe by the hinge joint between them. Strong adduction of the gnathal lobe on the basal segment is achieved by a large dorsal adductor muscle pulling on an apodeme from the gnathal lobe, essentially as in the Diplopoda, and unlike other arthropods (p. 105), but the gnathal lobe apodeme is composed of stiff cuticle not flexible tendon. This stiff apodeme enables promotion by the anterior tentorial apodeme to abduct the gnathal lobe by pressure applied to the base of the gnathal lobe apodeme. In Diplopoda the pressure is applied to an adjacent point on the gnathal lobe via the hypopharynx.

It is probable that the symphylan mandibular mechanism has evolved directly from a very simple jointed prehensile limb as suggested for the Diplopoda (§ 26),* the necessary simultaneous evolution of a new abductor mechanism being different in the two groups, although both utilize the mobility of the anterior tentorial apodeme but in different ways. It is probable that the Symphyla have never possessed a rolling type of mandible depending entirely upon the promotor-remotor movement of a walking leg, such as is possessed by the more primitive Thysanura. The demonstration that mandibular evolution in insects has probably proceeded in two directions from an archi-thysanuran-like condition, the one towards transverse biting of large food and the other towards piercing and the cutting of small food by a rotatory movement, means that the Symphyla and Pterygota have acquired their mandibular mechanisms independently. An animal with the symphylan type of mandible could not possibly be ancestral to any type of apterygote or pterygote insect.

The general form, the musculature and movements of maxilla 1 in the Thysanura, the more primitive Pterygota, the Collembola and Diplura have much in common (see §§ 19 (iii), 22 (iv) and 23). Maxilla 1 of the Symphyla shows little of this basic plan (cf. figure 57C with 22, 27, 34, 45). The articulation with the head is quite different (and there is no posterior tentorial apodeme); the morphologically posterior margin of the maxilla (marked 'inner margin' in figure 57C) is not used for muscle insertions; the principal retractor-adductor to the lacinia (muscle II) inserts on the under side of the anterior tentorial apodeme and not on the cranium; the distal abductor mechanism (muscles I and X) is unique and entirely unlike insects; some inexact similarity exists between the proximal protractor-abductor mechanism (muscles VII, VIII and IX) but for this a cardo-stipes articulation would not be useful and none exists; the intrinsic muscles III and XI are absent in insects; and adductors IV to VI arise from the anterior and not the posterior margin of the maxilla. Many of these differences are correlated with the assistance given by the maxilla towards mandibular abduction, but there is no evidence indicating that the Symphyla have evolved from an animal possessing the same basic type of maxilla 1 as present in the Thysanura, etc. Muscle VIII in *Scutigerella* is attached to the transverse maxillary tendon, yet its position is more like that of muscle XI than muscle X in *Petrobius*. So many differences suggest that the structure of the symphylan maxilla 1 as well as the mandible must have been evolved independently from those of hexapods.

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* No support is found for the suggestion by Snodgrass (1950) 'that the symphylid-diplopod jaw has been evolved from the more simple jaw of the chilopods'. The present account demonstrates that the chilopod jaw is so far from simple as to be intelligible only after consideration of all the types covered above. The chilopod mechanism is very different from that of both Symphyla and Diplopoda, and neither of the latter orders show any trace of entognathy in their jaw mechanisms.

29. General considerations concerning head structure of centipedes

The head anatomy of *Scolopendra subspinipes* Leach was described by Meinert (1883). His data in the main are confirmed, details are added and his muscle numbering has been adopted as far as is practicable. Fahlander (1938) has given more information concerning chilopod head structure, Applegarth (1952) has described the head musculature of *Lithobius*, and Lewis (1961) has provided a welcome account of the prey and feeding of the geophilomorph centipede *Strigamia maritima*, but no functionally adequate account of the working of the feeding mechanism of any centipede exists.

The anatomy and movements of the mandible of a centipede can only be interpreted with reference to the whole feeding mechanism. *Lithobius* resents close inspection of its feeding activities, but when hungry *Scolopendra* and related genera can be observed feeding under a microscope quite easily, and the head cuticle of young specimens is sufficiently transparent to show much of the muscular and cuticular movements going on within. The feeding behaviour of *Scolopendra subspinipes* Leach will be described shortly, the figures of anatomy depicting the very similar *Cormocephalus nitidosus* Por. The mandibles of *Lithobius* have been dubbed 'a masterpiece of inefficiency' by Applegarth (1952). Yet it is difficult to find a terrestrial fauna so poor as to contain no species of *Lithobius*. Among land invertebrates the Lithobiomorpha rank as an outstandingly successful group, and it would be strange indeed to find extreme inefficiency in their feeding mechanism. No confirmation of such a view has been obtained. The mandibular mechanism of *Lithobius* and of *Scolopendra*, while not identical, are similar in general principles and in much detail. Since these animals represent the Epimorpha and Anamorpha their feeding mechanisms may be taken as representative of the Chilopoda.*

The head morphology of centipedes, other than Scutigeromorpha, is correlated with head flattening sufficient to enable the catching and eating of active prey within a crevice of no greater dorso-ventral span than the tergite-sternite thickness of the trunk. The head flattening is so great that there is space for huge poison claws and other limbs to manipulate food below the preoral cavity. It would not be possible to design strongly cutting mandibles serving flesh eating on the lines of the transversely cutting, hinged mandibles of Pterygota Apterygota, Isopoda, etc., but set on so shallow a head. The centipede difficulties of obtaining transversely cutting mandibles and a suitable abductor mechanism have been resolved by the evolution of entognathy and the use of the endoskeleton, but the details differ entirely from those of other entognathous arthropods.

The relationships between the preoral space, the lateral gnathal pouches lodging the bases of the mandibles, and the other relevant structures are shown in the oral view and in the sagittal half of the head in figures 60 and 61. The lateral parts of the labrum and the 'pleural sclerite' (a fold of cuticle) bounding the preoral space are all slightly movable.

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* Divergencies from this basic type of mandible are found in the Geophilomorpha (listed by Verhoeff 1902–25, p. 482), which lack a transverse mandibular tendon (Fahlander 1952), and possess at least 3 mandibular sclerites (cf. 5 in Scolopendromorpha). The musculature of *Himantarium gabrielis* L, as far as it is shown by Verhoeff (1902–25, pl. 26, figs. 13–18), is generally disposed as in *Scolopendra*, including a distal adductor (muscle 20 below), a muscle said to be absent in an unidentified geophilid by Snodgrass (1950, 1952). For a fuller consideration of head structure and jaw mechanisms in Geophilomorpha and all principal groups of chilopoda see Manton (1964).

The broad outer lobe of maxilla 1 closes the orifice of the gnathal pouch, and can cover the mandible, the inner lobe of maxilla 1 prevents the posterior escape of food particles. The mandible, composed of 5 sclerites, is articulated to a rod-like suspensory sclerite in the gnathal pouch wall. This rod is movably jointed to the pleural sclerite (figures 62 to 64) and permits great proximal freedom of movement of the mandible. A corresponding freedom is found only in entognathous apterygotes and Onychophora.

As is well known, the mandible is twisted on its main axis, but it is set obliquely across the head in a manner not usually appreciated (figures 61, 63, 64). The narrow basal end in the gnathal pouch lies close to the dorsal cuticle of the head, and the wide distal end is slightly concave and set horizontally below the preoral cavity. Sclerite 5 is entire all round (mitten shaped) and projects freely into the preoral space, arthrodial membrane joining its proximal inner margin where a process from the anterior tentorial apodeme ends (see inset, figure 63). The strong cusps in the middle of the gnathal edge act as cutting carnassial teeth; the anterior distal corner is upturned as a soft flexible anterior lobe (labelled in figures 61, 63, 64); and the distal posterior corner is heavily spined. The whole distal mandibular margin fits neatly round the hypopharynx, which, owing to the mode of head flattening, forms the roof of the preoral space (cf. Diplopoda, figure 50).

The remaining 4 mandibular sclerites form the outer face of the mandible which is otherwise open to the haemocoel. Sclerite 4 forms the ventro-lateral margin proximal to sclerite 5, and bears a very strong articular process which hooks round the vertical anterior process of the anterior tentorial apodeme (figures 61, 64). Sclerite 4 is hinged to sclerite 5 on the lower (external) mandibular face, but is continuous with the anterior lobe on the upper (internal) face. Sclerite 2 is movably articulated all round, while sclerite 3 is continuous at its margin with sclerite 5. The basal sclerite 1 is very narrow, and its twisted shape gives it rigidity against deformation by the strong muscles arising from its concave face.

A pair of anterior tentorial apodemes is present whose component parts and movements resemble in essentials those of diplopods, and a transverse mandibular tendon is also present (see below).

30. The feeding mechanism of scolopendromorph centipedes

Scolopendromorph centipedes typically catch and eat living prey, they are also scavengers, but when hungry they take almost anything. *Scolopendra cingulata* when freshly caught in Sicily ate pieces of bread and cake, and 'licked' butter etc., but they are not hyaena-like. The feeding mechanism is suited to the soft fleshy contents of the prey and to small entire anthropods.

Prey is seized and bitten by the poison claws, and held by the clawed tip of the maxilla 2 telopodites and first few pairs of walking legs. The bite may be repeated several times, the prey being turned about by these limbs. When the prey has a firm exterior, a grip by the tips of the poison claws is followed by a sudden and strong flexure of these limbs and a forward movement horizontal to the body of the coxo-sternite of the poison-claw segment (figure 60). The toothed coxal endites cut into the prey like a spade or a tin opener. The oral field is then applied to the exposed flesh, or the head is inserted into the lesion (as is done by *Strigamia*), or the poison claws may themselves be thrust into the interior of the prey where they drag the flesh towards the oral field. Apart from such movements the tips of the poison claws and maxilla 2 telopodites are used only to hold the food mass in a convenient position while the mandibles and maxillae 1 carry out rhythmical feeding movements.

The mechanism of ingestion is speedy and efficient. Within $1\frac{1}{2}$ hours of intermittent feeding a young *S. subspinipes* 33 mm long and about 2 mm wide consumed the contents of two blow-fly maggots each about 15 × 2·5 mm. The body of the centipede was turgid in appearance after such a meal, and the cuticular body wall of the maggots were left clean and empty.

The maxillae 1 and mandibles carry out rhythmical movements each lasting about 0·5 s. The gnathal edge of the mandible is covered almost all the time by the more ventral spoon-shaped and mobile outer lobe of maxilla 1 (figure 61). This limb moves in similar phase with its fellow, the pair sweeping up a cone of flesh into which the pair of mandibles bite. The head is often rhythmically raised at this point, and so the mandibles as they bite drag up the cone of flesh, which is again swept up and gripped by the soft and very flexible maxillae 1. The head is then lowered and the mandibles part.

At rest two thirds of the mandibles are covered by the gnathal pouches and the maxillae 1 and the lateral parts of the labrum cover the rest (figure 60). The proximal ends of the mandibles are visible through the head capsule in young *Scolopendra* and in *Lithobius*, and much movement can be followed by direct observations from above and from the side through the overlying structures. Mandibular movement is akin to a see-saw, operating roughly about a transverse line passing through the head at the level of the articulation between the pleurite and the suspensory rod of the mandible and through transverse muscle 32. The proximal end of the mandible within the gnathal pouch is very mobile and performs wide excursions. A strong outward and downward sweep of the proximal end of the basal sclerite causes the opposite movements of the gnathal edge where adduction and levation take place. At the same time a backward movement of the whole mandible brings the proximal end of the basal sclerite close to the posterior wall of the cranium, so retracting the gnathal margin (the dotted white line in figure 63E gives a foreshortened indication of the movement). This see-saw combined with a protractor-retractor movement of the mandible causes the observable biting into the cone of food swept up by the maxillae 1. The 'carnassial' middle region of the gnathal edges cuts exactly and the degree of curvature of the whole mandible is controlled by intrinsic and extrinsic muscles which help the mandible to make the best use of its confined space. Great flexibility and powers of modification in detail characterize the movements, as in entognathous Collembola. The only modification of movement possible to strong transversely biting hinged mandibles of other arthropods resides in very slight out-of-phase effects.*

Movements of the labrum and anterior tentorial apodemes could not be observed directly, but the presence and positions of muscles to these parts (see below) indicate the movements which must occur in life, and which can be seen by manipulation of the skeleton. The whole anterior tentorial apodeme moves about its lateral union with the

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* Snodgrass (1950) states that a live centipede 'refuses to demonstrate any action whatever of its jaws' and he infers that 'in action...the mandibles rotate lengthwise'. This inference is not correct; all the morphology precludes lengthwise rotation, as can be seen in a living *Scolopendra* (see § 30 (ii)).

pleural fold, as in Diplopoda, and in so doing it moves the articular process of mandibular sclerite 4 and thereby the whole mandible. A downward, forward and outward swing of the anterior tentorial apodeme promotes depressor-protractor-abductor movements of the gnathal edge of the mandible and an upward, backward and inward swing of the anterior tentorial apodeme promotes levator-retractor-adductor movements of the biting parts.

Food enters the mouth by the tongue-like activities of the hypopharynx and anterior lobe of each mandible and by suction generated through the musculature and armature of the pharynx. The functions of the epipharyngeal armature have not been investigated. The whole feeding mechanism is characterized by flexibility, speed of action and efficiency. To what extent external digestion may take place has not been determined. An abundance of glands occupy much head space and extend down the trunk for several segments. They open both on the inner and the outer sides of the mouth parts (Fahlander 1938; Manton 1964) and are of various kinds. They could serve to lubricate the movements of the mandibles, cover food with salivary juice as it enters the mouth, and pour out juice into the prey, reaching the tissues both as and before they are swept up by the maxillae 1.

31. Skeleto-muscular basis of the mandibular movements of scolopendromorph centipedes

The movements of the head endoskeleton play an integral part in the jaw mechanism, and the mandibles alone are not capable of completing their own normal cycle of movements, although they are not as entirely dependent upon tentorial movements as are the mandibles of Diplopoda (see also Manton (1964)). The endoskeleton has been described many times (Verhoeff 1912 to 1925; Attems 1926; Fahlander 1938), but in a confused manner, and essential detail has been neglected.

(i) *Head endoskeleton, its muscles and movements in* Cormocephalus nitidosus *Por. and* Scolopendra subspinipes *Leach*

Paired *anterior tentorial apodemes* (the commandibulares Gerüst of Attems and Mandibelapodeme of Fahlander) arise from the walls of the preoral cavity on either side of the mouth. The general form is shown on the left inset diagram of figure 63. A hollow *posterior process* passes inwards and backwards lateral to and below the level of the pharynx (figures 61, 63E). The posterior process is strongly concave ventrally, as in *Scutigerella* (figure 59H), a shape conferring rigidity. This process ends in fibrils carrying the ventral longitudinal muscles and a stout muscle mesial to them passes from the posterior process to the vertical tendinous endoskeletal plate (thorax 1 suspension*). A strong dorsal crest on the posterior process bears mandibular muscles on its outer face and antennal muscles on its inner face (figure 62).

A short *hypopharyngeal process* passes downwards to the hypopharynx (figures 61, 63D), and close to it a curved narrow *mandibular process* curls down to join the proximal inner margin of sclerite 5 of the mandible (figure 63E where the mandibular process carries muscle 27 but is itself unlabelled and 64), its termination is shown in the right-hand inset diagram of figure 63.

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* The homology of this pair of plates is demonstrated in Manton (1964).

A thick strong *transverse process* extends as a surface sclerotization from the origin of the apodeme across the angle of the preoral cavity under the labrum, as in Diplopoda, and ends movably against the pleural sclerite (figures 62, 63), this joint corresponding with the clypeal notch of a diplopod.

A stout *anterior process* extends from the origin of the apodeme vertically downwards as a surface sclerotization on the anterior face of the preoral cavity (figure 61). The process is separated from the thick median epipharyngeal cuticle by a flexible area (permitting movement of the whole apodeme). This process in dorsal view looks like a peg (figure 63, 64), and round it hooks the articular process of mandibular sclerite 4. The large anterior process of the Chilopoda is comparable with the similarly named small process of a diplopod which supports the corner of the preoral cavity but does not touch the mandible (figures 51, 54).

The differences between the anterior tentorial apodemes of Diplopoda and Chilopoda relate mainly to the utilization of the hypopharyngeal process in the former and to the anterior process in the latter for causing mandibular movements. The mandibular process of the tentorial apodeme in the centipede is a specialization correlated with the see-saw mandibular movement and is not present in a diplopod.

The *muscles* controlling the position of the anterior tentorial apodemes are many and strong, as in Diplopoda, but differently arranged.

Muscles T7 to T10 from the dorsal edges of the transverse and posterior processes pass forwards, upwards and mesially to the cranial wall (figure 62A). Muscles T7 and T9 must protract the apodeme, and muscles T8 and T10 levate and adduct it.

Muscles T5 and T6 from the anterior edges of the transverse process pass forwards and downwards to the frons (figure 62C) and must protract, abduct and depress the apodeme.

Muscles T2 and T3 from the ventral face of the transverse process pass downwards to the ventral cuticle more steeply than drawn in figure 63E. They must depress the apodeme.

Muscle T4 from the anterior process passes forwards to the frons (figures 61, 63E) and must protract the apodeme.

The action of these muscles, when appropriately combined, can levate, depress and protract the anterior tentorial apodemes. The longitudinal musculature attached to the posterior process of the apodeme can retract them. As in diplopods the promotor muscles are strong, since they help to promote the mandibles as well as the tentorial apodemes. The use of longitudinal muscles for retraction, possibly effected largely by the sector inserting on the posterior endoskeletal plate above the poison claw (figure 61), is an arrangement corresponding in principle but not in detail with the diplopod retractor (*f*) from the post-occipital flange (figure 50).

A wide *transverse mandibular tendon* (the Tentorialkörper of Fahlander (1938)) is present in the Chilopoda (except in the Geophilomorpha, see Manton (1964)), and unlike those of most arthropods, it is a mobile tendon. Laterally it unites with the tips of the posterior processes of the anterior tentorial apodemes and not with the transverse mandibular muscles, and a fine strand links the tendon with the head arthrodial membrane (see Fahlander 1938). The tendon is T-shaped, the transverse mandibular muscle 32 being attached to it as shown in figure 63. Anteroposterior movements of the anterior tentorial apodemes about their pleural articulations are transmitted directly to the transverse mandibular tendon and its muscles 32. In Crustacea, *Limulus*, *Petrobius*, *Campodea* and a diplopod transverse tendons appear to be regions of considerable but not absolute stability (figures 3, 7 to 9, 14, 21, 44, 53). There is some movement of the endoskeletal apodemes and tendons of Collembola, and in *Scutigerella* small protractor movements of the apodemes must also protract the mandibular tendon and its transverse muscles (figures 57 to 59); but in Chilopoda the transverse mandibular muscles remain at the fulcrum of the see-saw movement at all stages of the wide protraction and retraction of the whole mandible, because the movements of the anterior tentorial apodemes are brought to bear upon the mandibles both via the articular process of the mandible and via the transverse mandibular tendon.

(ii) *The musculature and movements of the mandibles of scolopendromorph centipedes*

The mandibular muscles are shown in dorsal view at different depths in figures 62 and 63, and a plan is given in figure 64 of the muscle origins (except for muscle 33), their directions of pull, the mandibular sclerites, etc. The slopes of the muscles are clear in the figures and the brief diagnoses given in the legend to figure 64 states the origins and insertions of these muscles.

As in the entognathous Apterygota, the presence of entognathy permits the external face of the mandible to carry muscles, as well as the margins and internal concave face (muscles 25 and 26 in figures 62A, C, and 64*a*, *d*, cf. muscles 1 and 2 in figures 33, 36D, 44, 46A). Proximal to the articular process of sclerite 4 the sclerite expands into an upward and outwardly directed apodeme which passes under the arch formed by the anterior tentorial apodeme mesial to its origin. The mandibular apodeme of sclerite 4 bears the very large muscle 20 which fans widely over the upper and lateral surface of the cranium as shown in the figures.

The points limiting mandibular movements are the static pleural articulation of the mandibular suspensory sclerite, the fulcrum of movement (see below) at the level of muscle 32, and the contact between the articular process of the mandible and the anterior process of the anterior tentorial apodeme, the movements of the latter being transmitted to the mandible. The segmentation of the mandible permits an increase in its distal curvature to be effected by intrinsic muscles 29 and 31 during the adductor-levator movements of the gnathal margins, and the exact alinement of these margins is maintained by muscles 21, 27 and 30.

The fulcrum of the mandibular swing

The large transverse muscle 32, composed of several layers of fibres which unite the mandibles via the transverse mandibular tendon, moves but little and does not appear to be primarily an adductor or an abductor. The muscle forms the fulcrum of the see-saw mandibular movements and by its small adjustments and tone provides both support and rigidity to the mandibles which are otherwise so free (cf. muscles 15 and 16 of *Tomocerus*). The protractor-retractor movement of the whole muscle mass, imposed by the movements of the anterior tentorial apodemes via the transverse mandibular tendon, enables the muscle to give support to the mandibles with the minimum amount of length change. Contraction of the more distal fibres could assist adduction and contraction of the proximal fibres could assist abduction.

Muscles promoting the biting together and raising of the gnathal edges

These muscles extend between the mandible and the dorsal and lateral wall of the cranium, between the mandible and anterior tentorial apodeme and are aided by the tentorial muscles. The muscles comprise two functional groups:

(*a*) Those promoting adduction and levation of the gnathal edge: Mandibular muscles 20 and 33 and tentorial muscles T8 and T10, with minor adjustments to the curvature and alinement of the mandible by mandibular muscles 21, 27, 29, 30 and 31.

(*b*) Those promoting retraction of the mandible: mandibular muscles 24 and 25 and the ventral longitudinal muscles attached to the tentorial apodeme.

Muscles promoting the abduction and lowering of the gnathal edges of the mandibles

These muscles insert in the same manner as above, and comprise two functional groups:

(*c*) Those promoting abduction and depression of the gnathal edge: mandibular muscle 26 and tentorial muscles T2 and T3.

(*d*) Those promoting protraction of the mandibles: mandibular muscles 22 and 23 and tentorial muscles T4, T5, T7 and T9.

The short muscle 19, close to the pleural articulation of the suspensory rod of the mandible, passes from the rod directly up to the cranium. The muscle assists the raising of the rod on the recovery movement of the mandible without impairing the freedom of the mandibular end of the suspensory rod. As usual, the muscles concerned with the recovery movement (groups (*c*) and (*d*)) are much less bulky and numerous than those causing the effective stroke (groups (*a*) and (*b*)).

The narrow morphologically antero-posterior face of the mandible, from which muscles arise very close together even if located on the anterior or posterior parts (figure 64*a* to *d*), promotes the maximum range of movement within the confined space of the much flattened gnathal pouch, and inhibits any tendency for the muscles to cause rotator or counter-rotator movements.

The *hypopharynx* possesses three sets of muscles. Two pairs, h. 1 in figures 61, 62C and 63 (the retractor linguae duplex, d. 19, of Meinert), leave the anterior region close to the termination of the hypopharyngeal process of the anterior tentorial apodeme. They lie one above the other and insert on to the sternites of maxilla 1 and maxilla 2, not on to the transverse mandibular tendon. Paired muscles h. 2 and h. 3 (figure 62C) pass respectively outwards and backwards and outwards and forwards to the anterior tentorial apodeme (muscles d. 20 and d. 21 of Meinert who describes an additional levator, d. 22). These muscles suggest that the tongue-like activities of the hypopharynx may be accurately adjusted to mandibular movements and to swallowing. The main median part of the hypopharynx fits against the upwardly directed soft anterior lobes of the mandibles, and a small, but probably important, lateral lobe of the hypopharynx fits into the corner of the preoral cavity (figures 61 and 63D). There seems to be no reason for withholding the name superlingua from this lateral lobe because its functions are not the same as in the Apterygota. In the Symphyla the superlingua is intermediate in form between the lateral lobes in *Scolopendra* and the superlinguae of Apterygota, which are themselves very various in shape.

32. Conclusions concerning Chilopoda

The account of the feeding mechanism of *Scolopendra* shows that both mandibles and maxillae 1 carry out rhythmical movements suiting the eating of flesh, which is made available by the tin-opener action of the coxo-sternite of trunk segment 1, and whole small animals. Maxillae 2 and the anterior trunk limbs hold the food.

Entognathy confers proximal mobility on the mandibles, as in other entognathous arthropods. The mandibular mechanism of *Scolopendra*, although unique, could readily have been evolved from a jointed, transversely biting mandible of a primitive myriapod type, lacking the particular refinements of present-day Diplopoda and Symphyla, by the growth of a pleural fold (p. 54). A loosening of the mandibular articulation on the head would make possible the see-saw movements of the chilopod mandible about the transverse tendon, which lies at the middle level of the mandible in Chilopoda as in Diplopoda and Symphyla. This movement largely resolves the problem of abduction of a transversely biting mandible.

The stimulus for the evolution of a see-saw entognathous mandible in Chilopoda has doubtless been the crevice-living habit and carnivorous feeding, for which head flattening is so useful (Manton 1964). It has been possible to combine such flattening with the presence of large strongly cutting mandibles serving flesh eating by the evolution of gnathal pouches which occupy the whole post-oral length and the depth of the head, and this has permitted the changes in mandibular structure and movements.

The segmentation of the chilopod mandible into scutes which, except for sclerite 5, are not cylindrical or even half cylindrical in shape, is so unusual as to have been regarded as pseudo-segmentation. The cylindrical concept of a segment is, however, equally artificial, even if the phenomenon is very frequent in the jointing of bodies and limbs. The segmentation of the chilopod mandible serves the same purposes as the common linear cylindrical or half cylindrical segmentation in that it promotes movement of one part upon another. The useful intrinsic movements concerning the curvature of a long shallow mandible working in so confined a space are small, and had such small movements between the sclerites been not worth while, it is improbable that intrinsic muscles 29 and 31 would be there to make them (figure 64*b*, *e*) or muscles 21, 27 and 30 to effect further adjustments.

The basic uniformity of the anterior tentorial apodemes in the Diplopoda, Symphyla and Chilopoda shown by the main branches of the apodeme, its strong muscles, and its swinging movements, suggests that mobile anterior tentorial apodemes characterized archi-myriapods. The mobility of these structures has been used to promote mandibular abduction, and to different extents in these three classes. This myriapod type of resolution of the general problem concerning abduction of the mandibles is quite different from those employed by other classes of arthropods, where anterior tentorial apodemes, if present, are not used for this purpose, and where the whole course of evolution towards transverse biting has been quite different.

The basic similarities between the Chilopoda, Diplopoda and Symphyla in the morphology and movements of the mandibles and of the anterior tentorial apodemes, leading to the retention of segmental tendons of the mandibular and sometimes maxillary segment, are far reaching and impressive, and go far towards restoring faith in the validity of the Myriapoda as a taxonomic group of real affinity. The very great apparent differences between the trunk morphologies of these three classes is correlated in detail with habits and with locomotory mechanisms. These class characteristics could have evolved from a similar basic type of archi-myriapod in association with the advancement of divergent habits (Manton 1954, 1956, 1958*a*, 1961, 1964).

The entognathy of the Chilopoda contrasts with that of the Apterygota in detail, although the all-important proximal freedom of the mandible is similar in both. The rotator and counter-rotator movements of the apterygote mandibles is absent in Chilopoda and the protractor-retractor movements of the latter are achieved quite differently. The widely open preoral cavity and gnathal pouch of the Chilopoda suits flesh eating, while the narrow gnathal opening of the Collembola and Diplura serves their very different mandibular movements. Myriapod maxillae 1 differ greatly among themselves, but all are unlike the basic type found in the Thysanura, Collembola and Diplura and the less specialized Pterygota. Myriapodan entognathy has evolved in parallel with that of the Collembola and Diplura. Resemblances such as those between mandibular muscles 1 and 2 in the Apterygota and muscles 25 and 26 in the Chilopoda, all arising on the external face of the mandible, are due to convergence, and the stabilizing muscles 15 and 16 of *Tomocerus* and 32 of *Scolopendra* must also be so interpreted. In both animals these muscles reach the middle line, being here united by a thin sheet of fascia (cf. the wide tendons of the rolling mandibles of *Chirocephalus*, *Anaspides*, *Petrobius*, etc.)

It is clear that a belief (Snograss 1928) in the primitive state of chilopodan mouth parts is unfounded. Maxillae 2 are, of necessity, leg-like (§ 30) but the mandibles are as specialized and efficient as can be found among the Arthropoda. It is the lack of appreciation of the working of the mandibular and feeding mechanisms which has led to statements concerning the presence of generalized mandibular musculature in Chilopoda (Applegarth 1952); to the view 'that the Chilopoda are to be placed somewhere back in the line which ultimately led to the insects' (Applegarth 1952); and to the statement that the 'mandibles of chilopods seem to initiate a new line of jaw evolution, since their structure cannot be matched anywhere among the Crustacea, and...it appears to lead into the type of mandible characteristic of Diplopoda and Symphyla' (Snodgrass 1950). The place of the Chilopoda is squarely within the Myriapoda, whose mandibular evolution has been both separate and divergent from that of the Hexapoda. The chilopodan whole limb mandible has nothing to do with the gnathobasic mandible of Crustacea; chilopod mandibles do not rotate on their long axes (as stated by Snodgrass). The chilopod mandibular mechanism cannot be regarded as ancestral to that of Diplopoda or Symphyla although all three may have had a common origin. The Chilopoda cannot be interpreted as a persistent relict of any form of insect ancestor, whose mandible must have been unsegmented and of the rolling type, from which transverse biting in Pterygota has been evolved by a clear series of evolutionary stages. Chilopod peculiarities in mandibular structure and mechanism are dependent upon entognathy which has evolved here in independence from those of Onychophora and the apterygote classes.

33. MANDIBULAR MECHANISMS AND THE PHYLOGENETIC RELATIONSHIPS OF THE LARGER CLASSES OF ARTHROPODS

The elucidation of phylogenetic relationships within the Arthropoda is essentially speculative since the fossil record is non-committal, and much has been writen without advancing new data (e.g. Siewing 1960). The variety in compound eye structure which exists within the Crustacea alone has recently been pointed out by Dahl and others at a symposium on Evolution of Crustacea (Whittington & Rolfe 1963), where the importance of recognizing the parallel evolution of 'unique mechanisms', such as compound eyes, was stressed. The facts presented here brings to light considerable evidence concerning interrelationships and phylogeny within the Arthropoda which is not of a speculative nature. A brief consideration of the views which have been expressed on this subject has been given by Tiegs & Manton (1958). Their conclusion that a monophyletic derivation of the Arthropoda is untenable and that mandibles have originated more than once is supported.

(i) *General considerations*

A recognition of the several courses of mandibular evolution not only points out divergent lines of arthropodan evolutionary progress, but also shows which, among living types, are the more primitive. The four types of jaws indicated by the vertical columns in figure 65 appear to have been independently evolved, since the details of their mechanisms and structure precludes any one type giving rise to another. The Crustacea and Chelicerata both use a gnathobase, but from differently constructed legs. The Crustacea have evolved their various types of mandibular mechanisms from a promotor-remotor rolling movement while the Chelicerata have used a directly transverse bite, thus indicating a lack of affinity between these two groups of animals. The rolling jaw of the Hexapoda and the usually segmented mandibles of the Myriapoda which primitively bite transversely, indicate two divergent evolutionary lines within the Onychophora-Myriapoda-Insecta stem, but the common possession of a whole limb mandible supports the supposed relatedness of these terrestrial arthropods. Since only two types of leg movement have been utilized in jaw evolution it is not surprising to find that the same type of movement has been exploited more than once, as in the transverse gripping by the Chelicerata and Myriapoda, and the rolling movement by the Crustacea and Hexapoda, just as hexapodous walking has been independently acquired by certain Crustacea, Arachnida and insects. An appreciation of the functional significance of entognathy and the recognition that this state has been convergently acquired many times (figures 65, 66), is also of great importance in any consideration of arthropodan phylogenetic relationships.

Since mandibular mechanisms utilize the head endoskeleton in large and in varied measure, the presence throughout the Arthropoda of a unified system of functionally important structures (i) head apodemes, continuous with the surface cuticle and caste with it at ecdysis, and (ii) segmental transverse tendons composed of connective tissue-like fibres, ectodermal in ontogeny in so far as they are known, and carrying their own formative cells away from the surface, so growing with the body, is of much comparative significance. The previous accounts of many of these structures are confused, inaccurate and incomplete. Segmental tendons are well formed in the primitive members of all classes, and the apodemal system of the myriapod-hexapod series shows a basic uniformity which contrasts with the Crustacea, as has hitherto not been appreciated. These similarities and differences are clear pointers to phylogenetic relationships.

The appreciation that strong biting in the transverse plane is not a primitive or even a typical condition in arthropods is of great importance. Such biting is absent in most of the more primitive living types, and it can only be accomplished after the resolution of mechanical difficulties in the design of a suitable abductor mechanism. The resolutions occur as end terms to many evolutionary lines, and since the resolutions are mutually exclusive they indicate the independent evolution of both the biting mandibles and of their owners. The statement that the 'generalized mandible...of the entomostraca and some of the malacostracan Crustacea, and in the Machilidae...in order to be a functional jaw must be able to swing towards its fellow, the pendent mandible has no ventral point of articulation' (Snodgrass 1950) is very misleading because such so-called monocondylic mandibles do not function by swinging together in the transverse plane in the manner implied, and none of the more primitive mandibular mechanisms existing today has been found to be operated by three muscles comprising no abductors, the primitive condition envisaged by Snodgrass.

The assumption that primitive jaw mechanisms are worked by direct transverse adductor muscles, and that all transverse muscles attached to mandibular and maxillary transverse tendons are adductor in function, is widespread and without foundation, as is the view that elasticity provides the abductor force (Snodgrass 1950). Transverse segmental tendons along the head and trunk serve many purposes (§ 4 (ii)). The tendons are well developed in the heads of the more primitive Crustacea and Hexapoda, and they occur in Chelicerata and Myriapoda. The tendons, except in the Myriapoda, support the primitive rolling mandibular movement as seen in the Anostraca, the more primitive members of the Leptostraca, Peracarida, Syncarida and Thysanura, the Diplura and the ambulatory movement of the prosomal legs of *Limulus*. The tendons disappear with the evolution of strong transverse biting in Crustacea and Hexapoda for functional reasons (pp. 19, 28 and 47). Very rarely are the transverse muscles attached to the mandibular tendon exclusively adductor in function (as in Diplopoda), more often they are differentiated principally into promotor and remotor sectors (as in the above named Crustacea, *Petrobius* and *Campodea*), sometimes small adductor, levator and abductor sectors are also present (*Chirocephalus*, figure 3D), protractor sectors are well formed in *Campodea*, and the transverse muscles may be largely stabilizers (Collembola and Chilopoda). Similarly the transverse muscles attached to maxilla 1 tendon may be adductor (*Petrobius*), abductor (Symphyla), protractor (*Campodea*) or stabilizers (*Tomocerus*). Only in Chelicerata and Myriapoda does transverse biting appear to have evolved directly from the typical transverse movement of a trunk limb, and quite independently and by different means in the two groups.

Snodgrass goes further and interprets transverse mandibular muscles as 'primitive sternal adductors' without evidence of either function or phylogeny. The function of transverse muscles has been summarized above. There is no evidence in support of the view that transverse tendons are portions of sternal scutes which have become internal, forming first a true endosternite (presumably cuticular) and then becoming tendinous, as shown in the drawings of hypothetical stages by Snodgrass (1958). Embryologically the segmental tendons have nothing to do with sternites; they are not cuticular; and they are intersegmental in origin. Head apodemes are intuckings of surface ectoderm and cuticle, but the more primitive arthropods do not have the transverse mandibular or maxilla 1 muscles attached to the apodemal systems.

The 'primitive sternal adductors' of Snodgrass leave the proximal rim of the hypothetical coxa, but transverse mandibular and maxilla 1 muscles usually do not; they arise from the concave face of the limb. In the functional survey of terrestrial arthropod limb structure so far completed (Manton 1958*a*, *b*, 1961) no trunk limb has been found in which an extrinsic coxal muscle arises from the body of the coxa, such muscles arise from the rim, the intrinsic muscles utilizing the concave face of the coxa.* The transverse muscles of mandibles and maxillae have no counterparts in the existing less specialized ambulatory limbs of most Crustacea, myriapods and apterygotes, and may be new muscles, laid down by undifferentiated mesoderm of the mandibular somite when the coxal size becomes large enough to house them and when intrinsic muscles no longer need the coxal surface. But the very wide trunk limb coxae of the Cephalocarida (Hessler in preparation) and of Branchiopoda, which lack firm basal articulations and thickened proximal coxal margins, possess extrinsic muscles arising from the inner face of the coxa which insert on the segmental transverse tendons, resembling the mandibles in this respect. Whether the coxae of these Crustacea are more archaic than all others, and represent a primitive stage once common to whole classes of arthropods is open to question. The serial repetition of many muscles in the thoracic, maxillary, maxillulary and mandibular segments of *Hutchinsoniella* is very striking (Hessler). It is possible that small size (*Hutchinsoniella*) and/or a predominant use of the legs for swimming (Branchipoda) has led to the retention of a primative crustacean skeleto-musculature of the trunk, and that a predominant use of the legs for walking is associated with the coxal musculature refered to above.

It is not possible in a short space to refer to the many further points of difference between the present account and the works of Snodgrass (1928 to 1960) concerning mandibular structure and evolution, many of which stem from the basal concepts referred to above and from faith placed in hypothetical generalized conditions which are considered to represent realities appertaining to arthropods at some stage in their monophyletic evolution. The present work is based upon the complete and real anatomy and movements of living animals, and not on simplified generalizations. No support is found for the concepts:

(i) That transverse mandibular muscles are primitively sternal, or that muscle 10*a* (figure 26A) in *Ctenolepisma* represents the partial preservation of this state (see p. 50).

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* In certain myriapods small extrinsic leg muscles arise from the margins of the trochanter and prefemur; and the condition of the almost immobile coxa and of the extrinsic leg muscles in *Polyxenus* is aberrant (Manton 1956, 1958*a*). In *Limulus* transverse muscles (figure 14, muscles 41*a*, *p*) inserting on the endosternite (fused enlarged segmental tendons) arise from the anterior and posterior coxal margins. Contracting together these muscles could assist adduction in the manner supposed to be primitive by Snodgrass; but their usual alternate contraction assists the promotor-remotor ambulatory swing of the leg. Since the abductor mechanism of *Limulus* is unique among arthropods, the musculature of its prosomal limbs can hardly be taken to be basic for the Arthropoda.

(ii) That the ingrowth of tentorial apodemes of biting Thysanura and Pterygota carries with them part of the sternal adductors (muscles 8, 9 and 10 in *Ctenolepisma*, see p. 50); it has been shown here how the need for a wider gape is correlated with the abandonment of the transverse tendon in *Ctenolepisma* as in Isopoda, Decapoda and Pterygota, and other factors are involved in Stomatopoda.

(iii) That direct union of the transverse mandibular muscles via the segmental tendon is a secondary change. Since segmental tendons are of such widespread occurrence, and since muscle primordia all along the body use these tendons in the embryo as scaffolding along which they grow to reach their destinations, there appears to be no reason to suppose that transverse muscles have primitively been attached to any structures other than their tendons.

(iv) That the crustacean jaw primitively carries three muscles which become differentiated into a greater number in the more specialized species. Since no crustacean mandibular mechanism has been found which is dependent upon only three muscles, the postulated changes from such a basis cannot be seriously entertained.

(v) The suggestion that the anterior ends of some Crustacea show a persistent primitive protocephalon, bearing the antennules and antennae but no mandibles, and separated by the cervical groove from the rest of the body (figures 1*a*, 7); and that the mandibles of the Anostraca are articulated to the tergum of a mandibular segment, drawn and labelled as 'a distinct plate between the protocephalic head and the large tergal plate of the maxillary segments' Snodgrass (1950, and also 1960), are not borne out by the facts. The cervical groove in *Chirocephalus* and in *Anaspides* (figures 3 C, D, 7, 8) is of functional significance and there are no clearly defined dorsal plates. The groove braces the surface cuticle against deformation by the pull of the suspensory processes from the transverse mandibular tendon and against the pull of extrinsic mandibular muscles. These muscles, moreover, are inserted under the surface cuticle far in front as well as behind the cervical groove, and the anatomy and connexions of the mandible in no way suggest that surface ectoderm behind the cervical groove alone represents a mandibular segment. The embryology of Crustacea shows that the dorsal part of the head is derived from unsegmented ectoderm in the known examples. Segmentation of the mesodermal somites provides the basis for ventral segmentation of the anterior part of the body, and only parts of some of the anterior somites grow up to reach the dorsal side. The fallacy of regarding the anterior end of modern arthropods as a series of complete cylindrical segments has already been discussed (Manton 1960). The cervical groove of Crustacea is unlikely to represent a segmental boundary lying immediately above the apex of the mandible, an intrasegmental position, but it is clearly of functional significance, as are most of the so-called 'sutures' of insect heads (Strenger 1952) and most of the 'lines', etc., on the head of *Ligia* (see above).

Thus the form and connexions of the mandibles of Crustacea provides no sound evidence for the existence of a persistent clearly demarcated protocephalon devoid of mandibles among modern arthropods. It should also be noted that the extent of a segment cannot necessarily be determined by the range of insertion of muscles originating from it or from its limbs. Large muscles may be composite structures derived from more than one mesodermal somite, and muscles can also traverse two or more segments before reaching their insertions. Head segmentation cannot be mapped with justification by the range of muscle insertions as has been done by Applegarth (1952). The extrinsic muscles of antennules and antennae show a great range in insertions, some of which can only be interpreted as convenient sites suiting the functional needs of the animals (figures 8, 11, see legend; 20, 29, 32, 44, 51, 57, 58 and 62 show some antennulary and antennal muscles, but not all are drawn).

(vi) Snodgrass (1951) states that 'it can hardly be doubted' that the movably articulated gnathal lobe of Myriapoda represents the fixed gnathal lobe of other arthropods, and that it does not represent a segment of a telopodite. No evidence is advanced in support of this view. The myriapod gnathal lobe armature corresponds with the terminal armature of the mandible of *Ctenolepisma*, and this armature spreads to the base of the mandible in the locust (figures 21, 26, 30, 53, 57, 64), but ontogenetic evidence shows that the myriapod gnathal lobe armature does not correspond with the gnathobase of Crustacea and Chelicerata (§ 3 (ii)). The hexapod mandible is unsegmented, and its basic movements are seen most primitively in *Petrobius* among modern forms, these movements would be hindered or impossible if the mandible was segmented. The definition of a segment in an arthropod leg will be considered in another place, but segmentation in the myriapod mandible is just as real and functionally useful as it is in a telopodite.* The view that a joint is not a true joint if no muscles are inserted on either side of it is a very artificial concept, but in both Diplopoda and Chilopoda intrinsic mandibular muscles do in fact traverse mandibular joints. There appears to be no valid reason against considering the gnathal lobe of Symphyla and Diplopoda and mandibular sclerite 5 in the Scolopendromorpha to be terminal segments of the mandibles.

(ii) *Crustacea, Merostomata and Trilobita*

Does the detailed similarity between the mandibles of a Branchiopod (e.g. *Chirocephalus*) and one of the more primitive Malacostraca (e.g. *Hemimysis*) represent a persistent primitive type of crustacean mandible, or are the similar details convergently related to filter feeding? The mandibles of Branchiura, Cirrepedia and Ostracoda and 'higher' Malacostraca are more specialized and need not be considered here, but those of the Copepoda are ventrally situated, but bear no grinding molar areas, even in the filter feeding *Calanus finmarchicus*,† and the mandibles of *Hutchinsoniella* possess an insertion even more like that of a trunk leg.

The mandibles of *Calanus* perform promotor-remotor movements about a sloping axis (figure 12*c*) which passes through (i) a loose lateral articulation (homologous with the dorsal union marked by a cross in figures 1, 3, 5, 7, 9), and (ii) a close union with the head at a point corresponding with the black spot on the same figures; here in *Calanus* the thick cuticle of a transverse sclerite on the head doubles back as the anterior face of the mandible. An axis sloping in this manner has been shown above to promote biting by incisor

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* It is not implied that the segmented myriapodan mandibles have been derived by reduction from a hypothetical basic arthropodan limb composed of a fixed number of segments (of the order of 8), supposed to have been common to all classes (Snodgrass). The latter concept is not considered to be valid. Since mandibular evolution must have started at the onset of differentiation between the major classes, there is no justification for supposing that the present number of mandibular joints has been evolved from a limb possessing a greater number.

† *Calanus* can eat large food such as other copepods (Lebour 1922).

processes on the remotor roll, and the shape of the lateral mandibular articulation in *Calanus* is suited to support a strong remotor roll. As described by Perryman (1961) the cusped cutting edges of the mandible come together as they swing forwards and upwards on the remotor roll and part as they move backwards and downwards on the promotor roll. The muscles causing these movements are the dorsally inserting promotor and remotor muscles arising from the anterior and posterior mandibular margins (corresponding with muscles 3 and 4 of *Chirocephalus* and *Hemimysis*), and the most anterior and posterior of the transverse muscles, arising from the inner face of the mandible anteriorly and posteriorly at the lateral limits of the mandible, and inserting on the short transverse mandibular tendon. These transverse muscles are set at about 40° to one another and are suitably placed to be antagonistic in their effects. As in other Crustacea the remotor muscles are the more bulky and presumably the stronger.

Perryman (1961) shows that the major mandibular movement of *Calanus* is not transverse adduction as claimed by Snodgrass (1950). During the present work manipulation of a potash preparation of *Calanus* by a Harding–Labgear micro-manipulator indicates most plainly the predominance of promotor-remotor movements on all others. And much wider movements readily occur at the deeply incurved posterior margin amply provided with arthrodial membrane, that at the anterior border which is restricted by the tight union at the point marked by a black spot. But small movements of the mandibles can be elicited in various directions owing to the looseness of the lateral articulation. Three transverse muscles arise from the middle region of the mandible near and just posterior to its lateral articulation (figures 12*c*, *d*). The most dorsal of these muscles resembles muscle 6 of *Chirocephalus* (figure 3D), arising from a tendinous pillar and not directly from the mandibular wall, and inserts on the base of the suspensory arms of the mandibular tendon (figure 12*d*). It is possible that contraction of these muscles promotes mandibular abduction on the remotor roll, a movement assisted by the form of the mesial mandibular union with the head. Here a thickened mandibular rim is linked by discrete but short arthrodial membrane with a thickened rim of head cuticle (figure 12*d*). The mandibles of *Chirocephalus* and of *Hemimysis* gradually fade into arthrodial membrane at this point.

Thus all these Crustacea have in common the utilization of the remotor swing of the mandible in bringing together the gnathal margins of the mandibles. Since transverse biting has been shown to be a derived achievement in Crustacea, it is clear that the primitive mandibular action in the class is dependent upon the antagonistic action of sectors of both dorsal and transverse muscles which cause the promotor-remotor roll about an axis lying roughly in the transverse plane of the body; the axis may be situated mainly on the ventral surface or it may be ventro-lateral in position.

The basic movements of the locomotory limbs of *Limulus* and of Crustacea are the same, a promotor-remotor swing. The feeding movements of an anostracan mandible (§ 5) and the feeding movements of the series of trunk limbs in the Branchiopoda,* including those

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* Lowndes (1937) has demonstrated that sometimes but not always small adductor-abductor movements of the thoracic limbs of *Chirocephalus* occur during swimming. How far these movements are muscular in origin or due to the exact position of the axis of swing of the legs is not known; but whatever their cause may be, the essential movement of the thoracic legs is a forward and backward swing. Similar, but very small, adductor-abductor movements sometimes accompany the walking movements of *Limulus*.

of the Notostraca where each possesses a gnathobase (Cannon 1933 *a*), also depend on this movement, the phase difference between successive legs being small. But the feeding movements of prosomal limbs 2 to 6 of *Limulus* are entirely unlike those of any primitive crustacean, they are alternative to those of walking, and the phase difference between successive legs when feeding is as large as possible (0·5). The gnathobase of *Limulus* performs direct biting movements in the transverse plane which are not caused by the promotor-remotor swing. The axis for the latter movement lies in the transverse plane, obliquely, as for the mandible of *Chirocephalus*, but transverse biting in *Limulus* takes place about an axis at right angles to this, a condition found in no crustacean mandible or trunk limb.* Transverse biting in Crustacea, where it occurs several times as different end terms of mandibular evolution (for example Isopoda and Decapoda), takes place about the original axis of swing of the rolling mandible which changes its position in these orders so that the axis becomes oblique or horizontal (figures 5, 7, 10, 13).

The fundamental difference between the movements of the gnathobases of *Limulus* and of Crustacea is of great importance. This, and the associated morphology, must surely mean that the merostome and crustacean gnathobases have been independently acquired as a parallel evolution not indicative of affinity. If a common basis for the limulid and crustacean gnathobasic mechanisms has ever existed, it could only be sought for in a small arthropod possessing no basal articulations to its limbs, an undifferentiated link by arthrodial membrane permitting a variety of slow movements by promotor, remotor, adductor and abductor muscles. Increase in size or in strength of movements must have been accompanied by the evolution of close articulations at the limb bases. Thereafter the Crustacea have used direct adductor-abductor mandibular movements to a minor extent only (as in *Chirocephalus* and *Hemimysis*), the direct abductor muscles 6 of these two animals corresponding in general principle, but not in detail, with abductors 25 and 26 of *Limulus* limbs 2 to 6, while the Chelicerata have exploited this biting movement to a maximum.

It is significant that the second feature which the Merostomata and Crustacea have in common, a biramous leg, is also one of quite different construction. The outer ramus in the Merostomata, and in Trilobita, is a proximal exite (pre-epipodite, Størmer 1939), while the outer ramus in Crustacea is a more distal structure borne on the end of the protopodite, and one or two proximal exites may be present, as in *Anaspides*. A third fundamental difference between *Limulus* and Crustacea concerns the telescopic limb-bearing surface of the prosoma in the former and the rigid insertions of the limbs on the trunk in the latter, features associated with the differences between the limb movements.

Thus the study of jaw mechanisms emphasizes the depth of the cleft between the Merostomata-Chelicerata and the Crustacea. The Trilobita show clear general resemblances in leg form to the limbs of *Limulus*, but the Trilobita lack as good a gnathobase and possess pre-epipodites all along the series. There is also the resemblance in trilobation of the carapace which may have a functional significance in trilobites such as that in *Limulus*.

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* In the hoplocaridan Crustacea strong cutting by means of blade-like molar processes takes place at right angles to the vertical axis of swing of the mandible, and this biting is done in the horizontal plane (see figures of Snodgrass 1950). It appears to be a specialized method of strong biting found in no other major group of Crustacea and is in no way primitive or directly comparable to the biting found in any other arthropods which have been examined here.

Thus the evidence, as far as it goes, supports Størmer (1944) in suggesting closer affinity between Chelicerata and Trilobita than between either of them and the Crustacea.

In attempting to assess the taxonomic positions of the early arthropodan fossil animals, many showing some resemblances to Crustacea, one would like to see a much more careful study of both the basal regions of the head and the trunk limbs where the state of preservation may allow. There appears to be much too great a readiness to state that the limbs are of the biramous trilobite-type when in fact this is not proved. Details of the coxal articulations and of the outer rami of the appendages, if they were available, would indicate the types of biramous limbs and types of jaw-like structures, which may have existed, or, in the absence of gnathobasic structures, evidence might be obtained as to the type of limb movement which was employed. All such observations would be of service in correctly interpreting the fossil record.

(iii) *Crustacea and Hexapoda*

Since the crustacean mandible is primarily a gnathobase and the hexapod mandible a whole limb, it would be surprising to find more than convergent resemblances between them, as indeed is the case. No support has been found for the assumption (Snodgrass) that these mandibles are homologous coxal derivatives. It is the coxa-body joint only which is constant in all types of mandibles, and the proximal coxal rim carries comparable muscles. All the evidence points to an independent evolution of both primitive rolling and secondary transverse biting mandibles by means of a gnathobasic jaw in Crustacea and by a whole limb jaw in Hexapoda.

The mandibular mechanism which most nearly approaches a central primitive type among the Hexapoda is that of *Petrobius* (§§ 16 to 19) and this shows two similarities with Crustacea. The promotor-remotor rocking movement of its mandible bears a resemblance to the promotor-remotor roll of the mandibles of the more primitive Crustacea, *Chirocephalus* and *Paranaspides* (§§ 5, 6, 8 and 9). But there are only two movements of an ambulatory limb which are serviceable to mandibles (§ 3), and it would not be surprising to find the same movement employed independently by Crustacea and Hexapoda. *Petrobius* also resembles the more primitive Crustacea in the presence and mode of use of a transverse mandibular tendon. But this is a potential attribute of all body segments (§ 4 (ii)). The presence of well developed mandibular tendons functioning in the same manner is no indication of affinity but suggests the persistence of a primitive attribute.

The mandibular mechanisms of *Petrobius* and of the more primitive Crustacea show many deep-seated differences:

(1) the derivation from a gnathobase and from whole limb has already been noted.

(2) The long narrow mandible of *Petrobius* does not require the 'elbow room' needed by crustacean mandibles such as *Chirocephalus* and *Paranaspides*. The wide rolling movement of Crustacea is absent in *Petrobius* and instead rotator and counter-rotator movements take place, the mandible working in a confined space and rotating from a dorsal ball and socket joint about an incipient hinge line.

(3) A much fuller use of the anterior and posterior margins of the mandible for the origin of rotator and counter-rotator (promotor-remotor) muscles is found in *Petrobius* than in the Crustacea.

(4) The use by *Petrobius* of anterior tentorial apodemes for the insertions of mandibular muscles, such apodemes being absent in Crustacea.

(5) The whole hexapod endoskeletal system, composed of anterior and posterior tentorial apodemes and transverse segmental tendons is entirely different in detail from crustacean endoskeletal systems.

(6) The presence of intrinsic and extrinsic endoskeletal muscles. Endoskeletal suspensions in Crustacea are not muscular in *Chirocephalus* and *Paranaspides*, where there is no provision for vibratory movements. In some Decapoda muscles are present between parts of the endophragmal system but they are not at all like the muscles possessed by *Petrobius*.

(7) The form and functioning of the hypopharynx and superlinguae is unlike that of the paragnaths of Crustacea. Only in certain Isopoda is an additional median lobe from the body wall present bearing a very superficial resemblance to the hypopharynx of hexapods (p. 45). In *Petrobius* these outgrowths from the ventral head wall provide the hydraulic efficiency of the oral cone within which the mandibles and maxillae 1 work.

(8) The utilization of labial segmental organs for providing salivary juice is not found in Crustacea.

This list of differences between the mandibular mechanisms of *Petrobius* and Crustacea supports the view that these mechanisms have been independently evolved using the same promotor-remotor swing of a walking or swimming leg, and giving convergent evolution of similar primitive rolling types of mandible. From both these primitive types further advancement has led to mandibles which bite strongly in the transverse plane and to those which scratch, pull and pierce, but these changes have occurred several times independently from both the gnathobasic and the whole-limb types of mandible (figure 65). Only two of these specialized derivatives have been considered here, the Isopoda and some Decapoda, because they show the greatest superficial resemblances to hexapods. Ostracoda (Cannon 1931), and Stomatopoda (see footnote to p. 100) show other specialities. As yet we are at the beginning of an understanding of the functional significance of structure. The strongly hypognathous heads of *Ligia* and of *Petrobius*, both antero-posteriorly shortened, are doubtless correlated with similar ways of life, and other superficial similarities between certain Isopoda and Thysanura are probably cases of convergence.

(iv) *Myriapoda and Hexapoda*

In considering the interrelationships of the myriapod, pterygote and apterygote classes (Tiegs & Manton 1958) little reference was made to the evidence provided by mandibles and endoskeleton because the appropriate data were not then available. The present work was undertaken to remedy this deficiency, and the information it provides leads to a revision of some of the arguments presented in 1958. The evidence concerning mandibular evolution is important because it reflects the course of evolution of the animals concerned (see above).

Snodgrass (1928) considered that the series *Petrobius*, *Ctenolepisma* and the locust illustrate the derivation of the pterygote mandible. While the present work is in agreement with this conclusion, the argument differs considerably.

It has been shown in §§ 19 to 23 how the mandibular mechanisms of (i) *Ctenolepisma* and of the more primitive Pterygota, and of (ii) the entognathous Apterygota (Collembola and

Diplura) represent two divergent types of mandibular evolution which could have originated from an archi-*Petrobius* type. Trend (i) leads to an absence of the *Petrobius* type of hydraulic efficiency and to the acquisition of strongly hinged transversely biting mandibles, while trend (ii) leads towards a proximal freedom of the mandibles permitting protractor-retractor movements as well as free rotator and counter-rotator movements, made possible by the growth of a pleural fold, such as present in *Petrobius*, which leads to entognathy. The differences in the protractor-retractor mechanism of Collembola and Diplura suggest that their entognathy has been independently acquired (p. 66). All these changes indicate a closer relationship between some archi-*Petrobius* type of thysanuran and a pterygote than between either Collembola or Diplura and the Pterygota. But it does not follow that the actual ancestors of the Pterygota were archi-Thysanura; all that can be suggested from this evidence is that the Pterygota are descended from ancestors possessing rolling, whole-limb, unsegmented mandibles, and that such ancestors entirely lacked the entognathous features of Collembola, Dipleura and Protura (figures 65, 66).

The survey which has been given of the structure, composition and connexions of the pterygote and apterygote head endoskeleton shows a remarkable coherence in basic plan such as exists in no other group of arthropodan classes. The conflicting statements in the literature have arisen from a basic lack of data and need not be considered further (see §§ 17 (i), 19 (i), 22 (i), (v)). This coherence is reflected also in the structure and movements of maxillae 1, which shows a community of plan not shared by myriapod maxillae 1, even in the Symphyla (see §§ 27 (iii), 28, 30). The closer affinity of the pterygote and apterygote groups to each other than to Myriapoda is shown both in their head evolution (mandibular mechanisms including anterior and posterior tentorial apodemes) and by their hexapodous state. But there is always the possibility that the advantages of a hexapodous condition may have been evolved more than once by the ancestors of present-day hexapods, since the use of three pairs of legs only is functionally advantageous and seen in isolated examples from widely different classes (Manton 1952*a*).*

The Chilopoda, Diplopoda and Symphyla are clearly distantly associated with the pterygote-apterygote groups for the reasons reviewed by Tiegs & Manton (1958), but more information is now to hand. The possession by these three classes of:

(i) anterior tentorial apodemes, homologous with those of hexapods, but highly musculated and swinging within the head;

(ii) the absence of posterior tentorial apodemes;

(iii) the presence of segmented mandibles representing whole limbs;

(iv) the utilization of the anterior tentorial apodemes to promote mandibular abduction;

(v) so that biting in the transverse plane has apparently been evolved directly, without any preliminary typical rolling mandible as seen in *Petrobius*; points to a unity among these myriapods and a deep cleft between them and the hexapods. The differing external trunk characters of these myriapods are correlated in detail with habits of life and are readily derivable from a common type (see Manton 1954, 1956, 1958, 1961*a*, *b*, 1964).

The Diplopoda and Chilopoda show the result of early habit divergence between fast moving predatory animals and burrowing feeders on decaying vegetation. Only two pairs of mouth parts give closely integrated feeding movements in both classes. Chilopod

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* Work is in progress to test this possibility.

maxillae 2 and poison claws are more like trunk limbs than mouth parts in their use. The whole form of the chilopod mandibular mechanism is bound up with entognathy and crevice living, and could not have given rise to that of any other class of myriapod (see p. 92). The Symphyla have achieved a labiate condition, as in hexapods, and, although vegetarian, the mandible lacks a molar area, possessing only a cutting edge (molar areas usually need a rocking and not a transversely biting movement for effective trituration). The diplopod gnathochilarium assists mandibular abduction, as does the maxilla 1 of Symphyla, but not by mobility in the transverse plane, and so an additional labium is not required. The chilopod feeding mechanisms would be wrecked by the presence of a labiate maxilla 2. *Scolopendra* needs a freely open space below the maxillae 1 (§ 30) such as is provided by the form of the maxillae 2 (figure 60).

The structure of the pauropod head has been described by Tiegs (1947), and direct observations of the feeding movements of so minute and delicate an animal present difficulties. The myriapodan maxilla 1 salivary gland (segmental organ) and anterior tentorial apodemes (hypopharyngeal apophyses of Tiegs) are present. The latter provide the only firm bearing for mandibular movement, a distal 'articulation'. Proximally the mandibles are very free, they are protrusible and covered by a fold of clypeus except at their tips. The mandibles provide a scraping mechanism, and fluid and finely divided food is sucked up. The pauropod condition is another manifestation of entognathy, giving the same advantages as the entognathy of other myriapods and hexapods, but by different means and from a dignathan stage of advancement. There is as yet no further evidence of the functioning and past history of this specialized mandible.

Thus the phylogeny of the Myriapoda appears to have been a series of divergent evolutionary lines leading to present-day Pauropoda, Chilopoda, Diplopoda and Symphyla, and the common features displayed by these classes suggests a usefulness in retaining the name Myriapoda to signify their relatedness (figure 66 and below).

The differences in mandibular mechanism and in salivary juice production between the Symphyla and all types of hexapods are so great as to make it clear that a supposed archisymphylan ancestry of insects must be abandoned. It is a pleasure to record my agreement with Snodgrass (1951) on this point. The symphylan head is not essentially insectan, except in limb number, and its mandible could not be the forerunner of the thysanuran type. The features of similarity between insects and Symphyla which have been pointed out by Tiegs must be regarded as partly due to distant common inheritance and partly to parallel evolution. The common possession of a labiate maxilla 2 in insects and in Symphyla cannot indicate close relationship of these groups as has sometimes been suggested. The labium has similar usefulness in both groups, and its parallel appearance is no more remarkable than the parallel evolution of the heterodont mammalian dentition in unrelated mammal-like animals.

That a common number of fourteen trunk segments should occur in the Symphyla and in some hexapod groups may appear to be more than a coincidence. However, it has been shown (Manton 1952*b*) that the number of trunk legs used for running by *Lithobius* is most exactly correlated with the gaits which are used, and these gaits in turn must be associated with the potentialities of muscle physiology, etc. A smaller number of legs, such as used in early instars of *Lithobius*, necessitates the use of slower patterns of gait if the loading on a leg remains constant, and an increase in the number of legs beyond the thirteen used in fast running by the adult would bring the physiological disadvantage of uneven loading. If it should be demonstrated that trunk segment number in Symphyla is correlated with the type of locomotory movements, and if this type was also used by insect ancestors (as is probable) a parallel evolution of the same number of trunk segments in a myriapod and in a many-legged hexapod ancestor would not be surprising.

It appears likely that insectan features, just as mammalian or reptilian features, have turned up several times in different stocks of early animals, and differently combined with other characters. And that the particular stock of many-legged creatures, which had the potentiality of giving rise to the Pterygota, did so, leaving no persistent imperfect insects for us to see today. Present-day Thysanura suggest the type of head and feeding equipment possessed by the archi-pterygote. Sharov's work (1957*a*, *b*, 1960) on lower Permian Monura and other primitive hexapods demonstrates an earlier stage of thysanura-like evolution and a primitive series of hexapod ontogenetic stages. Modern Symphyla suggest the type of locomotory habits which preceded the hexapod state. The gaits, trunk morphology and jaw mechanisms of Diplopoda, Chilopoda and Pauropoda have all been too committed from the start to their own lines of advancement to have had the potentiality of conversion to an insectan type (Manton 1964). The remaining Apterygota were limited to their own lines of advance as soon as they embarked upon proximal mandibular mobility and entognathy. No new data has been brought forward here concerning the Protura. They are clearly another independent line of entognathous apterygote with stylet-like mandibles which has played no part in the evolution of any other group. Thus it is not reasonable to look to the archi-members of any existing myriapod and/or apterygote group, with the possible exception of the Thysanura, for the ancestors of the Pterygota.

(v) *Onychophora and other Arthropoda*

The unsegmented whole-limb jaws of *Peripatus* places the Onychophora squarely with the Myriapoda-Hexapoda assemblage, a conclusion in keeping with the many other considerations brought forward by Tiegs (1947), Manton (1949) and Tiegs & Manton (1958). The limited cephalization indicates perhaps a very early adoption of a jaw technique in feeding. The unique antero-posterior slicing by entognathous jaws (p. 56 and Manton 1937) is related to the onychophoran accomplishment of outstanding importance, that of being able to deform the body extremely so that access is gained, without pushing, to damp cavities where predators cannot follow (Manton 1959, 1961 *a*). Large sclerotized mandibles working on a transverse mandibular tendon would be an impossible mechanism for such a habit of life. Heavy sclerotization is limited to the terminal jaw blades and to the very long hollow jaw apodeme which extends through several trunk segments. An abundance of extrinsic muscles fan out from each jaw (Butt 1959),* the largest muscle being the remotor (retractor) arising from the long apodeme (Manton 1937, text-figs. 2 and 3) and causing the cutting movement. Mandibular apodemes have evolved independently (p. 74) even within the myriapod-hexapod series, those of the Thysanura and Pterygota springing from the posterior margin of the mandible and carrying their adductor muscles posterior to the transverse tendon, while those of the Diplopoda, Symphyla and Chilopoda arise more

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* A reply to the arguments put forward in this work has been given (Manton 1960).

distally, from the gnathal lobe in the two former classes, and their muscles pass anterior to the transverse tendon (as noted by Snodgrass). The early adoption of habits benefiting by body deformability permitting squeezing through narrow crevices accounts for the most conspicuous features of the Onychophora: their soft and muscular body wall, thin furrowed cuticle rich in sensory spines, type of limbs, unexploited slow gaits, unstriated muscles, connective tissue skeleton; and most of these are involved in the mode of action of the jaws, so intimately correlated with the habit of life of predominant evolutionary importance.

34. CONCLUSIONS

The evidence derived from mandibular mechanisms supports the view of Størmer (1944) concerning the lack of connexion between (i) the Onychophora-Myriapoda-Hexapoda stem, (ii) the Crustacea, and (iii) the Merostomata-Chelicerata-Trilobita assemblage. A biting gnathobase has been independently evolved in the Merostomata and in Crustacea, and a whole-limb mandible has evolved independently in the Onychophora, usually in segmented form in the Myriapoda, and unsegmented, using a different basic movement, in the Hexapoda. Some polyphyletic conception of arthropod evolution seems inescapable. But it is one thing to demonstrate the existence of clefts between modern groups of animals and quite another to speculate upon the depths of these clefts in geological time and to suggest what type of animal preceded the divergent lineages. Such speculation will not be indulged in here. To show that mandibles have been independently evolved is a concrete step forward, but this is no proof that divergence in head evolution dates back to a segmented soft bodied coelomate ancestor, as supporters of the validity of the Mandibulata are so ready to oppose.

The opponents of the idea of any form of polyphyletic derivation of the Arthropoda are unwilling to consider that convergence in detail of organs such as eyes is a conceivable phenomenon. It is salutary to consider the amazing similarity in detail, down to the electron microscope level, of the complex spiracular gills and plaston respiratory structures of pupae and eggs whose polyphyletic origin in some 15 groups of insects is undoubted (Hinton 1957 to 1962). Of great importance is the recognition of the limited range in form which is serviceable for certain organ systems. For example, the constancy of nine peripheral and two central fibrils in cilia and flagella throughout the living world would hardly have been maintained had divergencies from this plan been equally advantageous. If there was less limitation in the structure and performance of certain organs, such as eyes, much greater range in structural details might be present today. Where similarities exist which can reasonably be accounted for by convergence, such similarities cannot be considered to represent sound evidence of affinity in face of much contrary evidence (Tiegs & Manton 1958, § II).

Increase in knowledge of the fossil record shows that the reptilian and mammalian grades of organization have been reached independently many times. For example, the recent work on the Mesozoic mammals of South Wales (Kermack & Mussett 1959) has added greatly to our knowledge of the origin and classification of the Mammalia. The conclusion that 'the mammals are a polyphyletic group—by which is meant that mammals have no common ancestor which was itself a mammal. The common ancestor must be found among the reptiles'...and...'must have lived in the Middle or Lower Triassic' shows that mammalian evolution resembles that of the reptiles in possessing no common ancestor. In view of these conclusions on vertebrate evolution it would indeed be surprising to find no trace of polyphyletic evolution among so large a group as the arthropods.

The parallel evolution of jaws in arthropods must date from the earliest differentiation of the major classes, but there is no indication of the stage of advancement from which they came. In this sense only does the evidence presented here indicate polyphyletic evolution among arthropods. Jaws appear in the merostome-chelicerate stem and presumably came from some animal of the trilobite-like grade of advancement with jaw-less limb structure and with little anterior modification or tagmosis.

Recent work on the Onychophora recognizes for the first time the habits and correlated body features which are of paramount importance in the survival of these animals, and there is no reason to suppose that the absence of surface scutes is secondary. The flexible body wall of very particular construction is likely to be descended from an *Aysheaia*-like stage and the jaws to have been evolved very early before the preoral segmental shifts took place in the ancestors of the myriapod-hexapod groups. The functional significance of preoral segmentation in arthropods is too little understood for useful comment to be made, but a parallel evolution of this feature in Crustacea and in the myriapod-hexapod group is not an impossible supposition in view of the many other examples of convergence. A functional consideration of the structure and evolution of arthropod limbs will be given at a later date, but there is no reason to suppose that the biramous type of crustacean limb has had anything in common with the uniramous limbs of Onychophora, Myriapoda and Hexapoda. Thus basic limb differences in these two assemblages probably preceded their entirely different mode of development of jaws.

The time has come to recognize that certain terms, originally designed to indicate relatedness in groups of animals, should be used in a more restricted sense, and in some cases dropped:

Arthropoda, as a name for a large group of animals, is as useful as are the terms Reptilia or Mammalia, even if the Arthropoda may be polyphyletic to some extent, and, with the reptiles and mammals, represent a grade of advancement rather than a closely related unity.

Mandibulata (Snodgrass 1938). There is no justification for this term if it implies phylogenetic relationship between Crustacea, Myriapoda and Hexapoda in which mandibles of entirely different types have been evolved in parallel. The term may serve some useful purpose if the sense is restricted to indicate a grade of advancement which has been reached independently by different stocks.

Entognatha (Tuxen 1959) similarly indicates a grade of advancement, and not a taxonomic group. Comparable entognathy, evolved by different means but showing the same functional assets, occurs in Onychophora, Pauropoda, Chilopoda, Collembola, Diplura and Protura, although the Entognatha of Tuxen comprises only the last three hexapodous groups. Even these hexapods appear to have become entognathous independently but probably from the same archi-thysanuran like stock.

Labiata (Snodgrass 1939, etc.) serves little useful purpose as a taxonomic category but perhaps represents a grade of organization. Snodgrass (1938) included the whole of the

Myriapoda and Insecta within the Labiata although only the Symphyla among myriapods possess a labium. The Labiata of Tiegs (1947) and of Remington (1955) comprises the Symphyla and Insecta which all possess a labium, but in the sense of a taxonomic category uniting Symphyla, Collembola, Protura, Thysanura and Pterygota the Labiata is unacceptable since the symphylan mandible, maxilla 1, head endoskeleton, salivary segmental organ, etc., separate this group from all the hexapods, and it is clear that a labium would be functionally disadvantageous to Diplopoda and Chilopoda.

Myriapoda deserve to be reinstated to include Pauropoda, Chilopoda, Diplopoda and Symphyla because these classes show clear functional and structural affinity to one another and basic differences from the Hexapoda.

Dignatha and *Trignatha* (Tiegs 1947). Whether these types of animals represent grades of organization or something more cannot as yet be assessed, and it does not at present appear justifiable to use these terms in a taxonomic manner denoting superclasses, as has been suggested by Remington (1955).

Insecta. The extension of this term (Remington 1955) to include the myriapod, apterygote and pterygote groups has little to commend it since the gulf between the Myriapoda and Hexapoda is thereby masked and the more restricted sense is so widely used.

Myocerata (Remington 1955) links the entognathous Apterygota with the Myriapoda on the common possession of: intrinsic antennal muscles, and the absence of a phallus and ovipositor of the type found in Thysanura and the more primitive Pterygota and lacking amnion and serosa, in opposition to the *Amyocerata* (Remington 1955) which links the Thysanura and Pterygota on the common possession of the opposite of the above named features. While in agreement with the suggested close affinity between Thysanura and Pterygota, the present work does not support the alinement of the animals placed in the Myocerata because they show at least two types of inheritance and not one, they have evolved their mandibles very differently and have advanced their head endoskeleton and principal salivary organs in quite different ways. The common features of the Myocerata appear to be no more than generally primitive attributes of the myriapod-hexapod assemblage.

That the Onychophora, Myriapoda and Insecta represent three well defined taxa which are descended from an early group of land arthropods (Sedgwick 1909) is supported by the data presented above.

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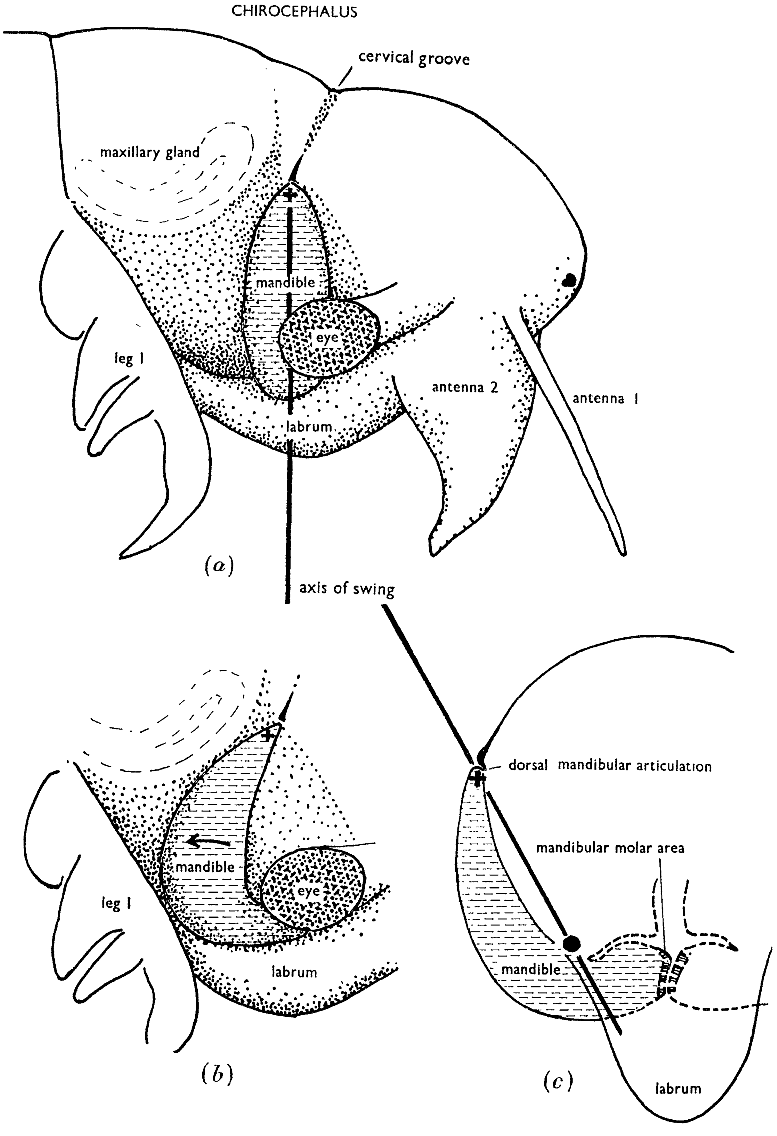


Figure 1. Lateral view of the head of *Chirocephalus diaphanus* Prevost showing the mandible in its position of extreme forward roll (promotor swing) about a dorso-ventral axis. The only point of close union with the head lies dorsally at the black cross (see figure 4*c*). (*b*) The eye and first trunk limb are in the same position as in (*a*) but the mandible is at the end of the backward roll (remotor swing), displaying the straight anterior mandibular margin and the inward and forwardly directed molar process. (*c*) Transverse view of the mandible on the body.

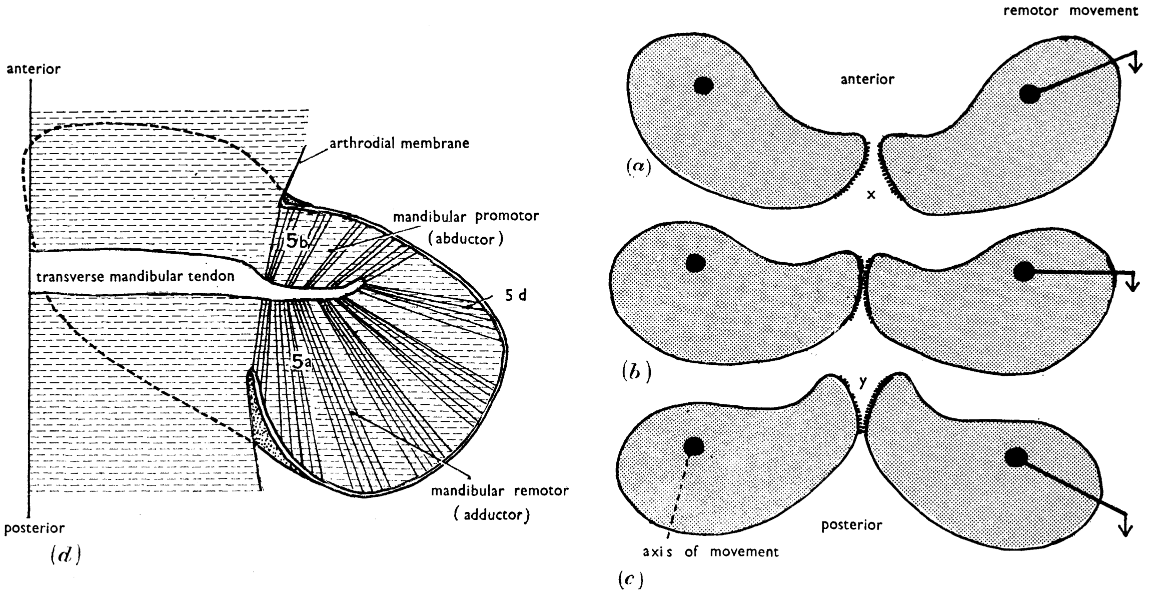


FIGURE 2. (*a*) to (*c*) Diagrams to show the effect of a backward remotor swing through 50° about a vertical axis of the lateral parts of a pair of cardboard shapes resembling an anostracan mandible in frontal view. For further description see text. (*d*) Represents a frontal section of the right mandible of *Chirocephalus* viewed from above, the position of the free portion of the mandible, bearing the molar area, being indicated by a dotted line. Muscles 5*a* cause the backward remotor roll of the lateral parts of the mandible, such as seen in figures (*a*) to (*c*), which swings the molar areas forwards and against each other; muscles 5*b* promotes the recovery swing.

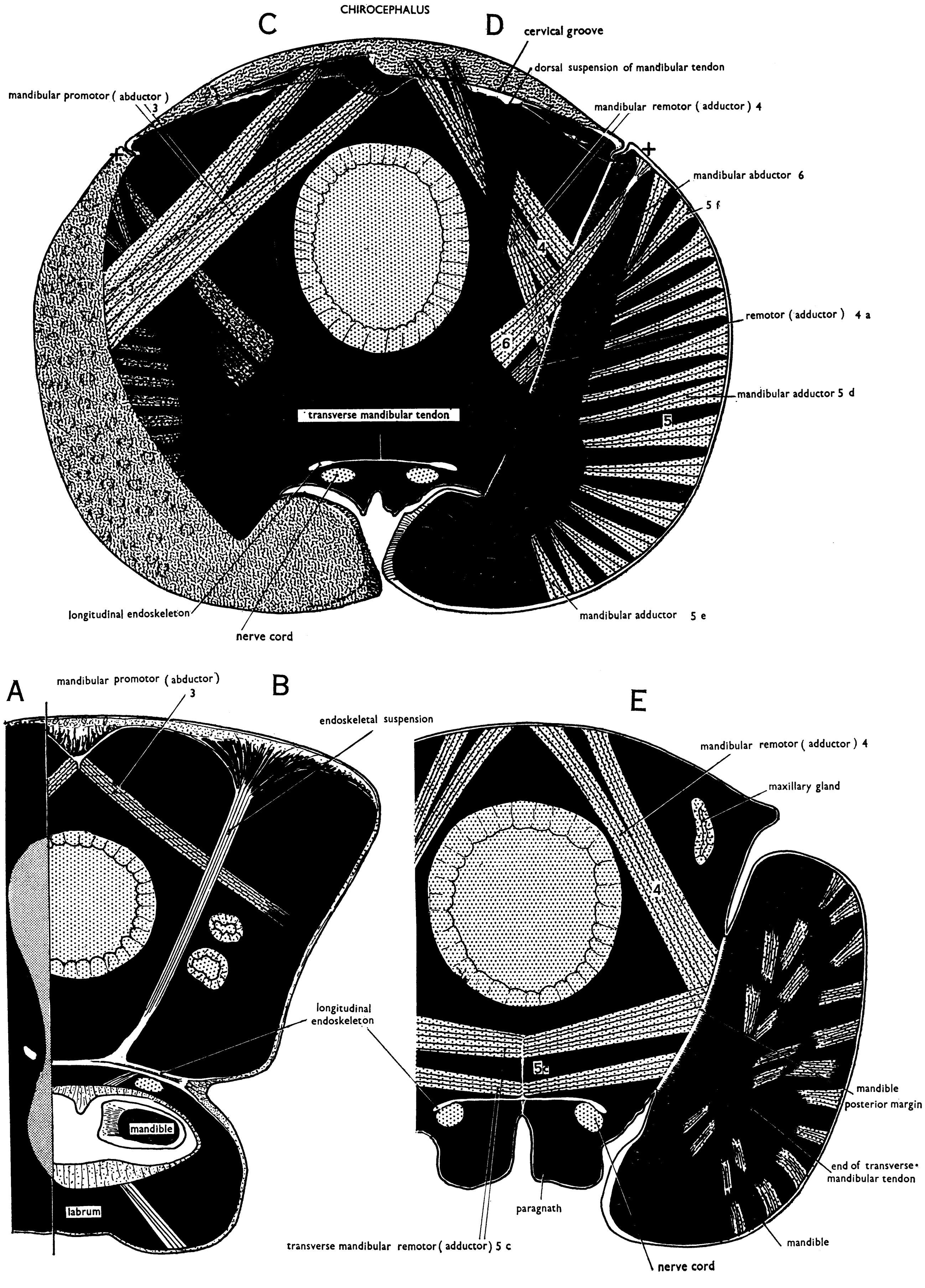


Figure 3. For legend see facing page.

FIGURE 3. Transverse views of the head of *Chirocephalus diaphanus* passing in front of and through the mandible at progressively more posterior levels. A–B lies just in front of the mandible.

Level A shows the oesophagus (stippled) uniting the mouth with the foregut and the cut longitudinal bar of head endoskeleton formed by an elaboration of the basement membrane.

Level B passes through the origin of this endoskeleton from the lateral basement membrane, the transverse connexion between the longitudinal endoskeletal bars, and their fibrillar suspension from the dorsal body wall. The mandibular promotor muscle 3 inserts dorsally on to a cone of basement membrane. Two lobes of digestive gland are cut.

Level C shows the anterior face of the mandible.

Level D passes through the middle of the mandible and its dorsal articulation (see figure 4*c*), the posterior margin of the mandible being visible behind. The median connexion between the mandibular tendon and the endoskeletal plate uniting the paired longitudinal endoskeletal bars lies on the posterior side of the mandibular tendon, and is shown also in level E.

Level E passes through the posterior margin of the mandible just in front of its union by ample arthrodial membrane with the head. The endoskeletal link between the interparagnath groove and the transverse plate uniting the paired longitudinal endoskeletal bars lies well behind the mandible. Muscles 3, 4, 5*a*, 5*b*, 5*c* and 6 are represented in *Paranaspides* (figures 7 to 9). The prefixes to muscle numbers 'adductor' and 'abductor' signify muscles causing direct movements in the transverse plane (type II movements, see § 3); 'remotor (adductor)' and 'promotor (abductor)' signify muscles primarily causing the remotor-promotor roll (type I movements) which facilitate the rolling together of the molar areas in *Chirocephalus*, or secondary transverse biting in derived crustacean types (figures 7–9, 11–13).

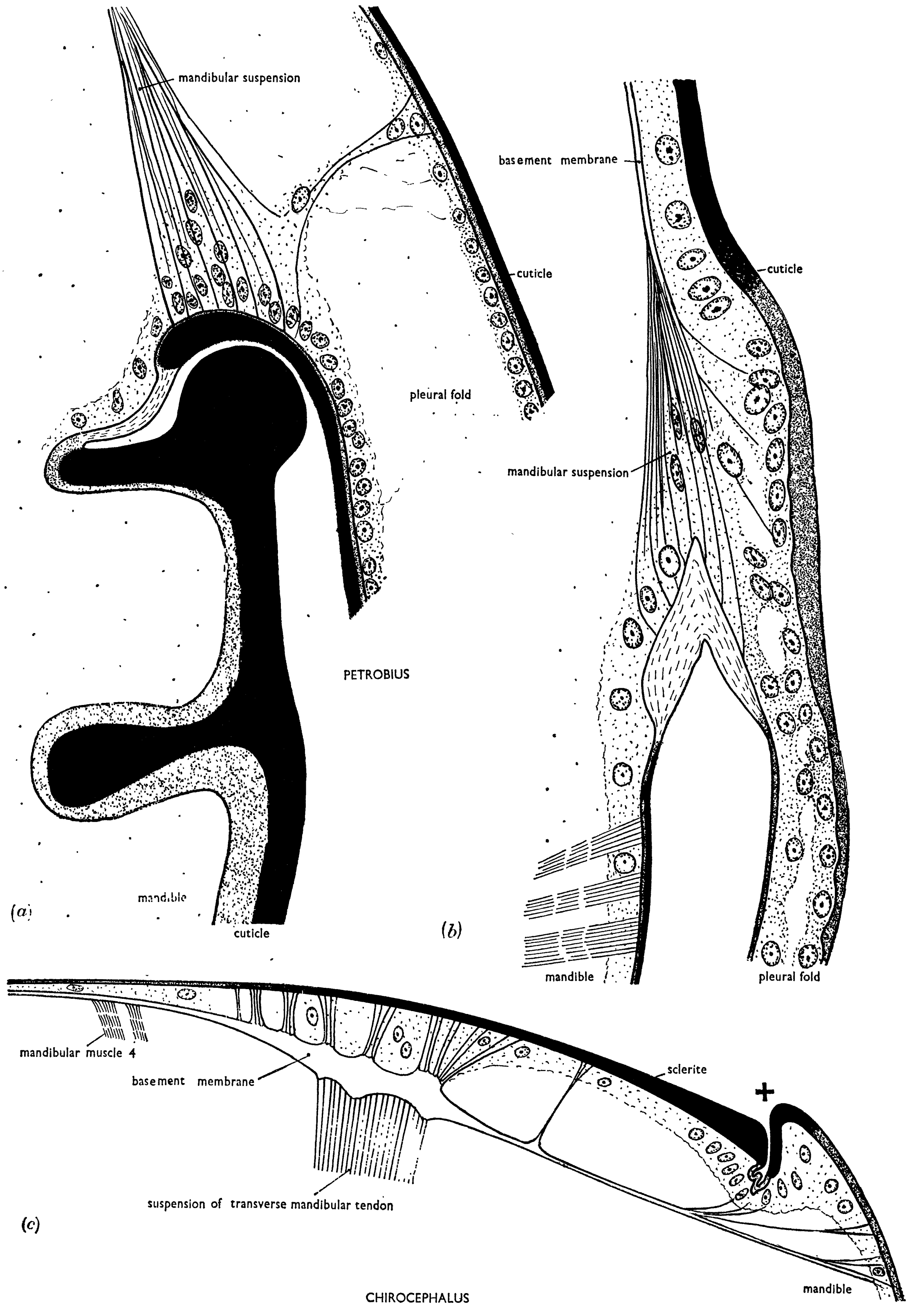


Figure 4. Transverse vertical sections showing the dorsal union of the mandible with the head in *Chirocephalus diaphanus*, *Hemimysis lamornae* and *Petrobius brevistylis*. Heavy sclerotized cuticle is shown in black, slighter sclerotization is indicated by grey tint, and arthrodial membranes by interrupted lines.

(*a*) Through the ball and socket joint of *Petrobius brevistylis* (see also figure 21). The ball is highly sclerotized, the inner layer of cuticle, staining blue with Mallory (grey here), becoming progressively thicker as distance from the ball increases. The socket is formed of thickened cuticle under the pleural fold, and is united by a stout fibrillar suspension to the dorsal wall of the cranium.

(*b*) Through the point of closest union of the head and mandible of *Hemimysis lamornae*, no articulation is present and the thick arthrodial membrane is united by a fibrillar suspension to the basement membrane of the side wall of the head.

(*c*) The dorsal articulation of the mandible of *Chirocephalus diaphanus*, formed between the sclerite of the cervical groove and the apex of the mandible, is often in the position shown, but the sclerite can project above the mandible, according to the position of the latter. The basement membrane is enlarged dorsally as shown.

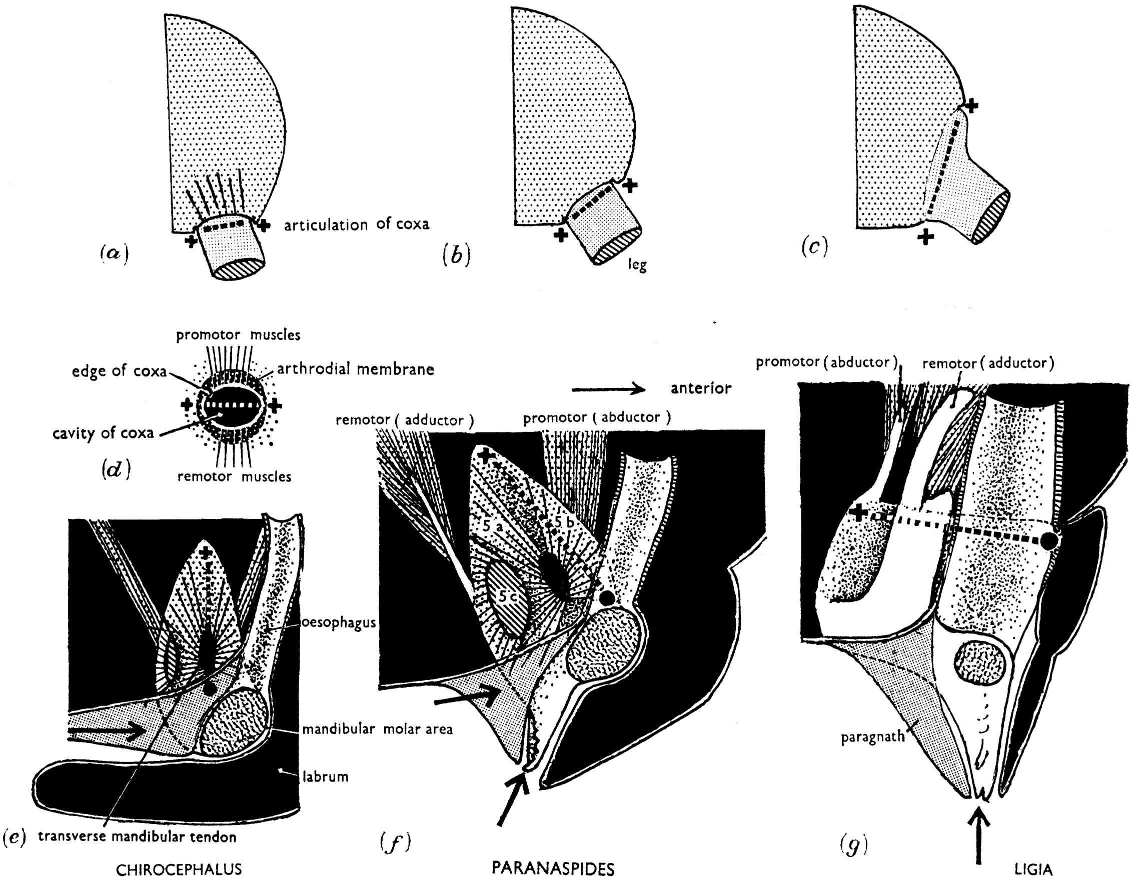


FIGURE 5. (*a*) to (*c*) Diagrammatic transverse views of half of the body of an arthropod to show the several positions of the axis of swing of the coxa on the body, dotted line between the crosses. In each case the axis lies in the transverse plane of the body, (*a*) as in Crustacea and Diplopoda, (*b*) as in Symphyla, (*c*) as in Chilopoda.

(*d*) Represents an end-on view of a typical coxa-body joint, the axis of swing being marked as in (*a*) to (*c*). This axis passes through the points where the arthrodial membrane (white stipple) between coxa and body is shortest (see Manton 1958*b*).

(*e*) to (*g*). Diagrammatic views of sagittal halves of the heads of *Chirocephalus diaphanus*, *Paranaspides lacustris* and *Ligia oceanica* to show the positions of the axis of the mandibular roll which is indicated by the interrupted line between the dorsal union of the mandible and cranium (marked by a cross) and the black spot; the positions of the molar areas and incisor processes with respect to this axis; and the routes to the mouth of fine food (upper arrows) and of large food (lower arrows). The direct transverse mandibular muscle 5*c* and the transverse mandibular tendon are cut. Promotor and remotor (abductor and adductor) muscles are homologous in the three animals, muscles 3 and 4 both possess apodemes in *Ligia* and a posterior remotor (adductor) apodeme is present in *Paranaspides*. Further details are shown in figures 1 to 3, 7 and 8, 10 and 11.

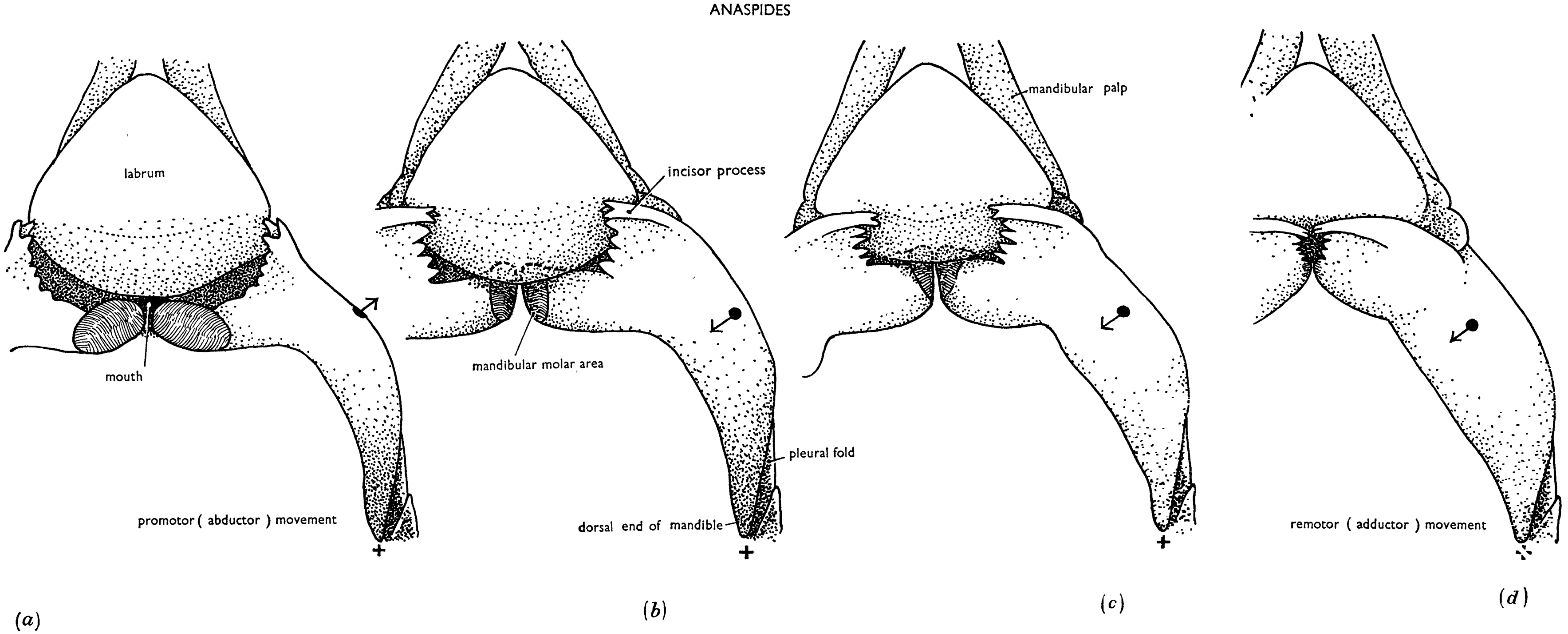


FIGURE 6. Ventral view of the mandibles of *Anaspides tasmaniae* Thomson to show the extreme range of movements about the axis of roll (see figures 5*f*, 7) which are possible to the animal. The dorsal end of the mandible and its point of closest union with the head lie far below the plane of the paper. The black spot bearing an arrow marks the same spot on the mandible in all figures. (*a*) Shows the extreme end of the forward (promotor) movement, rather more extreme than is usual in normal feeding, (*b*) to (*d*) show the progressive backward (remotor) roll which brings the incisor processes together in the transverse plane, moving along a hollow in the labrum.

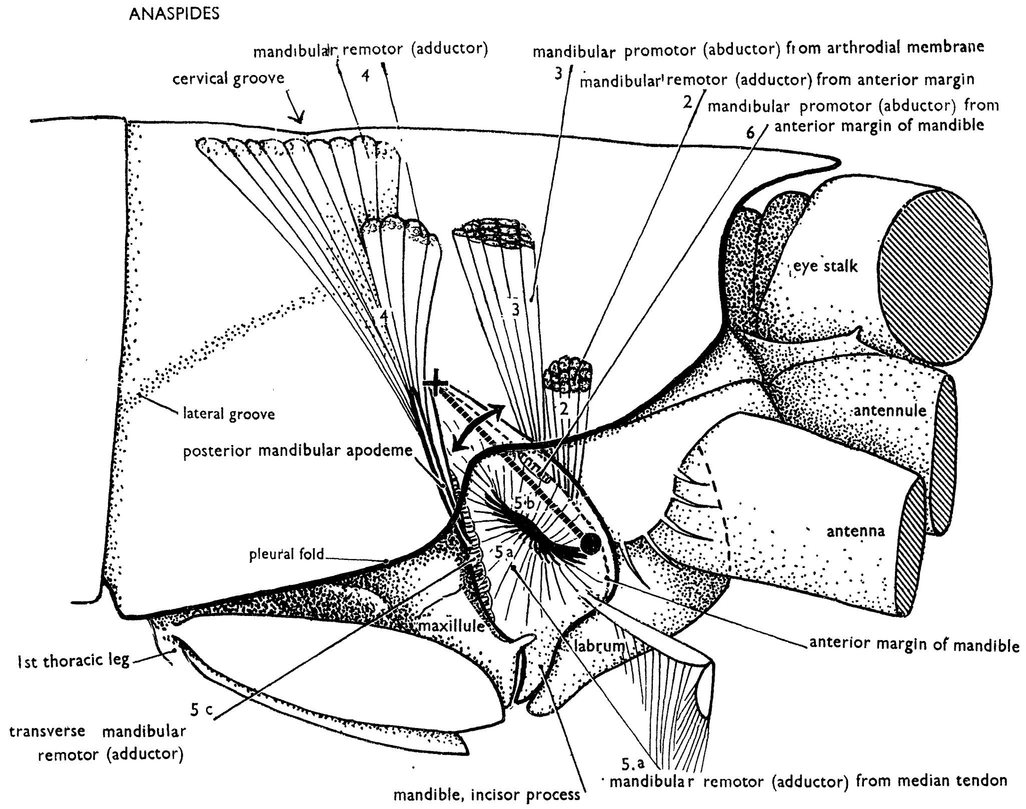


FIGURE 7. Lateral view of the head of *Anaspides tasmaniae* Thomson to show the positions of mandibular muscles and the direction of the principal mandibular movements. The cross indicates the close dorsal union of the mandible and head under the shallow pleural fold whose free margin is shown by a heavy line. The dotted line between the cross and black spot marks the axis of the rolling movement. The lightly dotted line shows the anterior margin of the mandible on to which muscles 3 and 6 pull. The posterior margin of the mandible gives origin to the hollow apodeme bearing dorso-lateral muscle 4, and from the posterior edge and posterior part of the mandibular face arises transverse muscle 5*c*. Muscle 3 and part of muscle 6 arise from arthrodial membrane near the mandibular edge. The lateral part of the transverse mandibular tendon is shown in black, from it muscles 5*a* and 5*b* pass outwards and backwards and outwards and forwards respectively to the concavity of the mandibular cuticle.

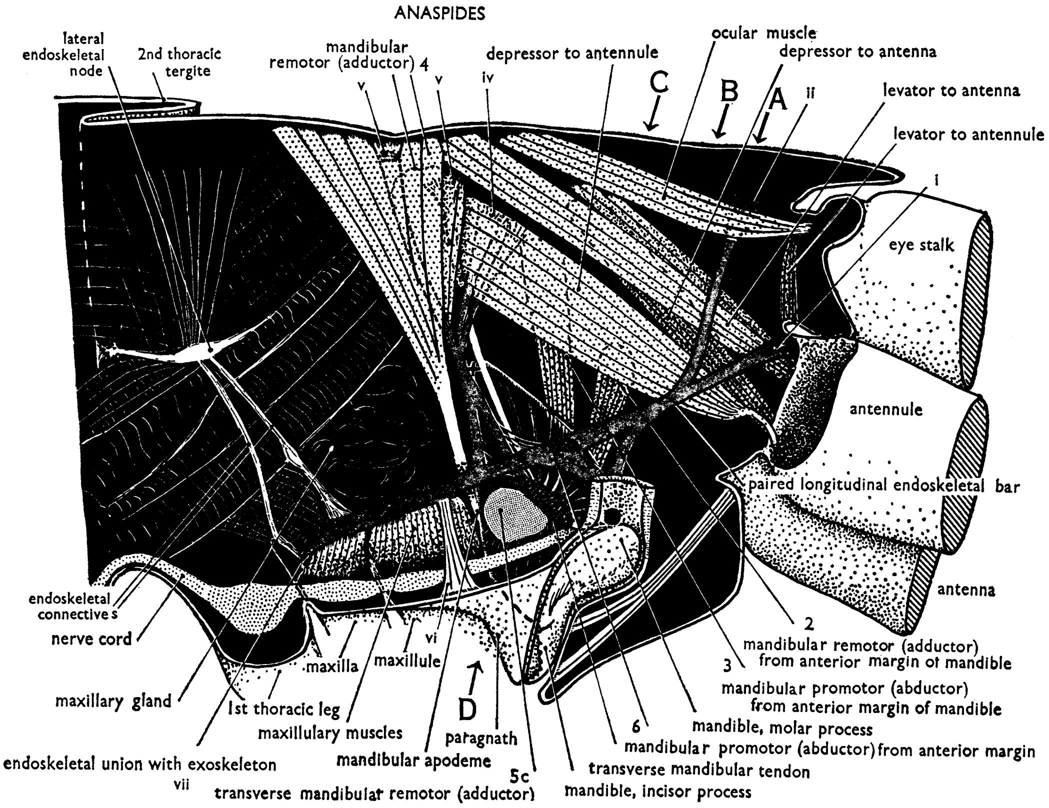


FIGURE 8. Sagittal half of the head of *Anaspides tasmaniae* Thomson with the alimentary canal and digestive gland removed to display the cephalic endoskeleton and mandibular musculature. The posterior mandibular apodeme is shown in white, and the transverse segmental tendons and their connectives are blue, the median endoskeletal bridges cut in the sagittal plane are hatched. The positions of the mandibular margins and of the axis of movement between the dorsal union with the head (a cross) and the black spot are indicated. The web of fibrous connexions between the transverse mandibular tendon, the lateral longitudinal tendinous bars and the three dorsolateral struts is more complex than shown. The levels A to D mark the planes of sections shown in figure 9. For further descriptions see text.

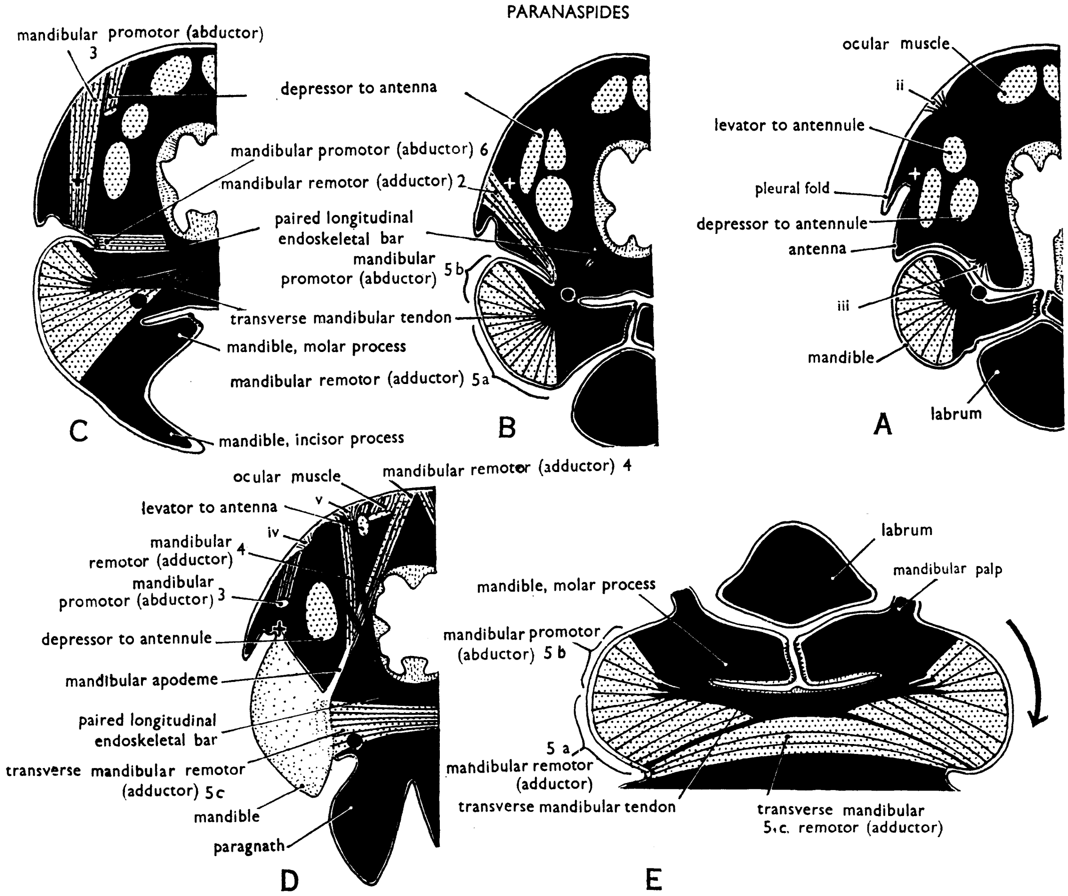


FIGURE 9. *Paranaspides lacustris* Smith. Thick diagrammatic transverse sections of the head at the levels indicated on figure 8 at A to D, to show the mandibular muscles and cephalic endoskeleton. The position of the axis of movement passing from the dorsal union of the mandible and head, marked by a cross in D, to the black spot in A is projected on to the other figures which show only part of the obliquely situated mandible. The designations (adductor) and (abductor) to the muscles shown is made in the sense described in the text; it does not signify a basic adduction and abduction in the transverse plane, but a remotor-promotor roll.

Level A shows the cuticular unions ii and iii of the paired longitudinal tendinous bars, iii being close to the oral angle braced by the termination of the transverse mandibular tendon shown in level B.

Level B shows the lateral longitudinal tendinous bar; the anterior dorso-lateral mandibular remotor (adductor) 2; and the anterior extension of the transverse mandibular tendon.

Level C shows the transverse mandibular tendon bearing remotor (adductor) and promotor (abductor) fibres (see labelling on level B); the transverse union of the paired longitudinal endoskeletal bars at the level where they bear abductor 6 (see the unlabelled dotted outline of the origin of muscle 6 in figure 8); and promotor (abductor) 3 arising mainly from the arthrodial membrane below the carapace fold. Level D shows the longitudinal endoskeletal bar and its tendinous suspensions iv and v; the hollow posterior mandibular apodeme with its dorso-lateral remotor (adductor) 4; and the transverse mandibular remotor (adductor) 5*c* lying behind and independent from the mandibular tendon.

Level E. Oblique horizontal section just below the mouth to show the mandibles and their molar processes at the end of the remotor roll; the transverse mandibular tendon, which supports the lower end of the axis of movement (black spot); and the transverse muscles.

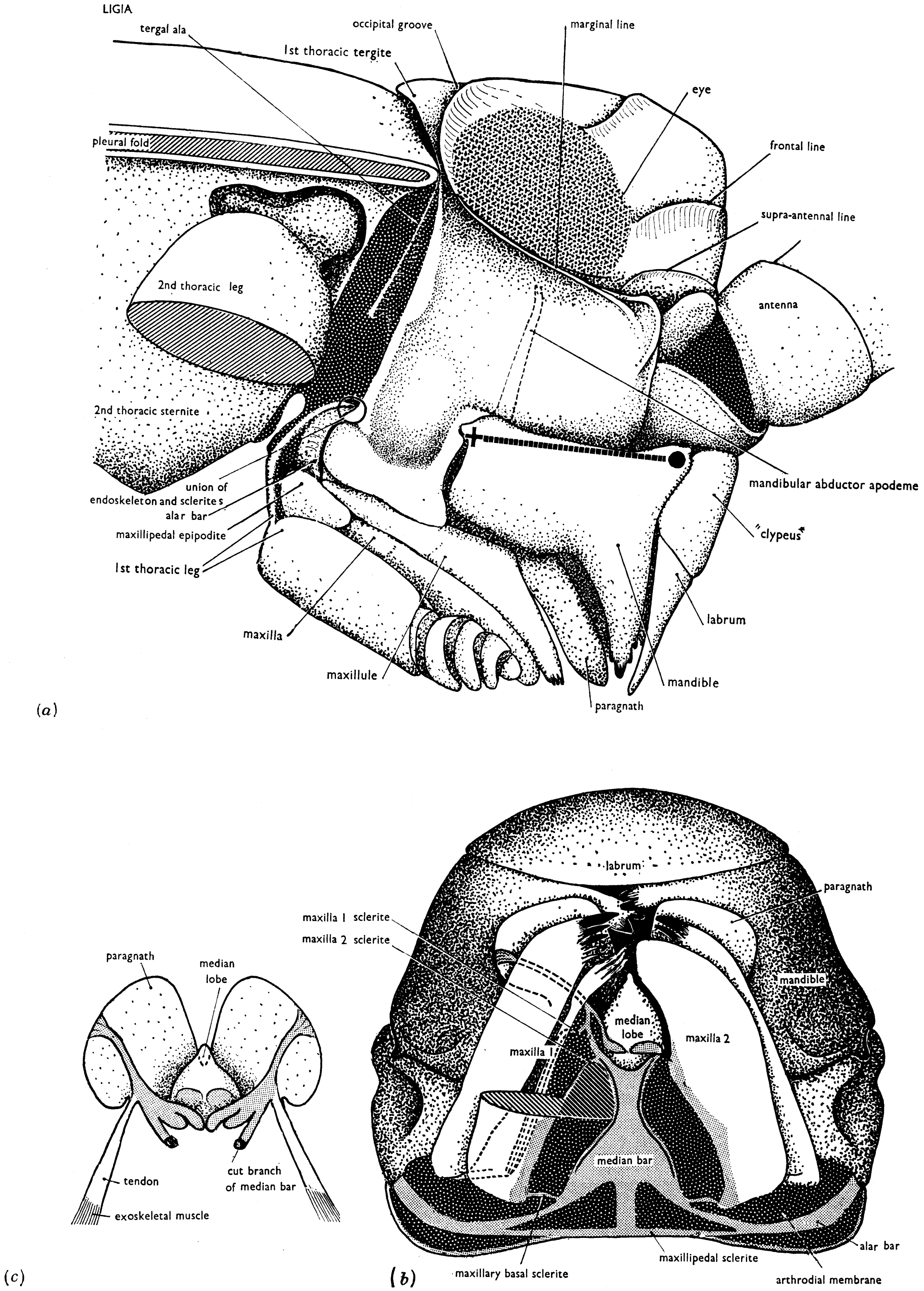


FIGURE 10. For legend see facing page.

FIGURE 10. *Ligia oceanica* Roux (*a*) Lateral view of the head with the pleural plate and leg of the second thoracic segment cut short. The heavy dotted line marks the axis of movement of the mandible, passing through the same morphological points marked by a cross and black spot as shown for *Chirocephalus* and *Anaspides* in figures 1, 3, 5, 7 and 9. Arthrodial membrane is indicated by white stipple on black. The 'tergal ala' apodeme of the head is visible through the arthrodial membrane passing to the second thoracic segment, here stretched a little. The notch, marked by a small circle, carries a cuticular thickening suspending: the maxillipedal sclerite, the alar bar of the superficial sclerite system of the head wall and the inferior lateral pterygoid process which forms one arm of the base of the 'sternal ala', a principal head apodeme; see figure 11.

(*b*) Ventral view of the head with the maxillipeds cut away from the maxillipedal sclerite and the animal's right maxilla 2 partly removed, in order to show the superficial sclerite system (maxillo-sternal framework of Jackson (1926)) which is finely stippled, the mouth parts and the median lobe. Arthrodial membrane (white stipple) separates the sclerites. Maxilla 2 sclerite almost encircles the base of maxilla 2. Butting on to the maxillary basal sclerite the mesial margin of the stiff part of maxilla 2 is strongly sclerotized forming an un-named rib along this edge. The median lobe is compressed a little on the animal's right in order to show the sclerite system.

(*c*) Posterior view of the median lobe and paragnaths as shown by a transverse slice through the head passing behind the paragnaths and cutting through the paired branches of the median bar (cut ends hatched), (compare with figures 11 and 12*a*).

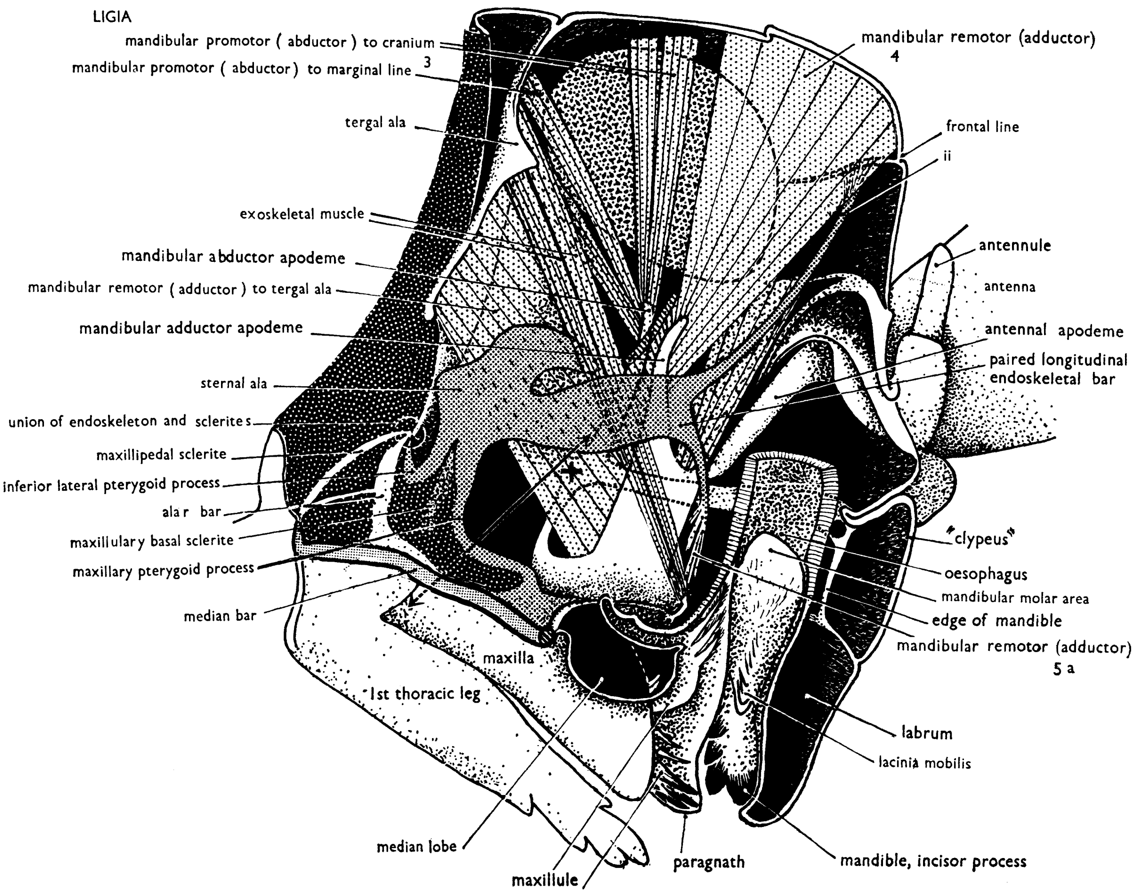


FIGURE 11. *Ligia oceanica* Roux. Sagittal view of left half of the head to show the longitudinal apodemal endoskeleton (red), the mandible and mandibular muscles. The mandibular cuticle is drawn alone in figure 12*b* from the same aspect. The cut through the ventral cuticle of the head passes along the 'median bar', a superficial scute, and one arm is shown of its anterior bifurcation which ends on the paragnath; the cut end of the other arm is hatched. The antennal muscles passing to the genal fossa region of the cranium (between the circle and cross in figure 10) are removed; they pass between the mandibular adductor and abductor muscles. The extrinsic muscles of the maxillule and maxilla to the tergal ala and sternal ala (see dotted arrow) and the maxillipedal muscles to the maxillipedal sclerite and alar bar are also omitted. The mandibular hinge on the head lies between the cross and black spot. The broad mandibular adductor apodeme leaves the parasagittal edge of the mandible and passes directly upwards (see figure 12*a*). The narrow posterior mandibular abductor apodeme leaves the antero-dorsal edge of the mandible close above the hinge and passes outwards and upwards (see left side of figure 12*a*). The mandibular remotor (adductor) muscle forms three main sectors, a posterior sheet passes from the proximal posterior edge of the apodeme upwards and backwards to the tergal ala; the most bulky sector fans out from the apex of the apodeme to the whole dorsal and antero-dorsal face of the cranium above the 'frontal line' (half of it is cut away to expose the abductor muscles); and an anterior sector arises from a tuft of fibres half way along the anterior edge of the apodeme and inserts on and around the 'supra-antennal line' (see figure 10) of the cranium. The mandibular promotor (abductor) comprises 4 sectors: two pass to the dorsal cranial wall just median to the eye; one passes to the 'marginal line' (see figure 10) behind the eye; and another to the anterior face of the tergal ala. The principal head apodeme the 'sternal ala' is shown in red. It arises from a maxilla 1–2 intucking (white stipple) bearing the inferior lateral pterygoid process and the maxillary pterygoid process in its outer and inner angles respectively. The maxillulary basal sclerite is attached laterally to the maxillary pterygoid process and can be seen through the membranous part of the apodemal intucking. The circle marks the union of the superficial scutes with the inferior lateral pterygoid process, a point also supported by the end of the tergal ala. Setae of maxilla 2 are drawn as if the median lobe was transparent.

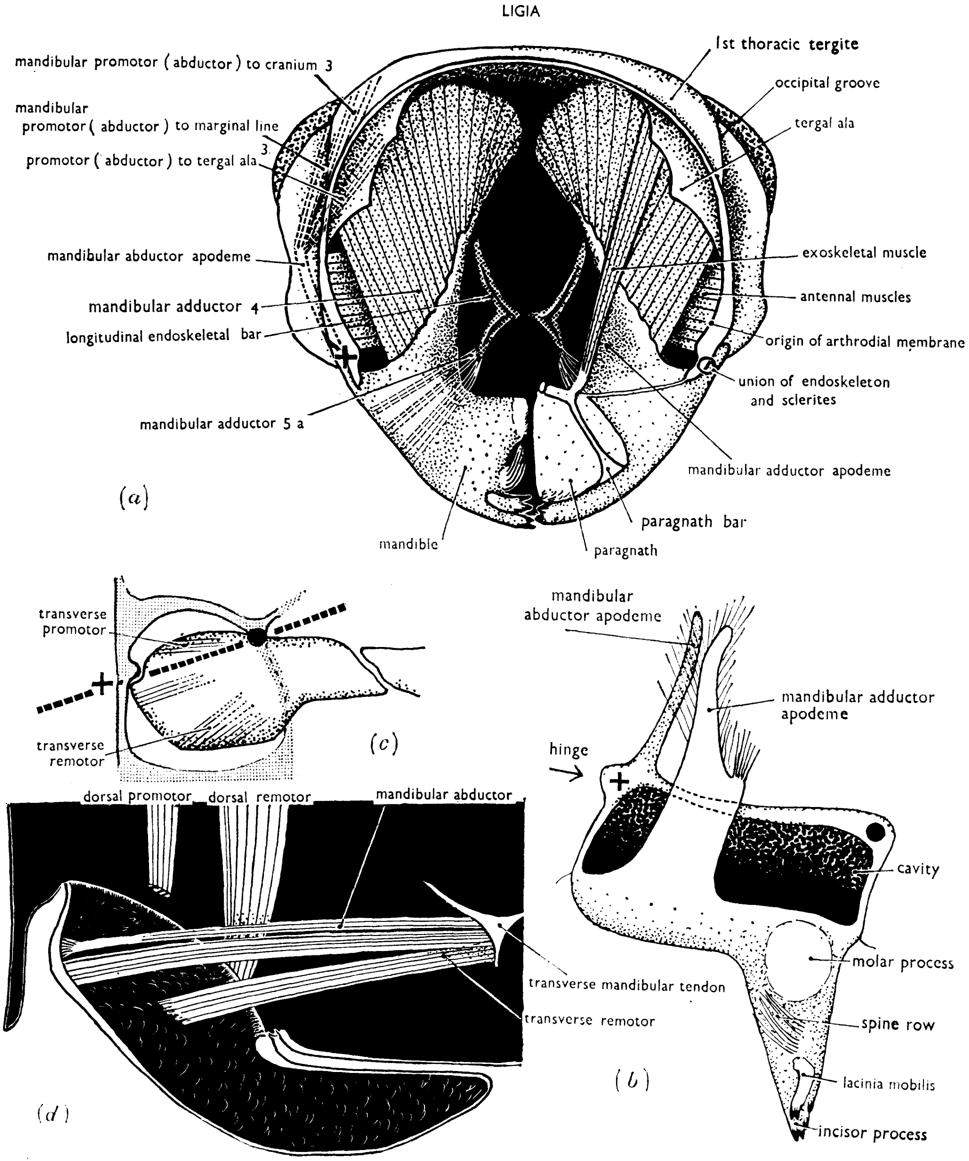


Figure 12. (*a*) Posterior view of the head of *Ligia oceanica* Roux, intact dorsally and laterally as far as the notch surrounded by the circle, marked as in figures 10 and 11. Ventrally the mouth parts are removed leaving the left mandible and the right paragnath and mandible. The principal head apodeme, the sternal ala, is cut and shown in red, and its process bears the small remains of mandibular remotor (adductor) 5*a* (cf. figures 7, 9).

(*b*) Sagittal view of the mandibular cuticle of *Ligia oceanica* devoid of muscles seen from the same aspect as in figure 11.

(*c*) *Calanus finmarchicus* Gunner, ventral view of right mandible. The interrupted line marks the axis of roll, the easiest movement elicited by micro-manipulation of a cuticle preparation devoid of muscles. The cross marks the loose lateral articulation with the head and the black spot the region of close hinge-like union with a transverse sclerite of the head. One arm of this sclerite curves posteriorly to form the inner margin of the mandibular socket.

(*d*) Diagrammatic thick transverse section through the right mandible of *C. finmarchicus* viewed from in front. The cut lies just behind the lateral articulation and through two of the three transverse muscle fibres (probably abductor) arising in this position (see (*c*)). The anterior (promotor) transverse fibres are cut away with the anterior part of the mandible and the origin of the dorsal promotor muscles, and the larger posterior (remotor) transverse muscle fibres are shown arising from the posterior shoulder of the mandible (see (*c*)). More anteriorly the transverse mandibular tendon is wider, the dorsal suspensory arms are cut. For further consideration see p. 98.

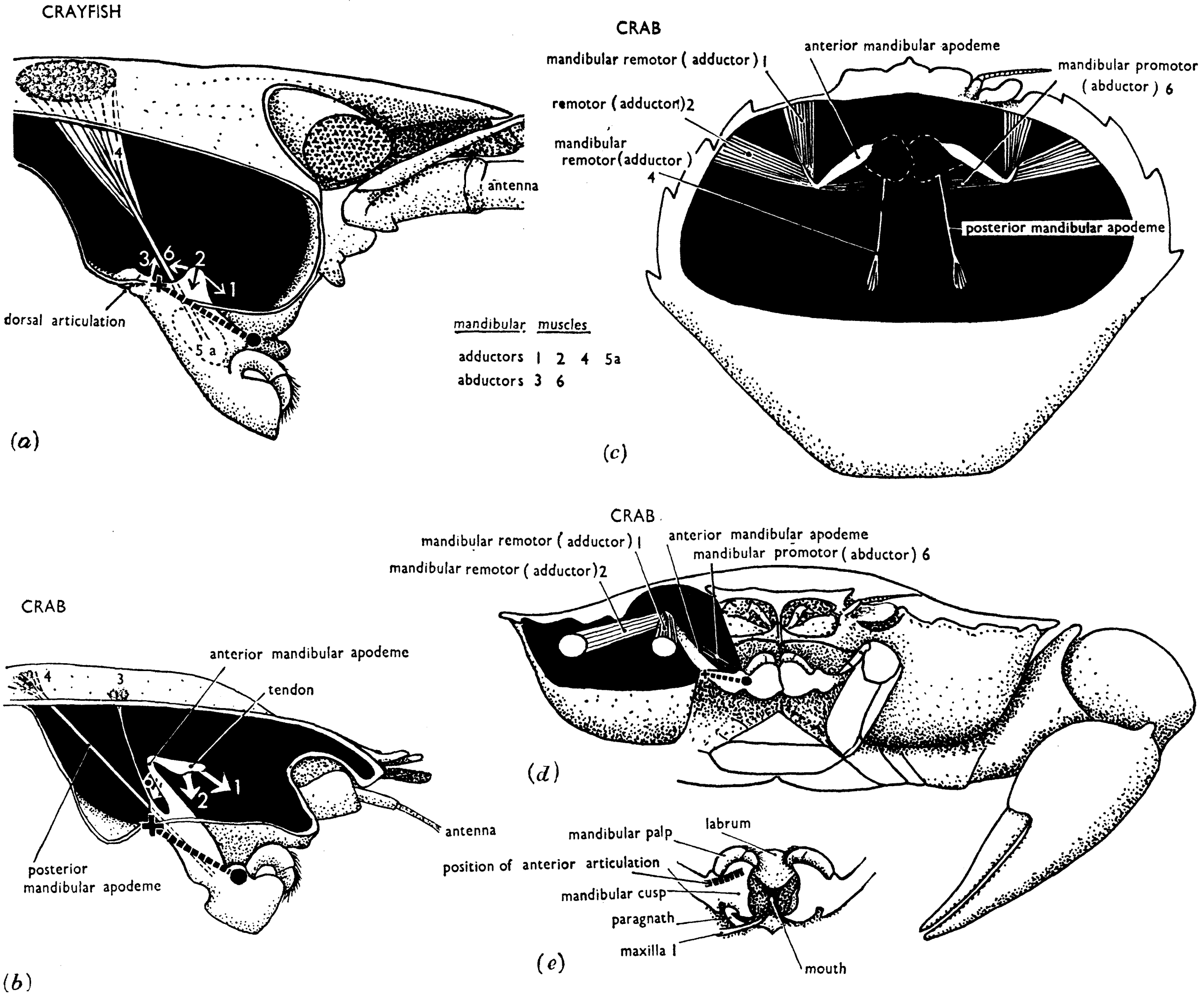


FIGURE 13. Diagrams showing the mandibles and their movements (*a*) in the crayfish *Astacus flaviatilis* (*Potamobius astacus* L.) and (*b*) to (*e*) in the shore crab *Carcinus maenas* (L.) for comparison with *Chirocephalus*, *Anaspides* and *Ligia*. The direction of pull of muscles 1–6 are shown by arrows in (*a*) and (*b*). For further details of the muscles see Schmidt (1915) for *Astacus* and Pearson (1908) for *Cancer*. (*a*) and (*b*) Lateral views of the right mandible of crayfish and crab with the head cut back; a tendon passes forwards from the apodeme to muscles 1 and 2 in the crab. (*c*) Dorsal view of the crab to show anterior and posterior mandibular apodemes and their muscles, the position of the gnathal lobe being shown by white dotted lines. (*d*) Anterior view of the crab with the head cut back to show the anterior mandibular apodeme and its muscles together with the anterior articulation of the mandible with the head. The mandible and its muscles are foreshortened in both (*b*) and (*d*). (*e*) Ventral view of mouth region of the crab with the mandibles fully open disclosing the labrum between the mandibular palps.

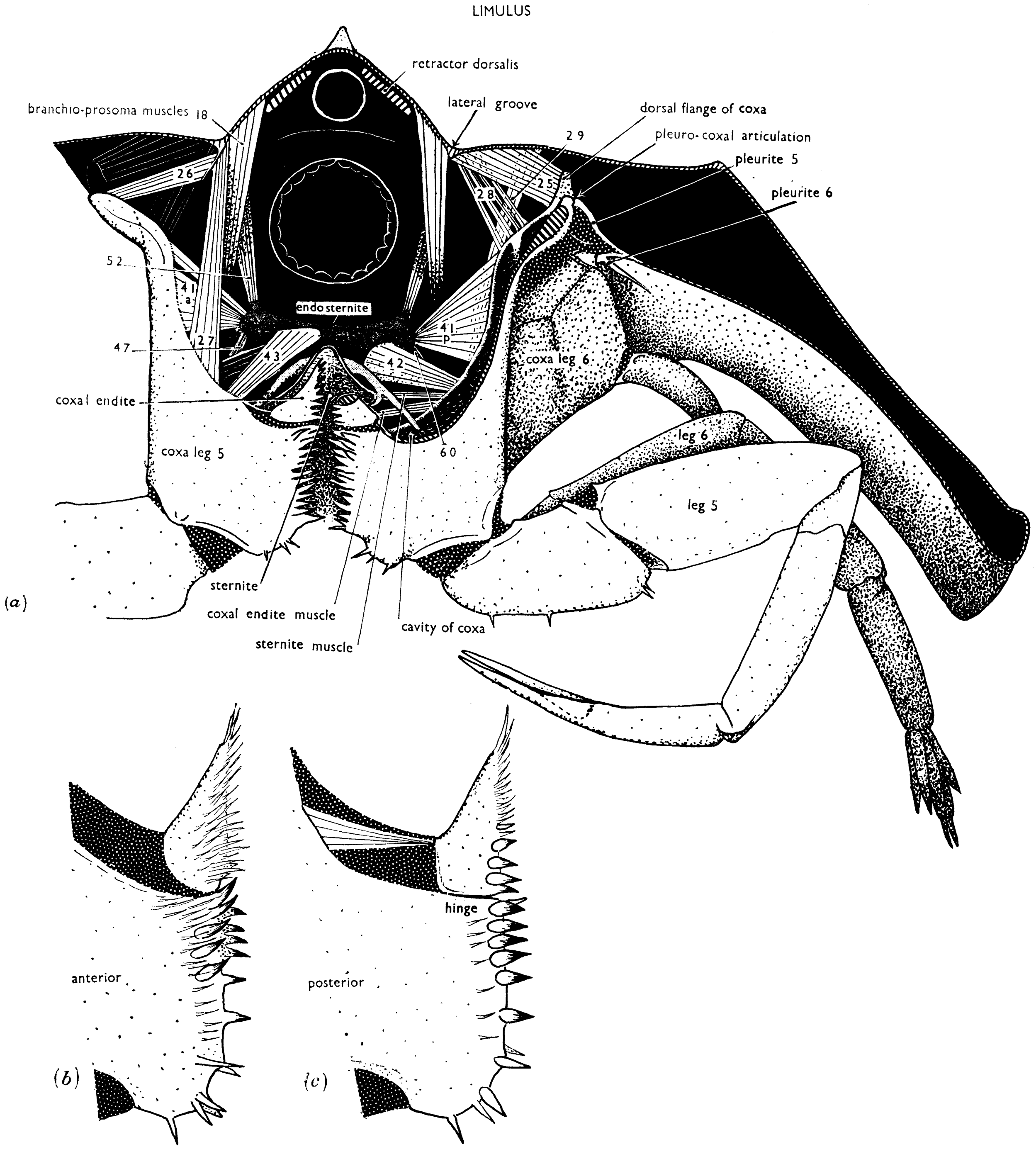


FIGURE 14. (*a*) The prosoma of *Tachypleus tridentatus* Leach cut transversely in front of legs 5 and viewed from in front to show the extrinsic limb muscles. The digestive gland is omitted; portions of the heart, pericardial floor and intestine are indicated but unlabelled; pedal nerves are stippled and arthrodial membranes are shown by white dots. Ventrally the anterior end of the sternite is passing upwards towards the oesophagus (see figure 16). The endosternite (blue) is cut transversely, its ventral surface and that of the ventral (pleural) surface of the carapace are foreshortened. Muscle numbers are those of Benham (Lankester, Benham & Beck 1885). Muscles 52 attach the dorsal cornua of the endosternite to the carapace and 18 comprise the branchio-thoracic muscles which pass forwards from the branchial limbs to the prosomal carapace.

The coxa of leg 5 is entire on the left and on the right it is cut away as far as its articulation with the pleurite, disclosing the 'dorsal flange' (marked) which is covered by a fold of arthrodial membrane (see figure 17*a*). On the right one limb of the Y-shaped pleurite, with which leg 5

(*Continued on p.* 130)

articulates, and the entire pleurite articulating with leg 6, are shown. The extrinsic muscles attached to the anterior thickened rim of the coxa are indicated in white on the left, some of the more posterior muscles being indicated in black. The extrinsic muscles attached to the posterior thickened rim of the coxa are shown on the right where the anterior rim and its muscles are cut away. The coxal endite is cut short on the right to show the sternite.

(*b*) Anterior view of the mesial part of the gnathobase of leg 5 to show the heavy spines (with black tips) and the endite set in ample arthrodial membrane which allows the proximal rim of the endite to tip into the rest of the gnathobase on forward flexure of the endite (see figure 16*b*).

(*c*) Posterior view of the same to show the straight hinge between the endite and the rest of the gnathobase and the muscle extending from the endite to the posterior rim of the coxa. Contraction of this muscle returns the endite into line with the rest of the gnathobase after the endite has been pushed forwards by adductor movements of the coxa which press the endite against food or against the roof of the food basin (see also figure 16*b*).

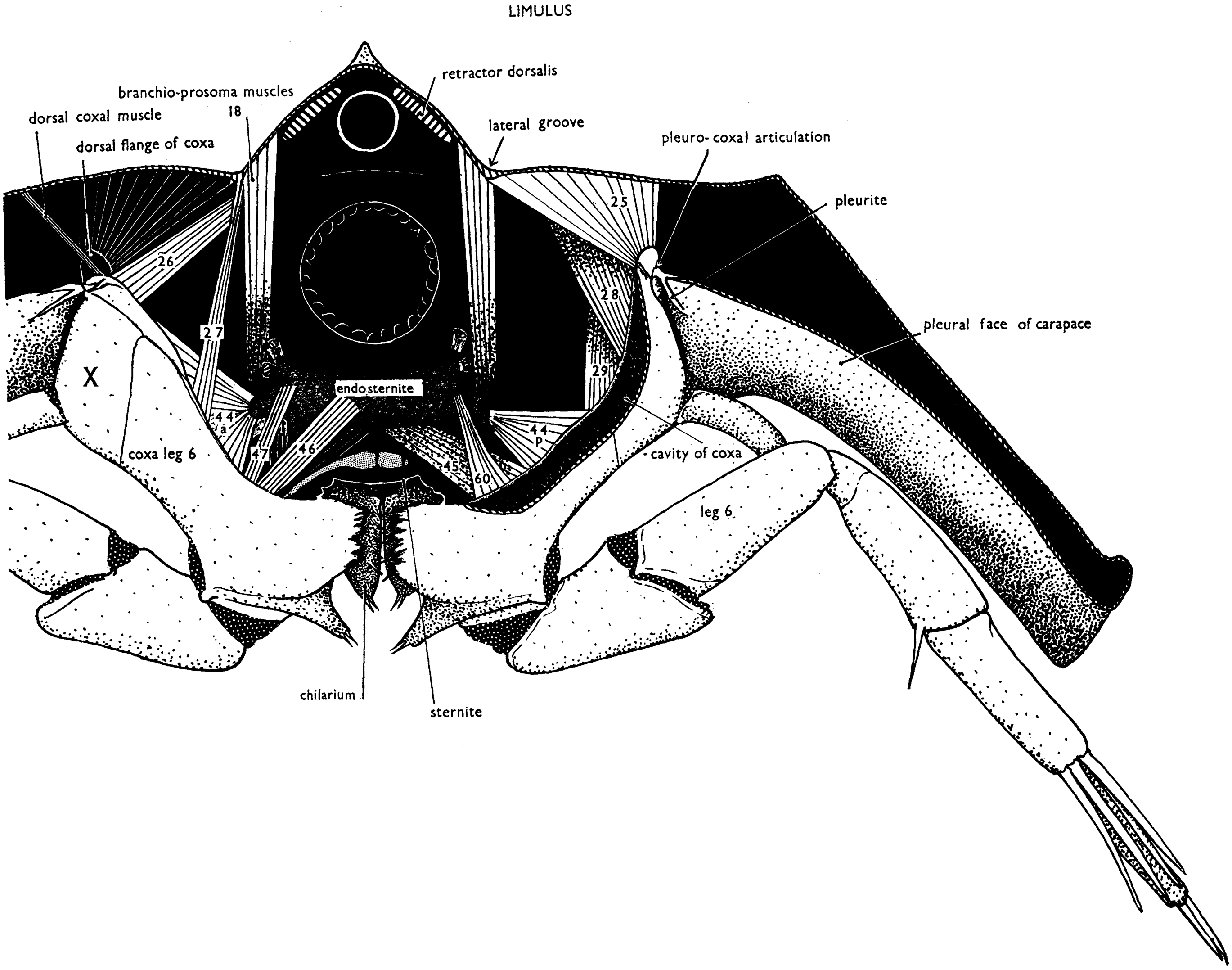


Figure 15. The prosoma of *Tachypleus tridentatus* Leach cut transversely as in figure 14 but the 5th limb pair and its muscles are cut away, the bases of muscles 52 and 41 (unlabelled, see figure 14) remaining on the endosternite (blue) which expands posteriorly to form the posterior cornua bearing muscles 44*a* and 44*p*. The thickened anterior coxal rim of leg 6, with its muscles, are shown on the left and are cut away on the right to disclose the muscles attached to the posterior rim of the coxa. Muscles 46 and 60 arise from the endosternite anterior to leg 6 and pass backwards to the anterior and posterior margins of coxa 6 (see figure 17*b*). Muscle 29 passes backwards from coxa 6 to insert laterally near the posterior margin of the carapace. A small muscle, marked dorsal coxal muscle, passes from the antero-dorsal margin of the coxa outwards and upwards to the carapace. It is not present on leg 5. The muscles 18 from the branchial limbs are shown in part. The area '*X*' marked on the coxa is similarly marked in the 5th and 6th coxae in figure 17*a* and *b* and has been claimed to be part of a precoxal segment (see text).

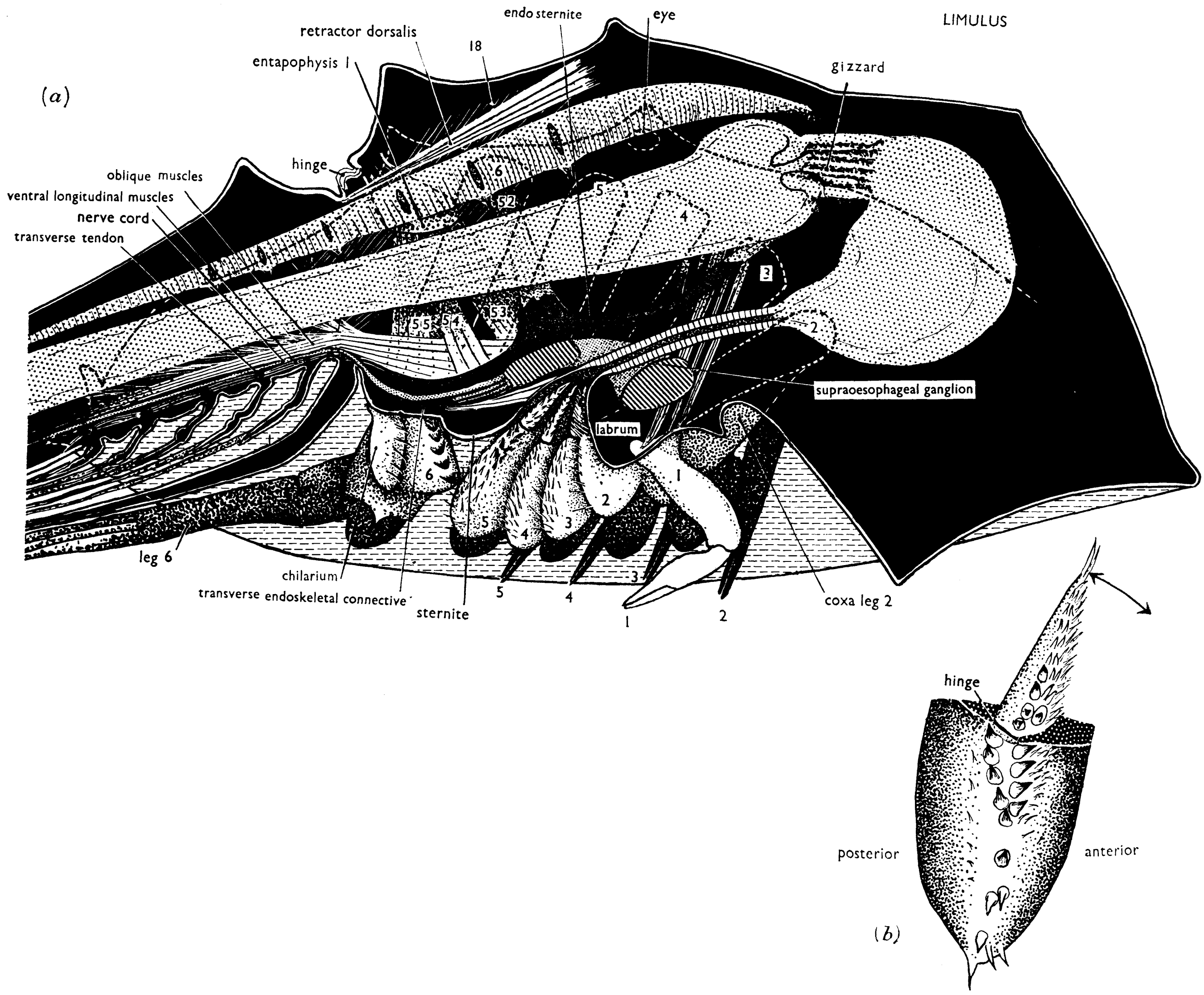


Figure 16. (*a*) Sagittal half of the prosoma of *Tachypleus tridentatus* Leach to show the form and positions of the gnathobases, the mouth and the endoskeleton with its attachments. The lateral prosomal ridge and the postero-lateral margin of the carapace are shown by a dotted line. Muscle numbers are those used by Benham (Lankester, Benham & Beck 1885). The heart, oesophagus, proventriculus and intestine are not labelled. Numbers 2 to 6 mark the gnathobases of legs 2 to 6; the movable coxal endites of legs 3 to 5, which are directed towards the mouth, are not labelled. The positions of the coxal margins of legs 2 to 6, which are attached by arthrodial membrane to the flanks of the animal, are indicated by dotted lines and marked 2 to 6. The anterior face of coxa 2 is visible lateral to leg 1. The supra- and suboesophageal ganglia are cut. The cut endosternite and its foreshortened dorsal face are shown in blue, the anterior cornu and two lateral cornua are attached by muscles (now shown) to the antero-lateral part of the carapace, the dorsal cornu is attached by muscle 52 to the carapace and by muscles 53 from the base of the dorsal cornu and muscles 54 and 55 from the dorsal face of the endosternite pass to entapophysis 1. A small 'transverse endoskeletal connective' lies below the nerve cord above the gnathobase of leg 6; this skeletal bridge is united laterally with the endosternite and carries a muscle to the anterior part of the sternite as shown (the occipital ring of Patten & Redenbaugh). The oblique and ventral longitudinal muscles are shown diagrammatically (for details see Benham (Lankester, Benham & Beck 1885, pl. 74–5, figs. 1–3) and Patten & Redenbaugh (1900, pl. 8, fig. 4)). Two large

(*Continued on p.* 132)

superimposed 'oblique muscles' comparable with oblique trunk muscles of other arthropods (see Manton 1961, and future publications), pass from the posterior dorsal face of the endosternite and branch to entapophyses 3 to 7 of the opisthosomal dorsal shield; these apodemes are not drawn but they lie in line with entapophysis 1, and arise from the opisthosomal cuticle on either side of the mid-dorsal line. These muscles are the dorsal and ventral entapophysio-plastral muscles of Benham, and they form part of the longitudinal abdominal muscles of Patten & Redenbaugh. The ventral longitudinal muscles form two series: one arising from the dorsal face of the endosternite and sending branches to (i) transverse segmental tendons 2 to 6 in the opisthosoma (the mesosomatic entochondrites of Benham, which also bear the muscles to the branchial limbs), and to (ii) entapophyses 4 to 7, and the muscle ends on the opisthosomal sternite; and the other forms a series of fibres linking one transverse tendon with the next and also ends on the opisthosomal sternite. The dorsal longitudinal 'retractor dorsalis' muscles comprise the large submedian arthro-tergal muscles of Benham, but in *L. longispinus* this muscle arises from the anterior border of the opisthosomal dorsal shield and passes forwards to the prosomal carapace. The series of muscles which extend from entapophysis 1 to entapophyses 2 to 5 as a fan of almost parallel strands (not drawn) are probably comparable with the lateral longitudinal or paratergal muscles of other arthropods. Muscles 18 extend from the branchial limbs to the prosomal carapace (see also figures 14 and 15). Three extrinsic cheliceral muscles insert on the carapace; the largest and most posterior is the flexor and the most anterior is the extensor.

(*b*) View of the gnathobase of leg 5 from the sagittal plane to show the free anterior and tight posterior union of the endite with the stiff cuticle of the rest of the gnathobase, and the range of movement of the endite in the parasagittal plane (see also figures 14*b*, *c*).

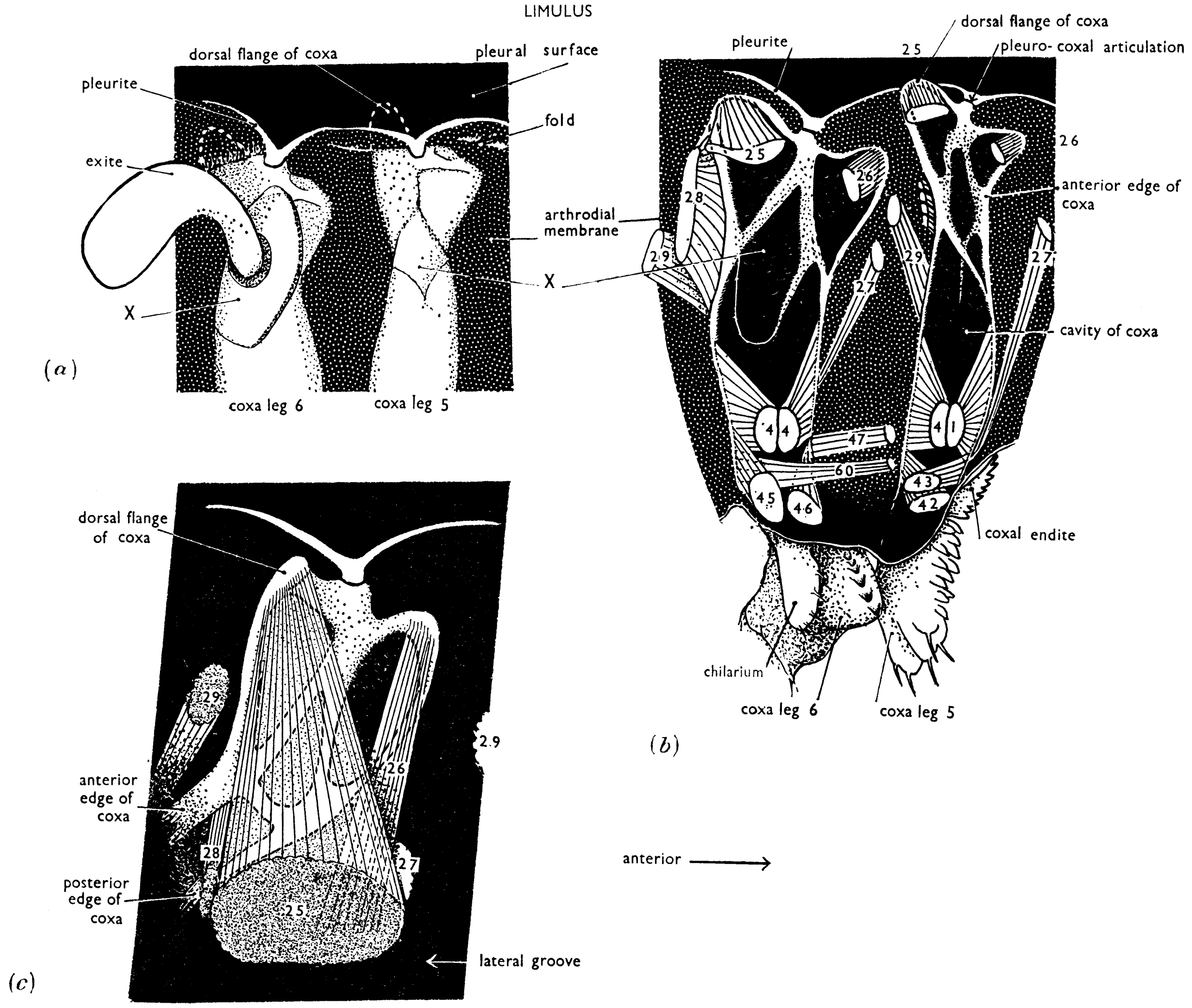


Figure 17. (*a*) Lateral external view of the dorsal ends of the coxae of legs 5 and 6 of *Tachypleus tridentatus* Leach to show their articulations with the Y-shaped pleurites lying at the junction of the under surface of the carapace and the pleural arthrodial membrane. A fold of this membrane covers the intucked dorsal flange of each coxa.

(*b*) Internal view from the sagittal plane of the coxae of legs 5 and 6 after removal of the viscera and endosternite. The cuticular thickenings forming the coxal rims and internal ridges are shown in white.

(*c*) Dorsal view of the upper end of left coxa 5 to show the size of muscles 25 to 29 and the position of their carapace insertions. Muscle 27 is attached to a tendinous sheet projecting below muscle 25 from the lateral groove of the carapace (see figure 14, left side). The dorsal flange of the coxa is foreshortened, and the anterior and posterior coxal margins slope downwards and to the left because the proximal rim of the coxa does not lie in the exact transverse plane (see figure 16 dotted outline of the base of the coxa of leg 5).

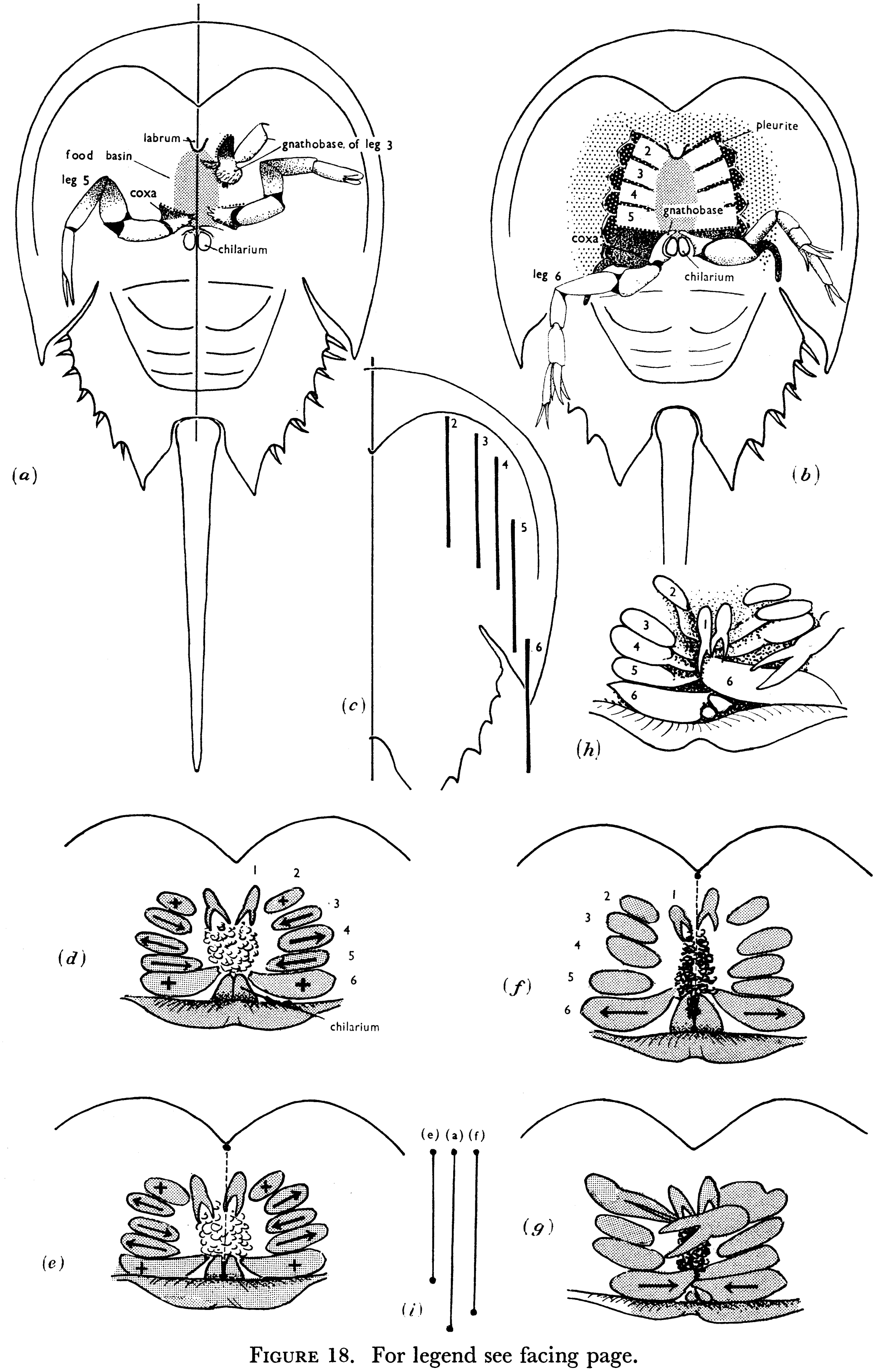


FIGURE 18. For legend see facing page.

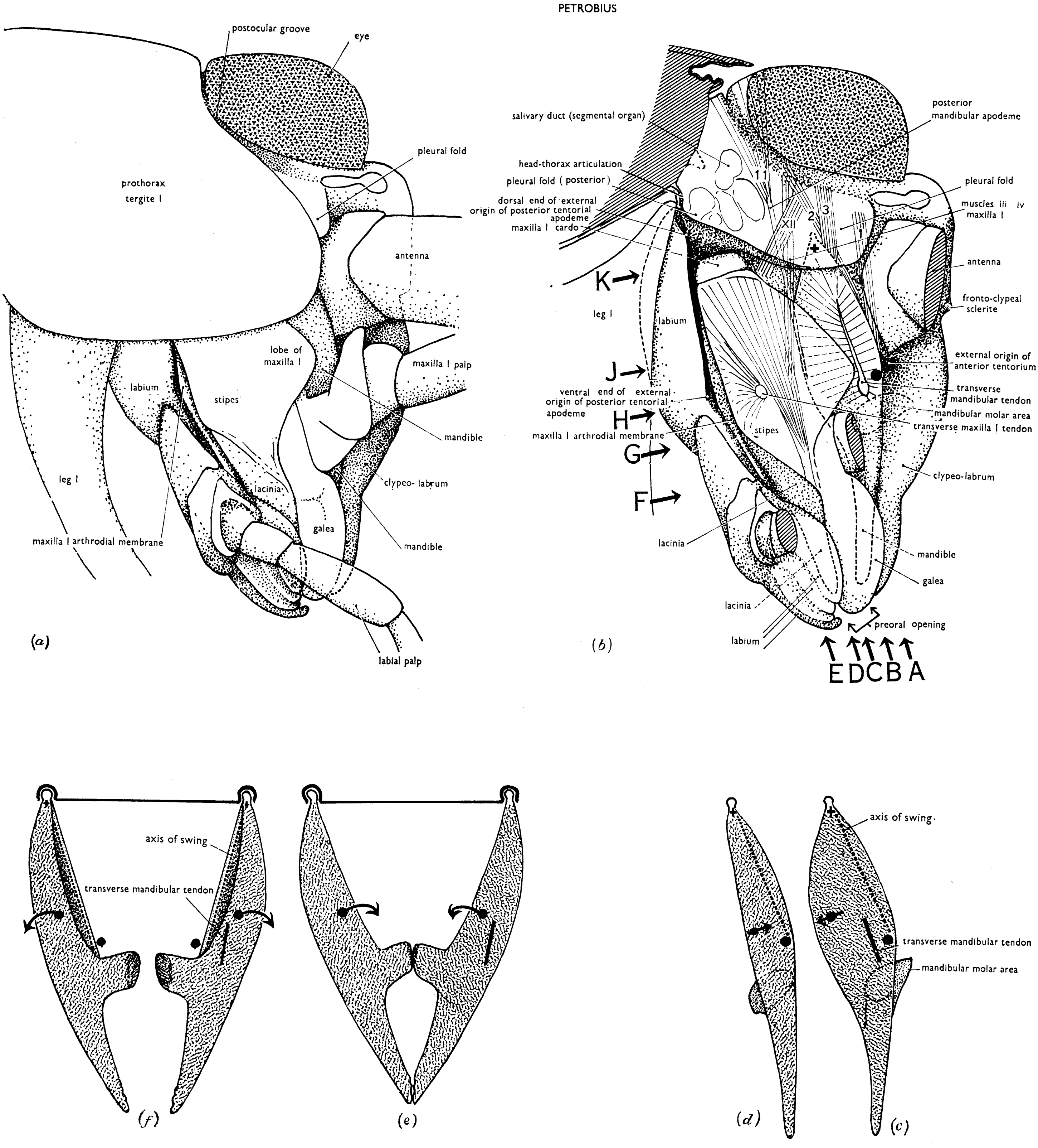
FIGURE 18. Diagrammatic views of the ventral aspect of living *Limulus polyphemus* L. The food basin between labrum, chilaria and the gnathobases of prosomal legs 2 to 6 is finely stippled. The flexible part of the ventral cuticle is coarsely stippled and arthrodial membrane below the pleurites and between the diagrammatic leg bases of (*b*) is stippled in white. The data concerning leg positions is derived from photographs taken through the bottom of a glass tank during normal walking (see figures 68 and 69, plate 1). The legs of a pair normally move in the same phase; prosomal legs 5 and 6 are shown at the extreme forward and backward positions on opposite sides of the same diagrams in (*a*) and (*b*). The extreme abduction of the gnathobases delimits the food basin.

(*a*) Left side shows the animal's right leg 5 at the end of the backstroke. The gnathobasal spines reach the middle line; the right side shows the animal's left leg 5 at the end of the forward stroke, the gnathobasal spines are turned a little forwards and outwards. The gnathobase of left leg 3 is shown in a position of extreme abduction; during feeding, the point marked by a spot can be adducted to the middle line. The proximal endite of leg 3 is directed mesially but not forward, adduction of the gnathobases of legs 3 turns the endites more forwards.

(*b*) The opposite positions of leg 6 are shown as for leg 5 on (*a*); the gnathobases do not alter their positions of adduction during the promotor and remotor swing of the leg.

(*c*) The heavy lines show the fields of movement of the limb tips on the ground during the backstroke, relative to the body.

(*d*) to (*h*) Tracings of frames from a cinematograph film of *Limulus polyphemus* showing feeding movements in ventral view. The animal and the camera were fixed so that all measurements are comparable. The outlines of: the trochanter of prosomal legs 2 to 5, of the distal part of the chelicerae and of the trochanter and gnathobase of prosomal legs 6 are shown, the rest of the legs being omitted. In all figures the genital operculum is raised (promoted) so that it is seen end on (cf. figures 68 and 69, plate 1). (*d*) and (*e*) show the eating of soft food (*Mytilus* mantle), the limbs in (*d*) being in opposite phase to those in (*e*), and legs 2 and 6 are stationary (marked by a cross). The chilaria are forwardly directed, keeping food opposite the chewing gnathobases of prosomal legs 3 to 5, which rhythmically adduct and abduct in the direction of the arrows. Adduction and abduction are of about equal duration and the phase difference between successive pairs of legs is 0·5 of a cycle. (*f*) and (*g*) show the eating of harder food (foot of *Mytilus*). The 6th prosomal coxae execute strong transverse biting; extreme abduction is shown in (*f*), and adduction in (*g*) where the chilaria swing back to a vertical position. The terminal chelae of many legs assist in manipulating the food in the food basin. (*h*) Shows the end of strong adduction of the 6th prosomal coxae followed by a forward heave of the left 6th coxa so that its teeth are level with the gnathobase of leg 3 as it pushed the stiff food forward. (i) The lines show the distances between the ventral skeletal 'V' of the carapace and the base of the chilaria in (*e*), (*a*) and (*f*), the scales being the same for all. These distances are marked by a dotted line in (*e*) and (*f*). For further description see text.



PROMOTOR ABDUCTOR MOVEMENT REMOTOR ADDUCTOR MOVEMENT PROMOTOR ABDUCTOR MOVEMENT REMOTOR ADDUCTOR MOVEMENT

FIGURE 19. *Petrobius brevistylis* Carpenter. (*a*) Side view of the entire head. (*b*) Side view of the head with the prothoracic tergite cut away to expose the pleural fold of the head, the dorsal ends of the mouth parts and the position of the external openings of the anterior and posterior tentorial apodemes. The arrows show the levels of transverse sections A to E and frontal sections F to K shown in figures 21 to 24. (*c*, *d*) Diagrammatic lateral views of mandible at the end of the remotor and promotor swing about the axis of movement. (*e*, *f*) Diagrammatic transverse views from behind of a pair of mandibles at the end of the remotor and promotor swing about the axis of movement. For further descriptions see text.

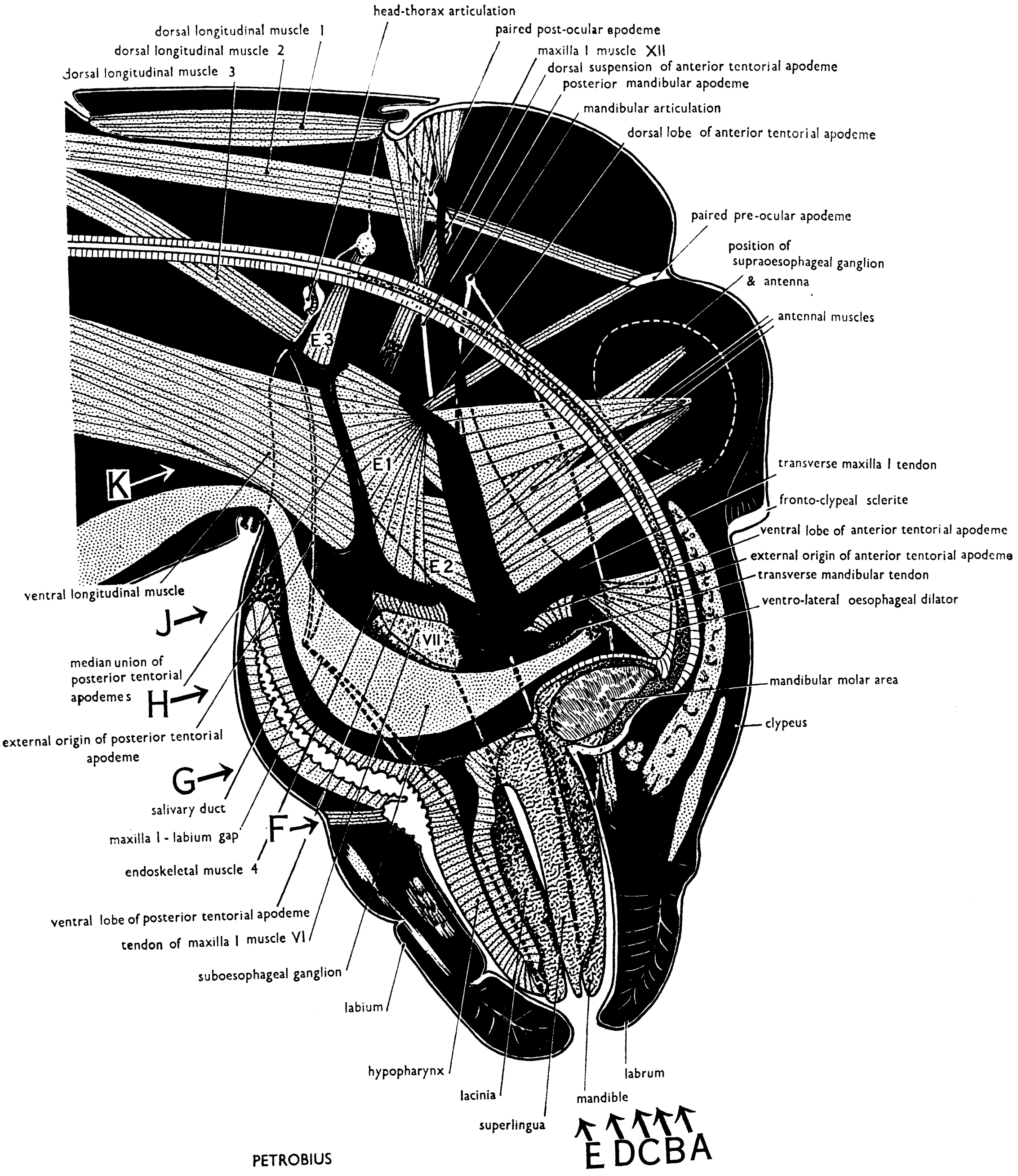


Figure 20. Sagittal half of the head of *Petrobius brevistylis* Carpenter. The suboesophageal ganglion and circumoesophageal commissures are in position but the cerebral ganglion has been removed to display the antennal muscles, the ganglion outline in this view is superimposed on the base of the antenna marked by a dotted line. The edge of the whole mandible is shown as if the head was transparent; only the distal part of maxilla 1 is marked by dotted lines. The median bridge formed by the union of the posterior tentorial apodemes is cut, its cavity passes anteriorly into the paired ventral lobes and the long slit-like external opening is shown by dotted lines at the maxilla 1-labium intersegment. Endoskeletal muscles E1 to E3 are shown and maxilla 1 muscle VII is marked, no distinction being shown between muscles VI and VII, see figure 22E. Clypeo-labral muscles are only roughly indicated. The arrows show the positions of transverse sections A to E and frontal sections F to K in figures 21 to 24. The three sectors of the dorsal longitudinal muscles are drawn but the ventral longitudinal muscle is more complex than shown. The lateral parts of the labium, labrum and the galea, which neatly close in the sides of the mouth part cone, are omitted in order to indicate the boundaries between the structures shown, which are closely packed together. For further description see text.

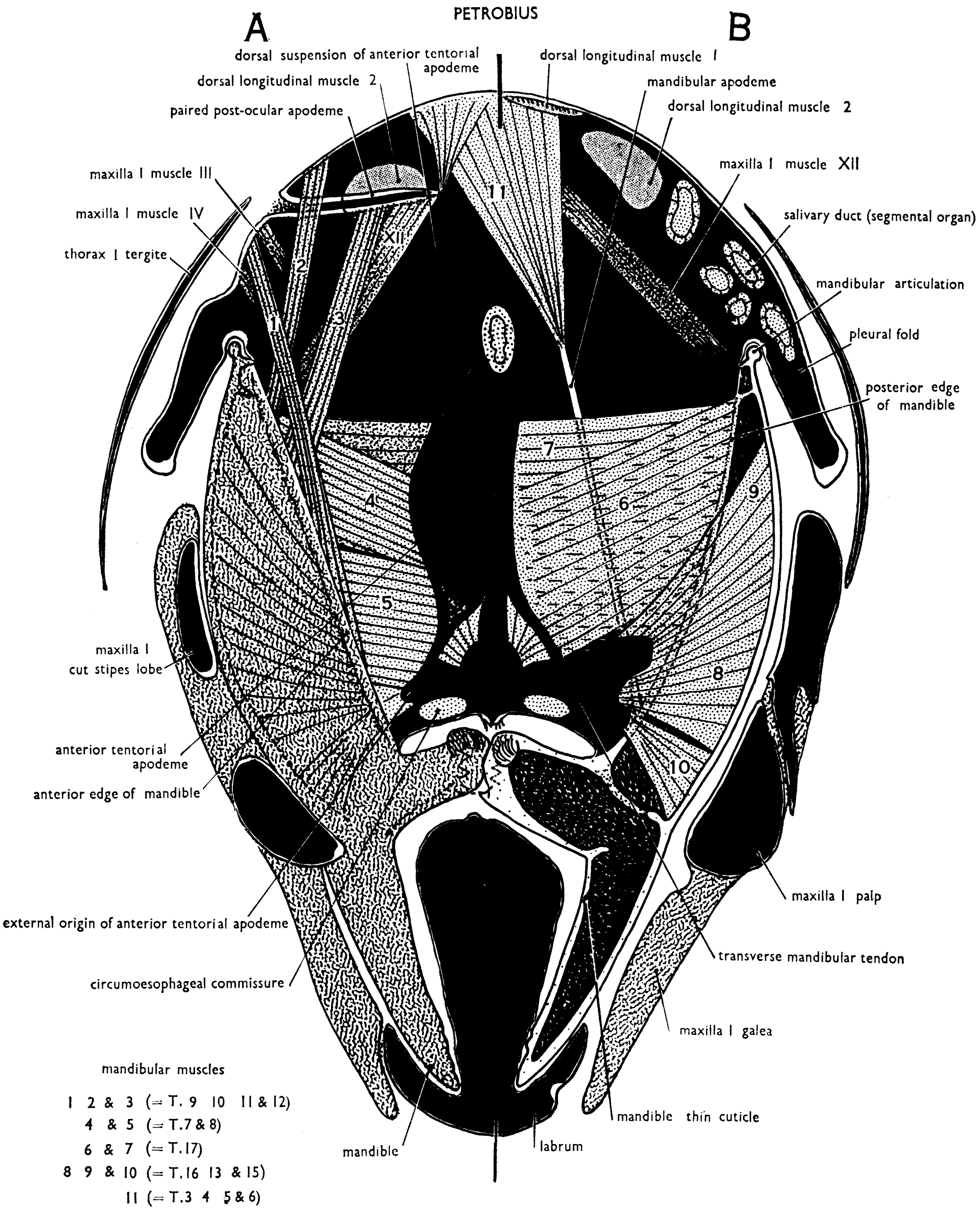


FIGURE 21. Transverse view from in front of the head of *Petrobius brevistylis* at the levels indicated in figures 19 and 20 to show the mandible, endoskeleton, muscles and general anatomy. The anterior face of the mandibular cuticle is seen in level A and a section through the mandible in level B. The insertion of sector 1 of the dorsal longitudinal muscle lies posterior to mandibular muscle 11 (see figure 20). The insertion of sector 2 of the dorsal longitudinal muscle on to the postocular apodeme is shown in A. A larger scale diagram of the dorsal mandibular articulation is given in figure 4*a*; the cusps on the molar lobe lie across its posterior edge (see figure 20). The suggested homologies between the mandibular muscles of *Petrobius* and *Tomocerus* are listed below on the left, the muscle numbers of *Tomocerus* being given in brackets (see figures 32 to 40). The dorsal end of promotor muscle XII to the maxilla 1 cardo is shown, the rest of the muscle being drawn in figure 22C (see also figure 19*b*).

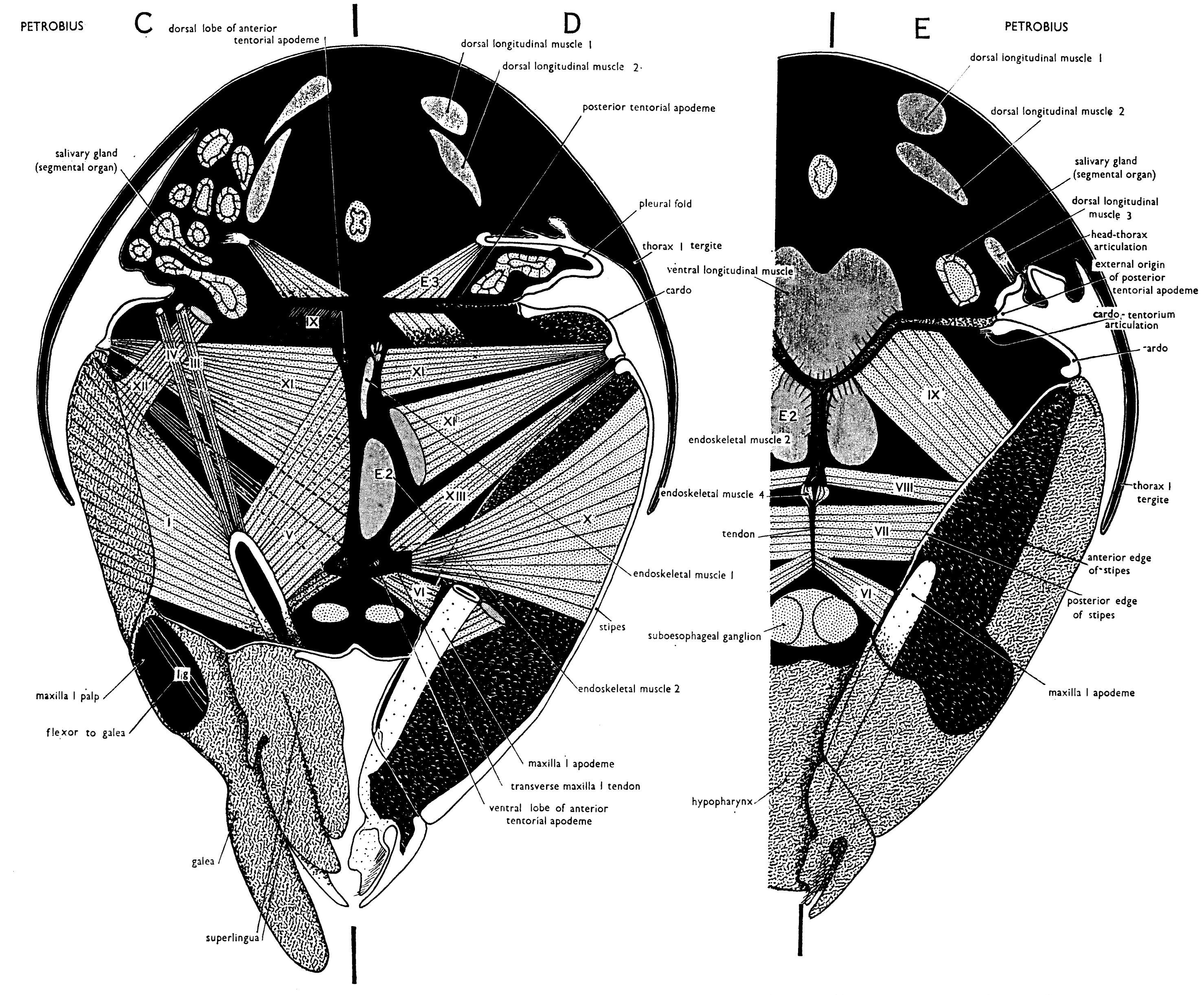


FIGURE 22. Transverse views from in front of the head of *Petrobius brevistylis* at the levels shown by the arrows C, D and E in figures 19 and 20 to show the maxilla 1 and its muscles, the anterior and posterior tentorial apodemes and transverse maxilla 1 tendon. The cuticle on the anterior face of the maxilla 1 stipes is seen in C and a section through the stipes and cardo in D, in E the whole anterior stipes cuticle above and below the palp base is intact but the muscles in the stipes cavity are omitted in order to show the muscles extending from the posterior rim of the stipes (see also figures 24H and J which show the antero-posterior thickness of these muscles). The shape of the cut posterior tentorium in E is due to the curvature of the transverse bridge (see figure 20); the ventral lobes pass forwards from the small ventral bifurcation seen here. Muscle E.3 from the posterior tentorial bridge inserts on the most anterior part of the prothoracic section of the head-thorax articulation. The union of the circumoesophageal commissures with the suboesophageal ganglion is indicated.

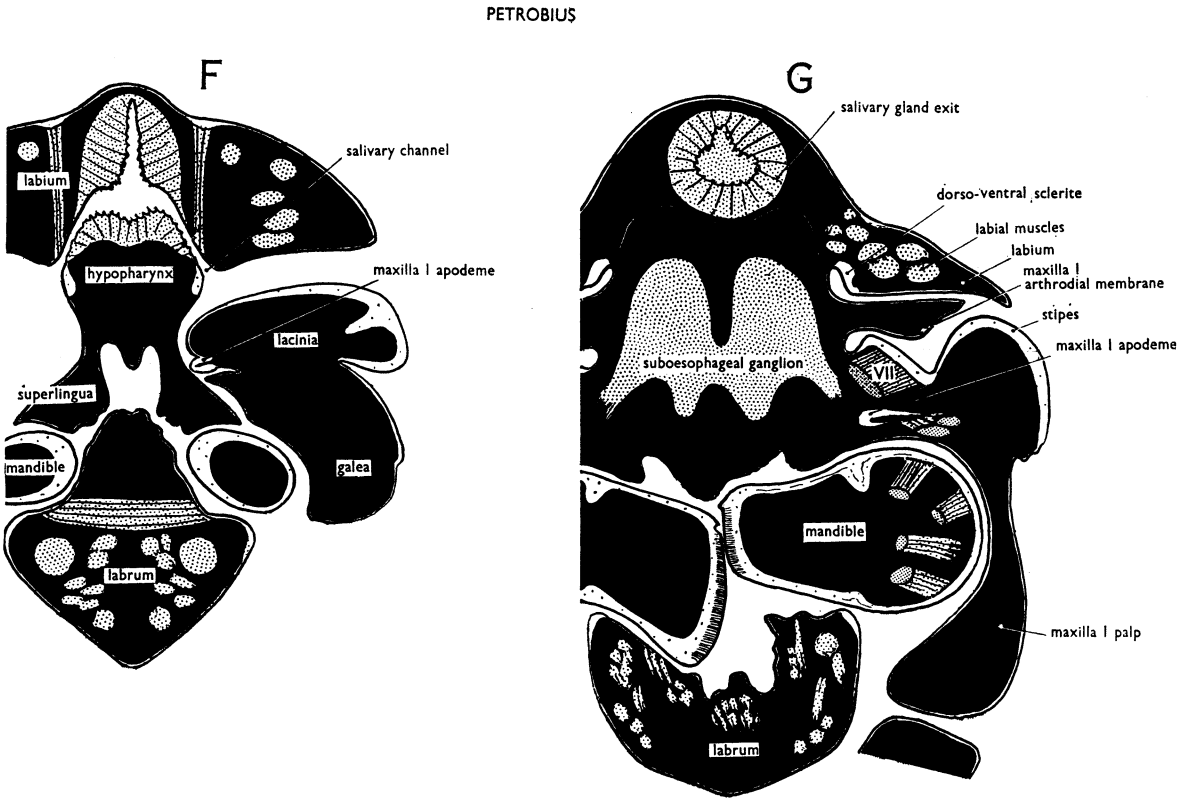


FIGURE 23

FIGURES 23 and 24. Dorsal views of frontal sections through the head of *Petrobius brevistylis* at the levels given by the arrows F to K in figures 19 and 20, to show the general anatomy. Mandibular muscles are marked by Arabic numerals and maxilla 1 muscles by Roman numerals.

Level F shows the food channel, not labelled, between the hypopharynx, superlinguae and labrum, the enclosed mandibular spike below the molar lobe, the origin of the lacinia apodeme and the salivary exit channels from the median part of the salivary duct.

Level G shows the molar lobes of the mandibles projecting into the preoral cavity (see figure 20), the lacinia (maxilla 1) apodeme is now internal, and the maxilla 1 palp embraces the mandible.

Level H shows the origin of the anterior tentorial apodemes, also the transverse mandibular and maxilla 1 tendons and the limb musculature. The maxilla 1 arthrodial membrane behind the stipes is folded in front of the labium and bears muscles VII and another muscle, unlabelled, from the labium.

Level J shows the relationship of the lobes from the anterior and posterior tentorial apodemes, the muscles E 1 and E 2 between them, and the mandibular and maxilla 1 muscles.

Level K shows the dorsal part of the posterior tentorial bridge and muscle XI, which depresses the cardo and so protracts and abducts stipes and lacinia. The positions of the dorsal suspension and dorsal lobe of the anterior tentorial apodeme and of the posterior mandibular apodeme are shown in relation to other structures, unlabelled. Muscles from both dorsal lobes of the anterior tentorial apodemes pass to the preocular apodeme on each side (see also figure 20, unlabelled muscle).

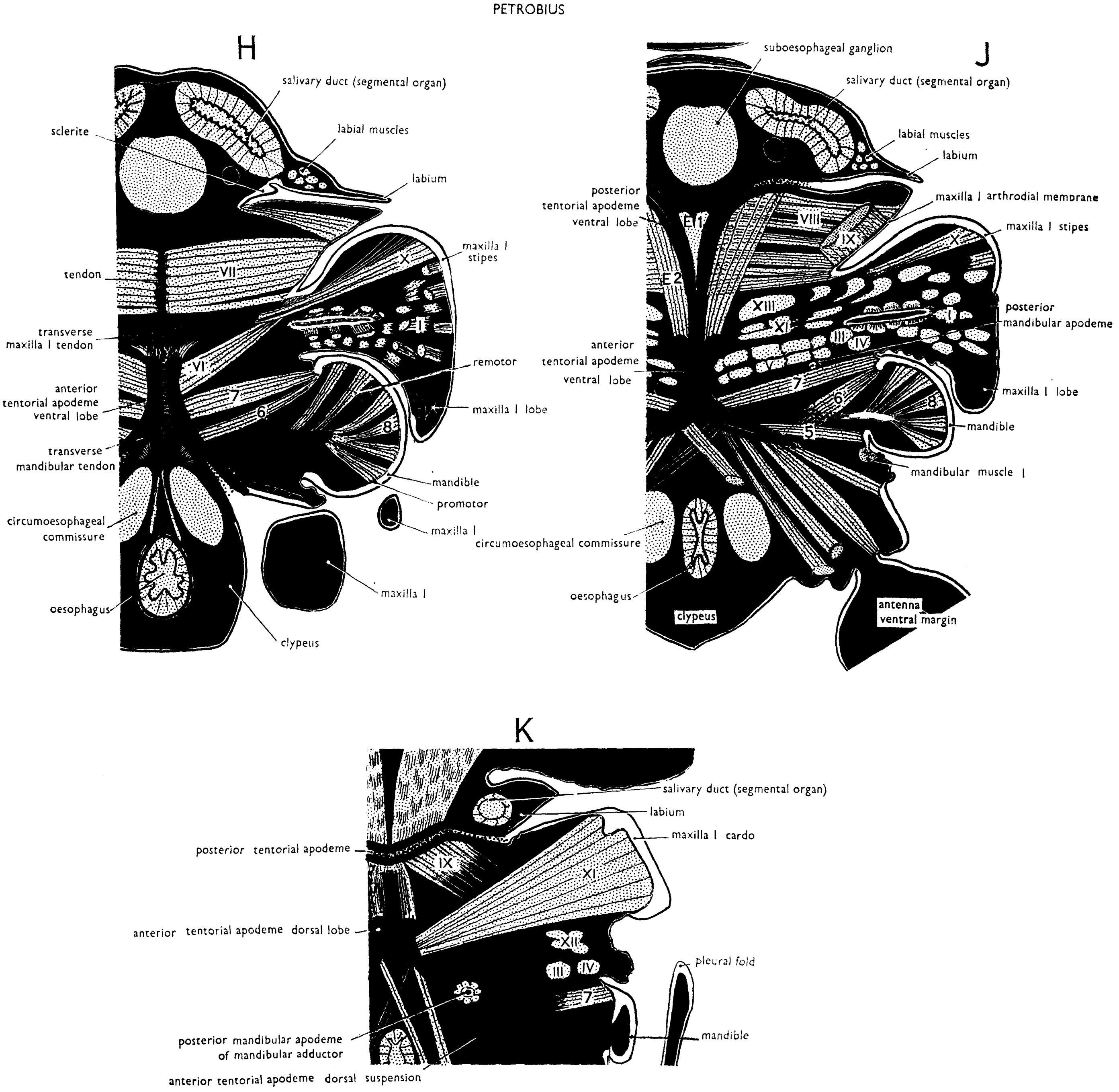

PETROBIUS
H
salivary duct (segmental organ)
sclerite
labial muscles
labium
maxilla I stipes
X
tendon
VII
transverse maxilla I tendon
I
VI
remotor
anterior tentorial apodeme ventral lobe
7
6
maxilla I lobe
8
transverse mandibular tendon
mandible
promotor
circumoesophageal commissure
maxilla I
oesophagus
maxilla I
clypeus
J
suboesophageal ganglion
salivary duct (segmental organ)
labial muscles
labium
posterior tentorial apodeme ventral lobe
E1
VIII
IX
maxilla I arthrodial membrane
maxilla I stipes
X
E2
XIII
XI
posterior mandibular apodeme
III
IV
anterior tentorial apodeme ventral lobe
7
6
maxilla I lobe
8
5
mandible
mandibular muscle I
circumoesophageal commissure
oesophagus
clypeus
antenna ventral margin
K
salivary duct (segmental organ)
labium
maxilla I cardo
posterior tentorial apodeme
IX
XI
anterior tentorial apodeme dorsal lobe
XII
III
IV
pleural fold
7
posterior mandibular apodeme of mandibular adductor
mandible
anterior tentorial apodeme dorsal suspension

FIGURE 24

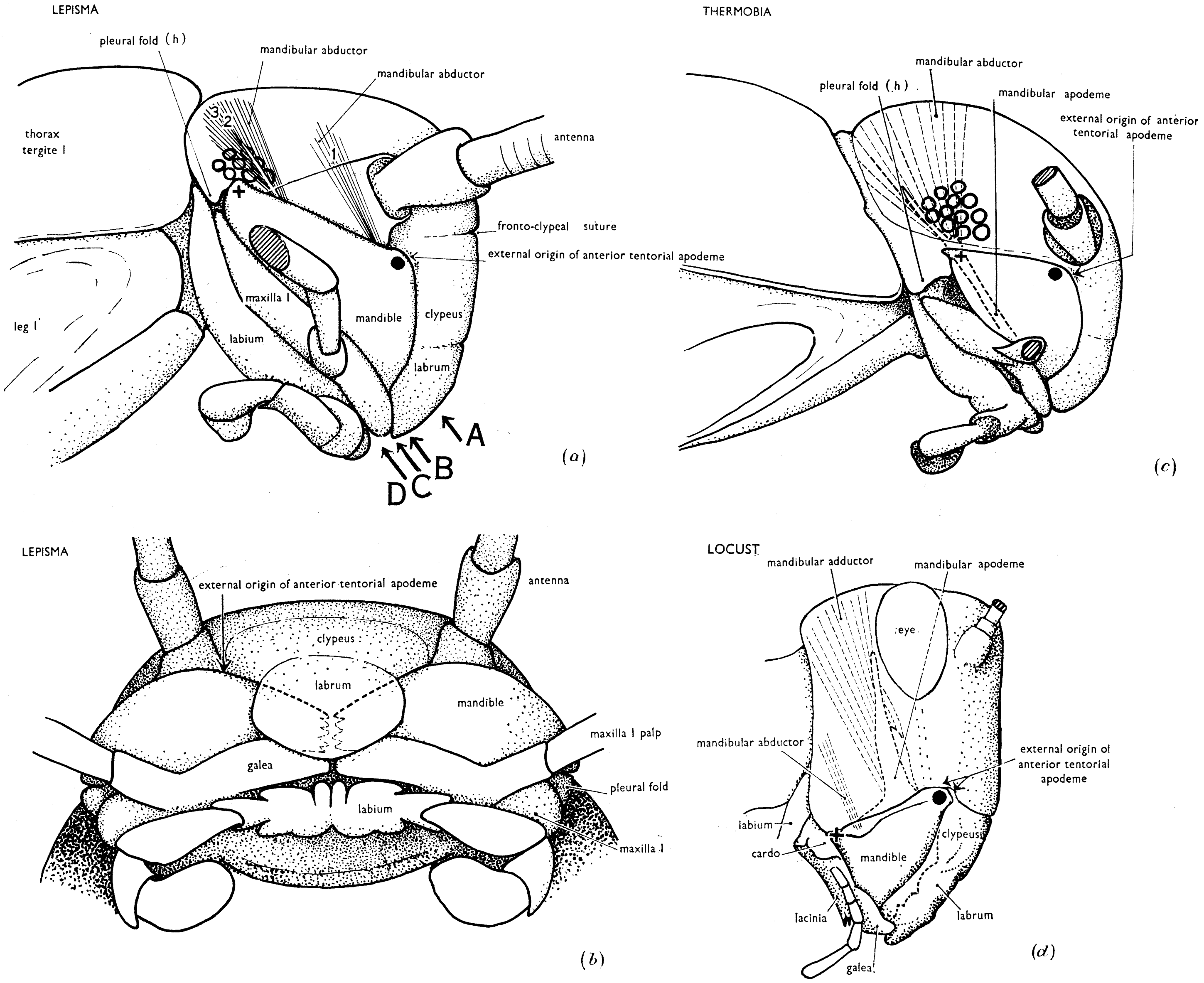


FIGURE 25. Comparative diagrams of the head of (*a*) *Ctenolepisma ciliata* Dufour side view, (*b*) same, ventral view, (*c*) *Thermobia domestica* (Packard) side view and (*d*) migratory locust side view, to show the positions of the mandibular hinge between the cross (dorsal articulation) and the black spot (anterior articulation), the positions of the main adductor and abductor muscles and the width of the labrum of *Ctenolepisma*. The arrows indicate the levels of the sections shown in figures 26 and 27.

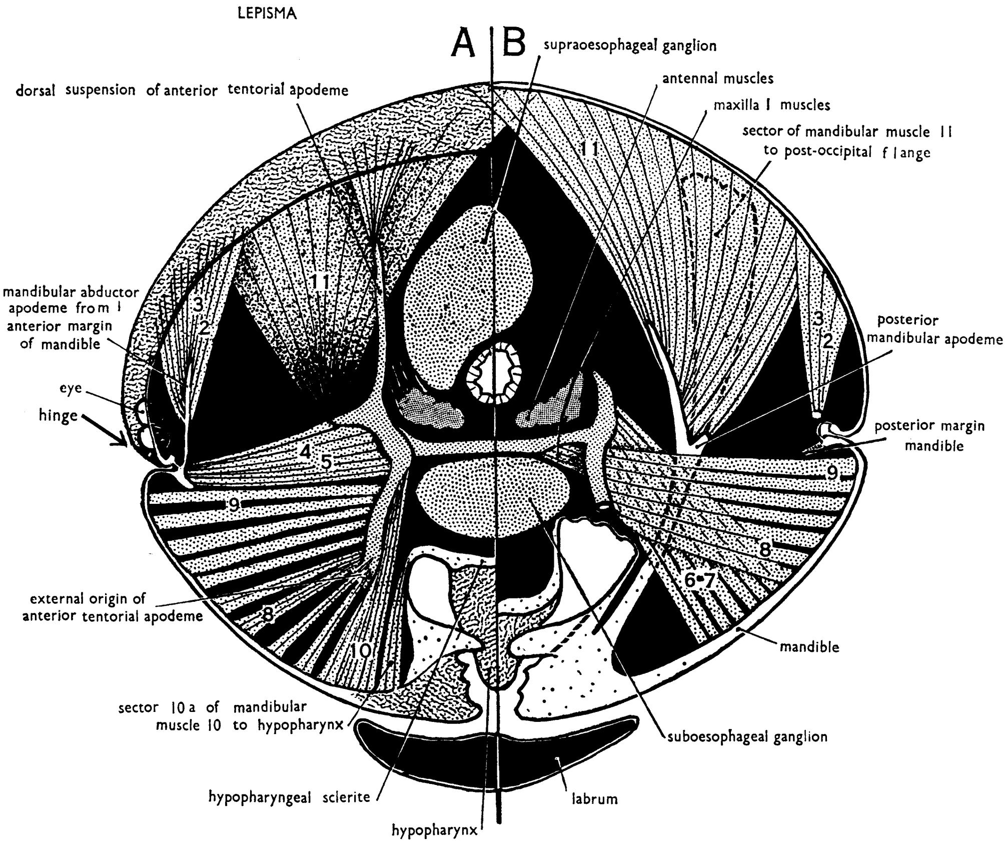


Figure 26. Thick transverse sections of the head of *Ctenolepisma ciliata* Dufour passing through the mandible and viewed from in front. The levels A and B are indicated in figure 25*a*, A being anterior to B. The external origin of the anterior tentorial apodeme is shown in A but the anterior face of the mandible has been removed to display the muscles. The transverse bridge formed by union of the anterior tentorial apodemes is shown in both levels. Muscle numbering corresponds with that of *Petrobius.* Mandibular abductor 5 is shown and abductor 4 lies just behind it. The apodeme bearing mandibular abductor 2 plus 3 (corresponding with the separate muscles 2 and 3 in *Petrobius*), is entire in A and cut short in B; the long cranial insertion of these muscles is also seen in figure 27C. Muscles 2 plus 3, 4 and 5 pull on the very short pre-axial border of the mandible (cf. muscles 3 and 6 in *Paranaspides* passing to the cranial wall and to the endoskeleton in figure 9C). The fan of adductor fibres 8, 9 and 10 from the inner face of the whole mandible to the anterior tentorial apodeme is entire in A and cut away ventrally in B to display the more posterior adductor muscle corresponding with 6 and 7 of *Petrobius*, Adductor muscle 11 is more complex than shown, one large and some small sectors passing behind to the post-occipital flange.

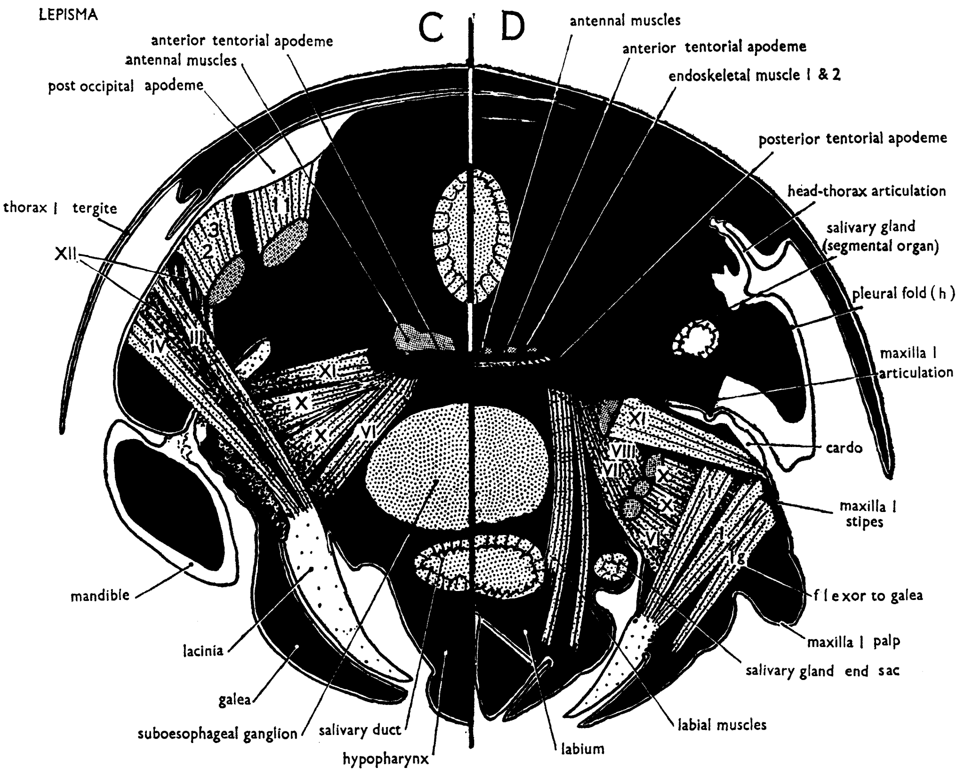


Figure 27. Thick transverse sections of the head of *Ctenolepisma ciliata* Dufour passing through the maxilla 1 and viewed from in front, level C being anterior to level D; the planes are indicated on figure 25*a*. Muscle numbering corresponds with that of *Petrobius*. Muscle XI, the protractor-depressor to the cardo-stipes hinge, and the stipes muscles VI and X are shown inserting on to the anterior tentorial plate in C; muscles VI and X are cut in D so displaying the more posterior stipes muscles VII and VIII which insert on the posterior tentorial plate. Muscle X runs in several sectors. The cranial retractors of the lacinia, muscles III and IV, are shown in C and the promotor of the cardo, muscle XII, in two sectors, lies immediately behind muscles III and IV; the sectors of muscle XII resemble those drawn more clearly for *Thermobia* by Chaudonneret (1950, fig. 42 *rl*, *rm*). The labial segmental organ is cut showing the end sac (marked) from which a duct passes up to the pleural fold and down to the median exit duct.

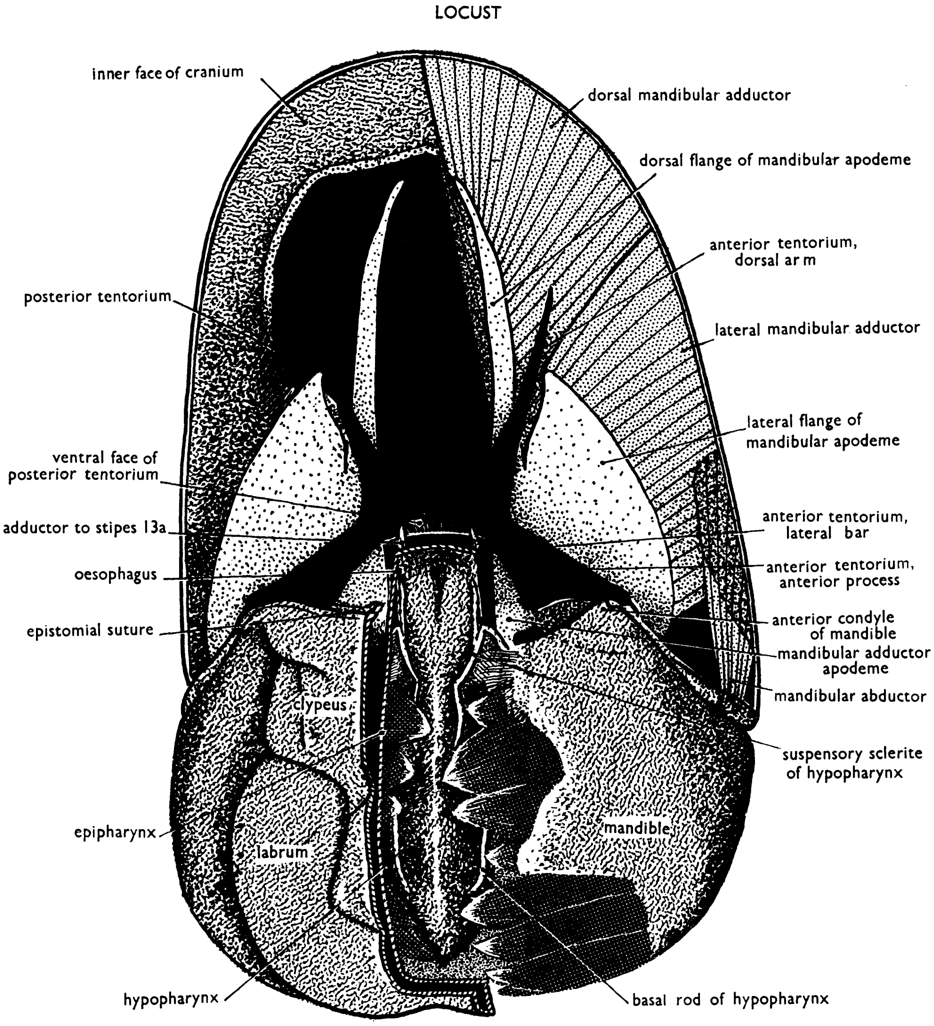


FIGURE 28. Oblique anterior view of the head of *Locusta migratoria* L., the mandibular hinge on the animal's left side being visible. Part of the clypeo-labrum is removed together with the whole front wall of the head. The cerebral ganglia, alimentary canal and antennal muscles have been removed to display the tentorium and mandibular muscles.

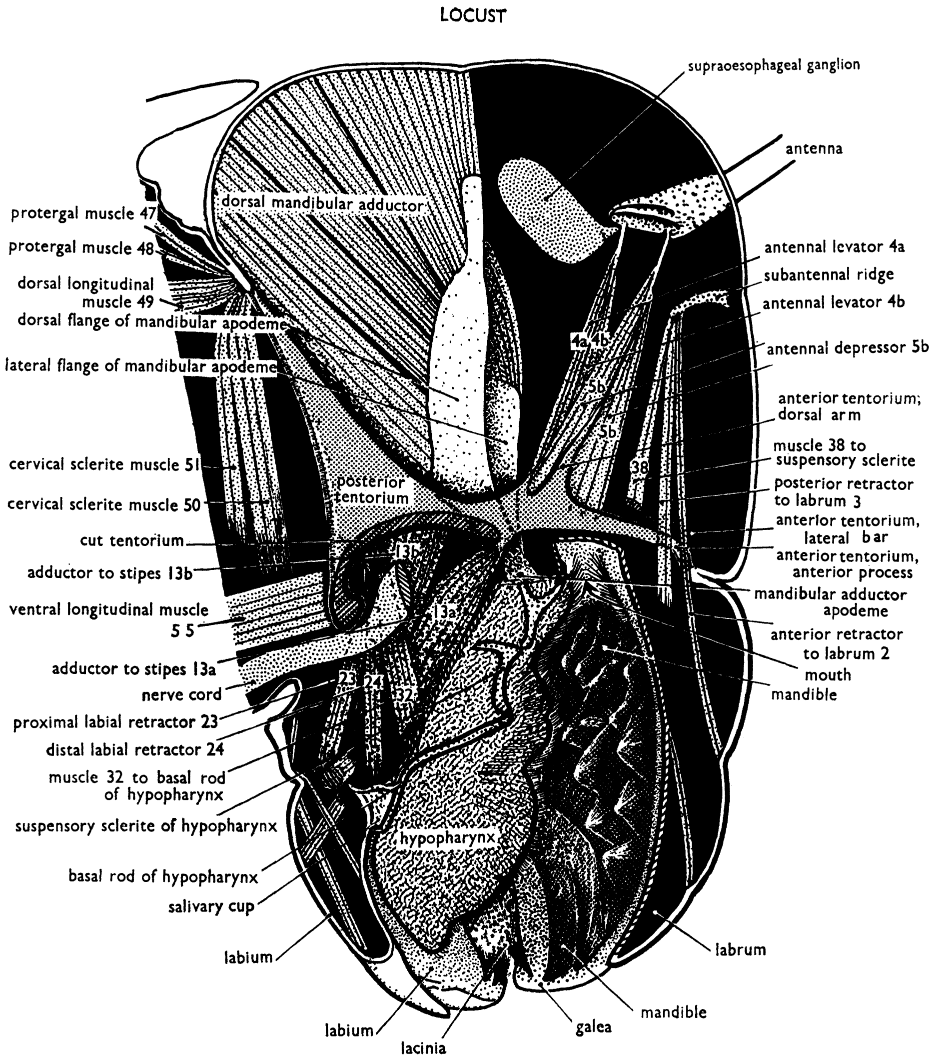


Figure 29. Sagittal half of the head of *Locusta migratoria* L. the hypopharynx being left intact. The circumoesophageal commissures have been removed in order to display the antennal and mandibular muscles and the tentorium. The upper sector of the suspensory sclerite of the hypopharynx sends one branch to the oesophagus and the other unites with the mandible close to the origin of the mandibular apodeme. The mandibular muscles are removed on the left to show the posterior part of the cranium and tentorium. The muscle numbers are those of Albrecht (1953).

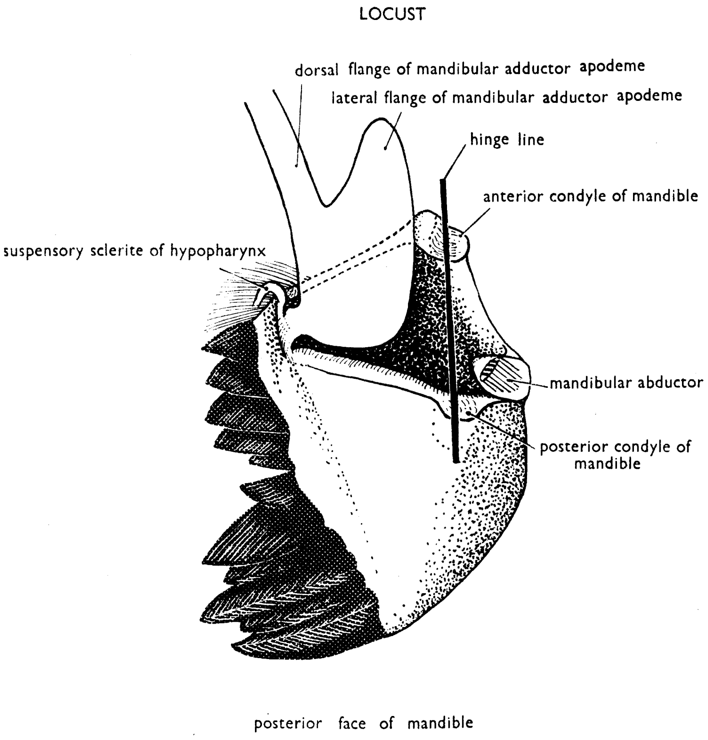


FIGURE 30. Posterior view of the isolated right mandible of the locust for comparison with the other mandibles illustrated here. The hinge line slopes downwards posteriorly. The abductor muscle is cut short and the adductor muscles, which arise on the apodeme, are omitted (see figures 28, 29).

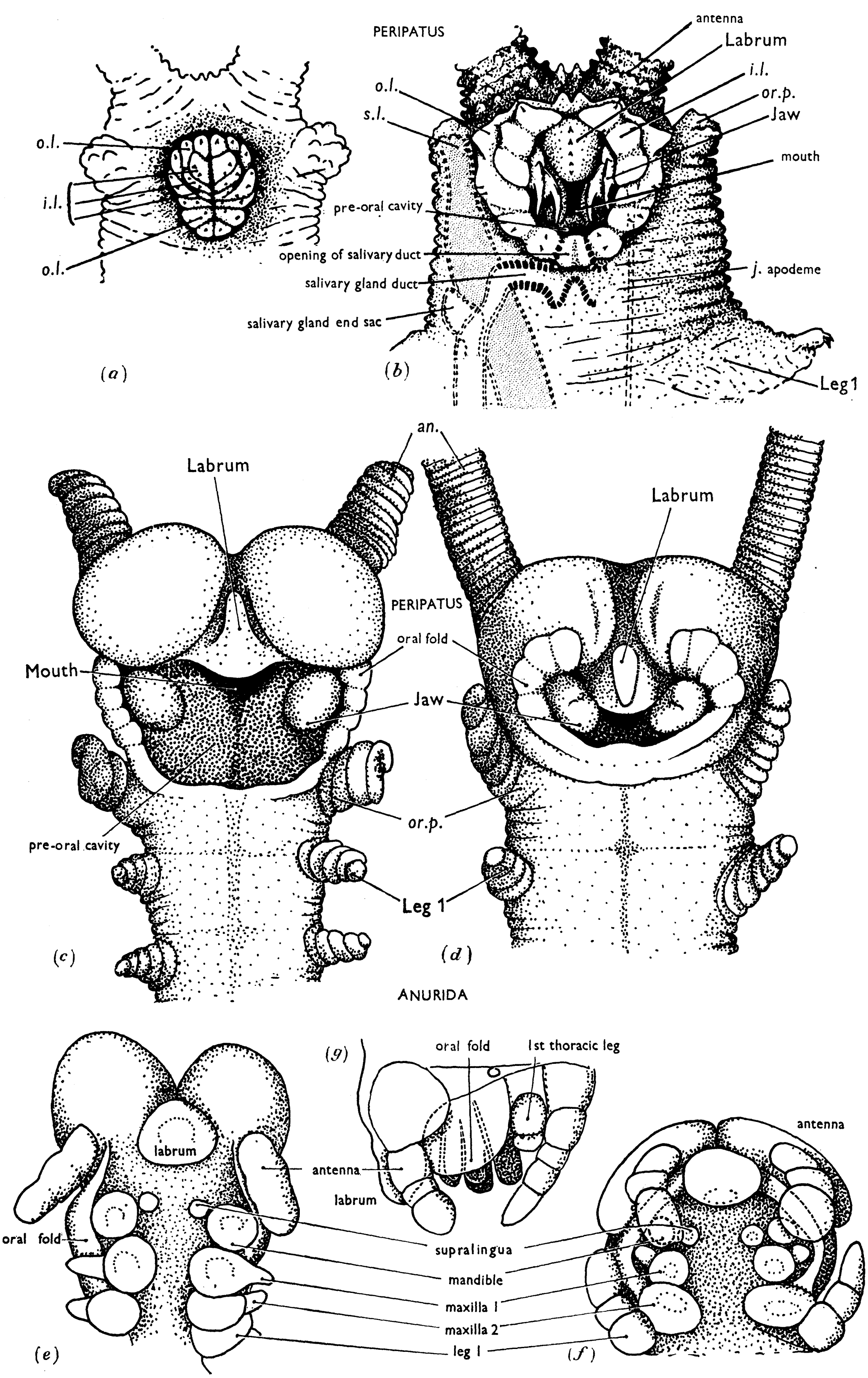


FIGURE 31. The form and development of a gnathal pouch in arthropods. (*a*) and (*b*) Ventral views of the oral region of *Peripatopsis sedgwicki* Purc. with the round lip closed over the jaws and pre-oral cavity in (*a*) and with the lip open, as it is when pressed on to the surface of prey, in (*b*). The mouth lies behind the labrum, the jaw blades, two to each jaw, slice widely from before

backwards at the sides of the mouth, the jaw apodeme(*j* apodeme) being shown by dotted lines. The circular lip is composed of inner (*i.l.*) and outer (*o.l.*) lip folds. The opening of the salivary duct lies within the lip as shown, the salivary gland end sac and duct being marked. The slime gland duct (*s.l.*) opens on the oral papilla, slime ejection is defensive and not employed in feeding (Manton 1937).

(*c*) and (*d*) Oral views of embryos of *Peripatus edwardsii* Blanch., the younger in (*c*), redrawn from Kennel (1886). Paired oral folds lie at the sides of the jaws and then unite with each other behind them (*d*) enclosing the preoral cavity. Later the folds unite in front of the labrum.

(*e*),(*f*)and (*g*) Oral views of embryos of *Anurida maritima* Laboulbene, the younger in (*e*) redrawn from Folsom (1900). The oral folds at first (*e*) lie lateral to both mandibles and maxillae 1 and unite later (*f*) with the labrum and labium (maxillae 2) to form the gnathal pouch. (*g*) Lateral view of the same stage shown in (*f*).

FIGURES 32 to 34. Frontal reconstruction of the head of *Tomocerus longicornis* (Müller) viewed from above at progressively lower levels (R, S, T, U and V) to show the endoskeleton, gnathal pouch and the form and musculature of the mandible and maxilla 1. Tentorial apodemes are shown in red, transverse segmental tendons and their connectives are shown in blue and the posterior endoskeletal plate is lightly stippled, the gnathal pouch cavity being white. Uncut surfaces of mandibular and maxilla 1 cuticle are mechanically mottled and muscle insertions on the dorsal cuticle are shown by the convention most in evidence on level R. Cut muscle ends are finely stippled. Mandibular muscles are marked by Arabic numerals (the numbering of Hoffmann (1908)) and the maxilla 1 muscles I to XII are marked by Roman numerals. The oesophagus is partly shown but its dilator muscles are omitted (see figures 35, 36). The levels of the transverse sections shown in figures 36 to 40 are given by the corresponding letters A to Q.

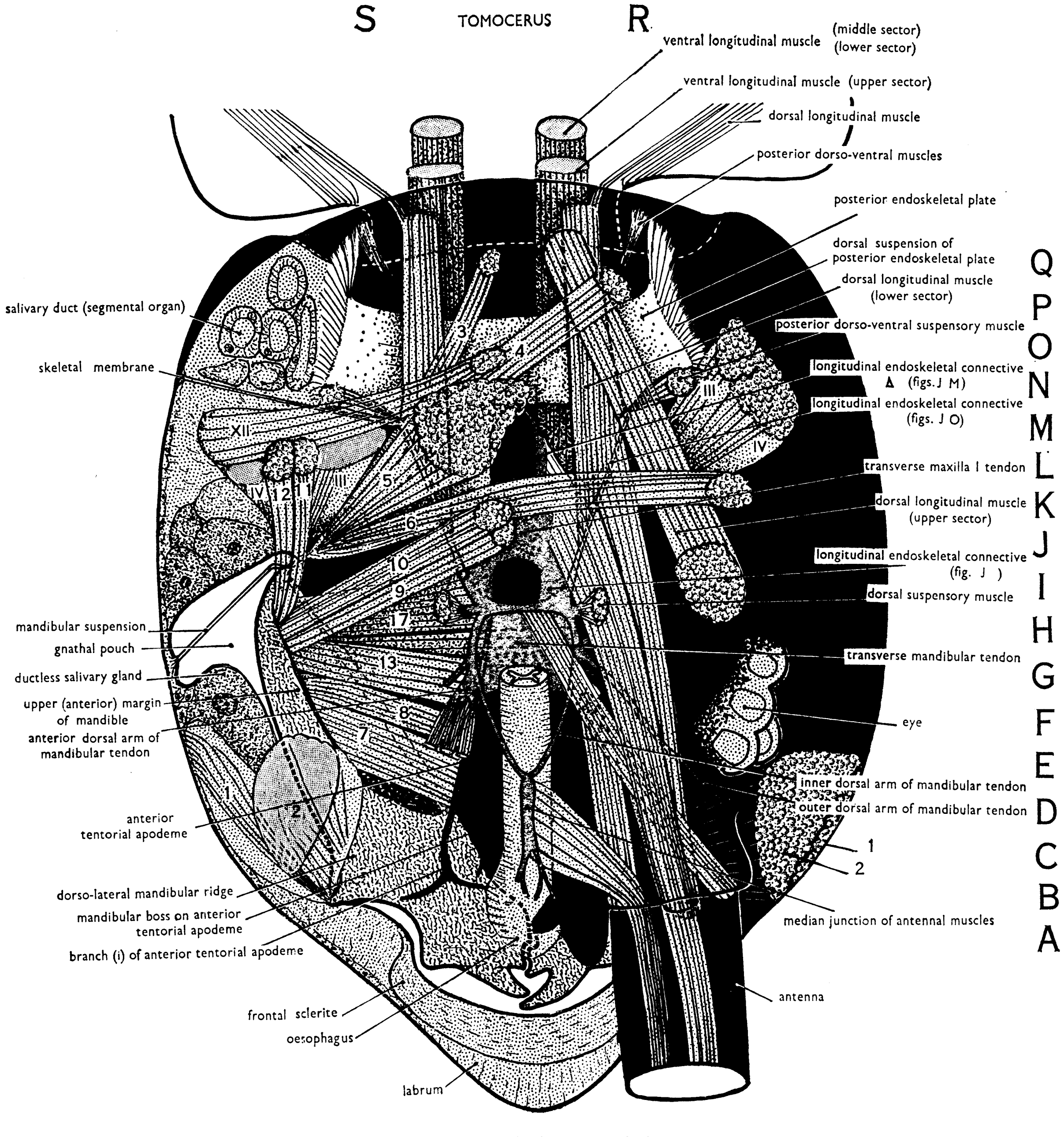


FIGURE 32 (see also legend on p. 149). Level R is superficial, the muscles and their antero-dorsal insertions being shown as if the head wall was transparent. The ocelli and the base of the antenna are shown, and the tip of the animal's left mandible is drawn as if the front of the head was transparent (see sagittal view in figure 35). Muscles from the animal's left mandible are omitted except for the dorso-lateral insertions of muscles 1 and 2.

Level S shows the entire right mandible and its most superficial muscles, muscles 4 to 6 crossing over to the other side. Muscles 7 to 12 arise from the anterior margin of the mandible, muscles 3 to 6 from the homologue of the posterior mandibular apodeme, here a short chitinous process at the postero-ventral corner of the mandible (see origin of muscle 6 in figure 37I), and muscles 13–17 arise from the mandibular concavity. Muscle 2 is cut short, it arises with muscle 1 from the dorso-lateral mandibular ridge (figures 33, 42 and 36D). The antenna and some of its muscles are omitted, others are cut short. Branch (i) of the anterior tentorial apodeme lies in the head above the gnathal pouch and has been drawn superimposed upon the mandible; its natural position is seen in level T and figure 36D. Maxilla 1 muscles III and IV are cut short their dorsal insertions appear in level R.

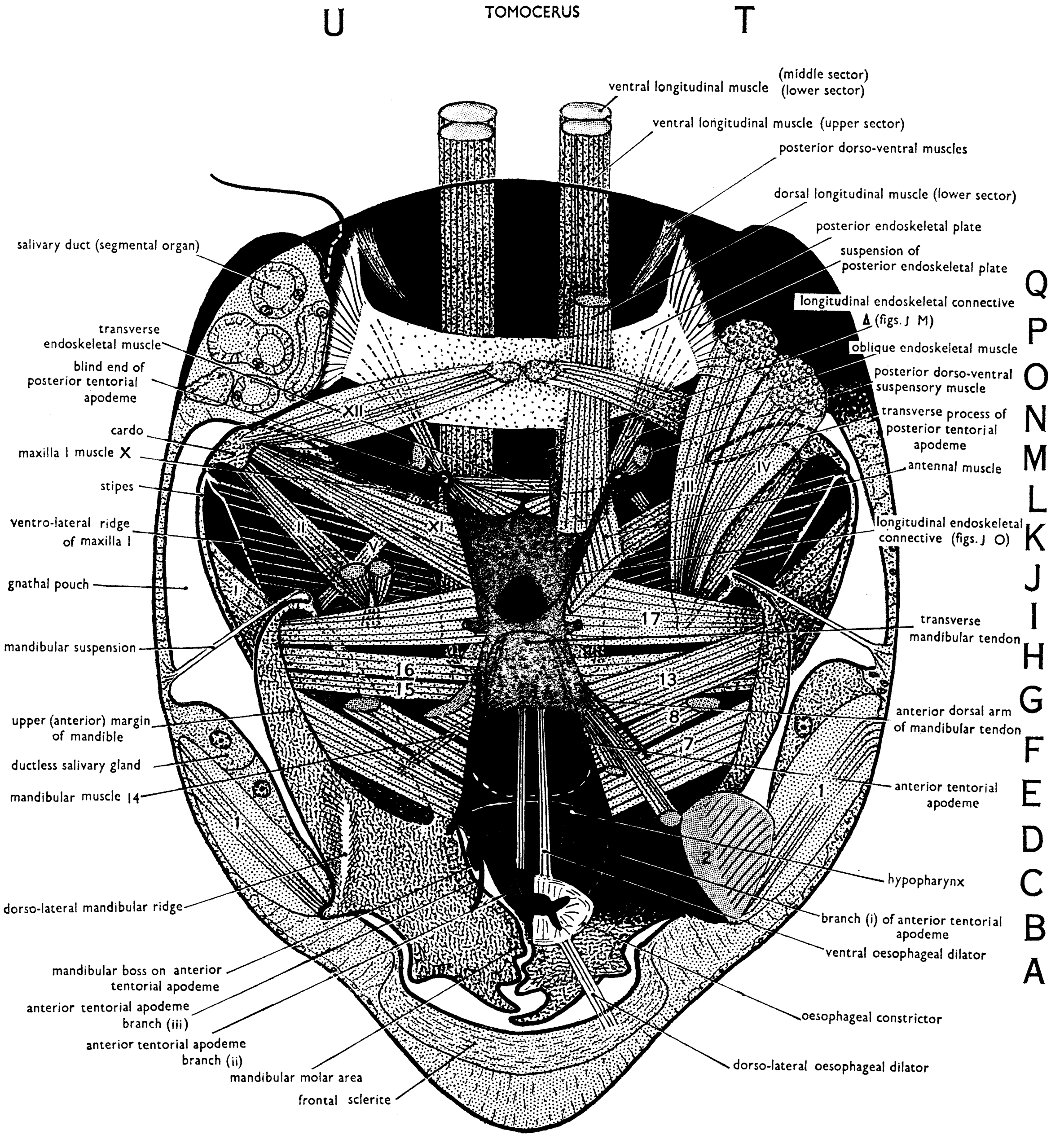


FIGURE 33 (continuation of figure 32). Conventions as on figure 32. Level T shows a deeper view of the mandibular muscles, which are further cut away in level U to show the transverse mandibular muscles 15 and 16 which unite with their fellows below the transverse mandibular tendon. The counter-rotator (promotor) muscles from the anterior margin of the mandible are removed. In level U muscle 2 and part of muscle 1 are cut away from their origins on the dorso-lateral mandibular ridge; the antennal muscles, the dorsal suspensory muscle, and the posterior dorso-ventral suspensory muscle are all removed; the latter is entire in level T. The proximal parts of maxillae 1 are shown, muscles III and IV being entire in level T and cut short in level U. The lower sector of the dorsal longitudinal muscle is omitted in level U and the longitudinal tendinous connective, marked by a triangle here and on the transverse sections, is cut away from the maxilla 1 tendon in U. The anterior tentorial apodeme is almost entirely shown in level T, branch ii to the superlingua and branch iii to the preoral cuticle above (anterior to) the mandible being marked on level U. The edge of the suboesophageal ganglion is indicated by a dotted white line.

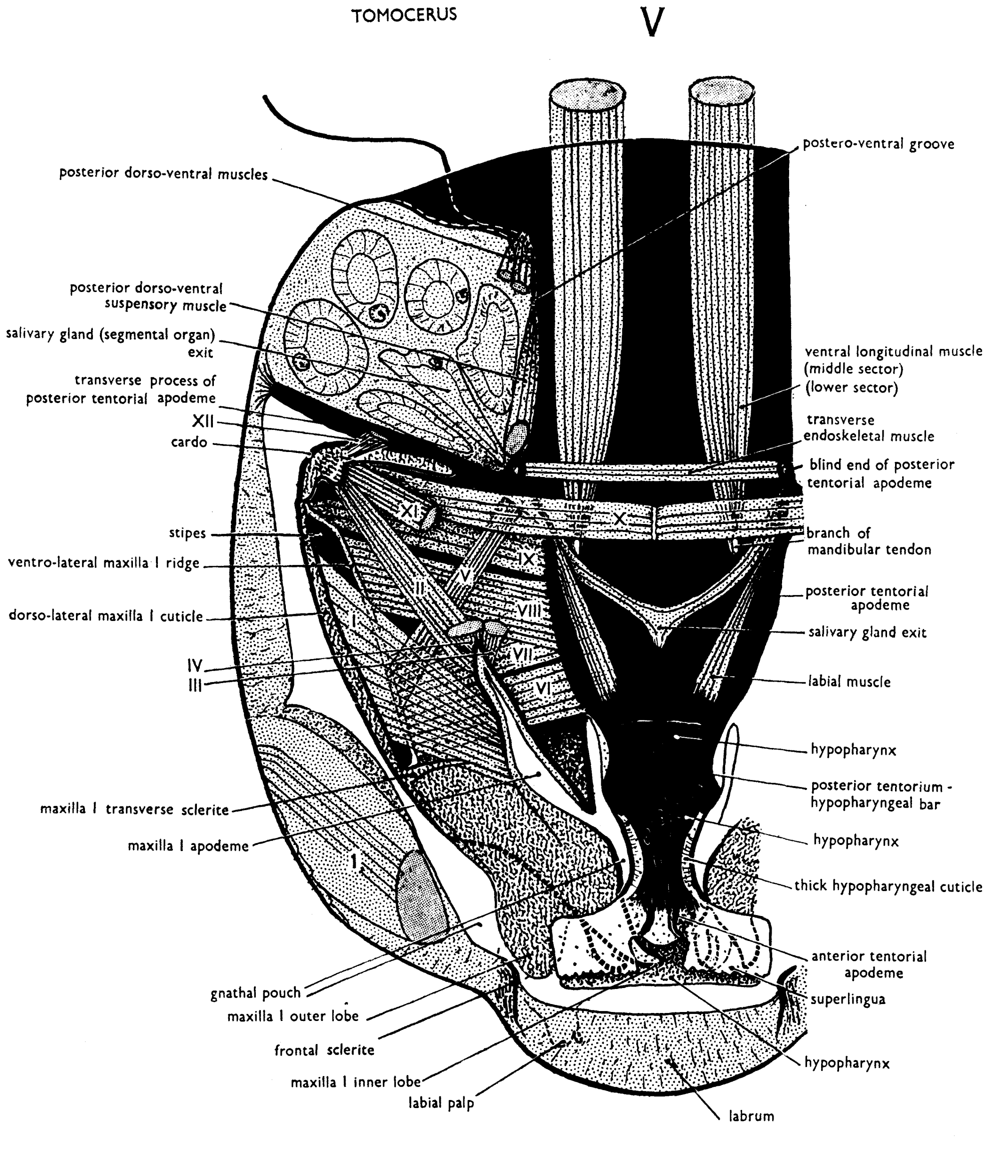


FIGURE 34 (continuation of figures 32 and 33). Conventions as on figure 32. A deeper level than figure 33 U displaying the whole of the posterior tentorial apodeme and maxilla 1 with maxilla 1 muscles other than III, IV, XI and XII which are cut short or omitted, they are shown in levels T and U. The blind end of the posterior tentorial apodeme rises in the head and is foreshortened in this view. The mandible with its muscles, the transverse segmental tendons of the mandible and maxilla 1 and the posterior endoskeletal plate have been removed. The point of exit of salivary juice from the paired ducts is shown diagrammatically. The whole oesophagus has been removed, leaving the hypopharynx and superlinguae between which the inner maxillary lobe projects. A cut portion of the anterior surface extension of the anterior tentorial apodeme lies on the hypopharynx, but the spines which this apodeme supports are omitted (see figure 36 B). The complexities in form of the biting end of the inner maxillary lobe are not shown; they are indicated roughly in figure 42 (for details see Hoffmann (1908)).

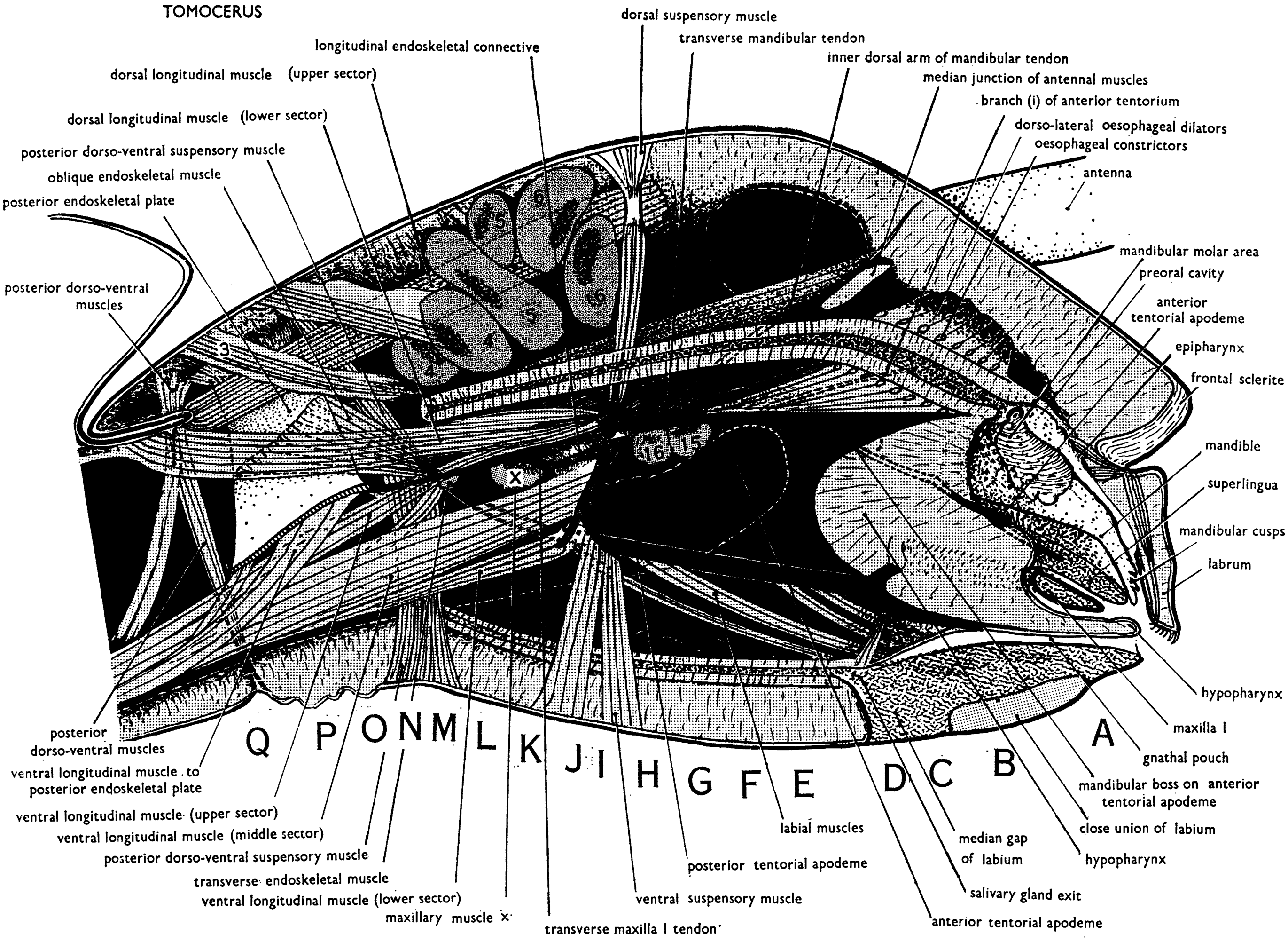


Figure 35. Reconstruction of a sagittal half of the head of *Tomocerus longicornis* viewed from the middle line. Conventions as on figure 32. The transverse maxilla 1 and mandibular tendons and the posterior endoskeletal plate are cut, as are the mandibular muscles 4 to 6 which cross to the other side of the head, and mandibular muscles 15 and 16 and maxillary muscle X which are transverse in position. These muscles cut transversely show the small central area of cut fibrils (dark) surrounded by bulky nucleated cytoplasm (stippled). Almost the whole of the anterior tentorial apodeme is shown, branch i being indicated by dotted lines. The internal part of the posterior tentorial apodeme is shown with its superficial arm alongside the maxilla 1, but the details of its fade out into the elaborate cuticular thickenings of the hypopharynx are not shown. The more important branches of the tendinous endoskeleton visible in this aspect are shown.

The dorsal longitudinal muscle runs in two sectors, the upper inserting dorso-laterally on the head wall and the lower on to the outer fork of longitudinal endoskeletal connective, marked by a cross on the transverse sections in figures 38K, 39L to O and 40P, Q. The ventral longitudinal muscle forms an upper sector inserting on the longitudinal endoskeletal connective (see figures 39, 40L to Q); a middle sector inserting on the upper part of the ventral suspensory arm of the transverse mandibular tendon (figures 38J, 37H, I); and a small lower sector inserts on a branch of the ventral suspensory arm (figures 39M, 38K). A branch of the ventral longitudinal muscle inserts on the hollow part of the posterior tentorial apodeme (unlabelled) (see also figures 39M, N).

The median opening of the paired (salivary) ducts of the labial segmental organs is more complex than shown, the ducts open into a median diverticulum of the gnathal pouch (see figures 37E and 36D). The gnathal pouch is freely open to the exterior between the paired parts at the marked median gap (see figure 36D), but distal to this there is a close, possibly fused, union between the two halves of the labium over the finely stippled area, see (figure 36B).

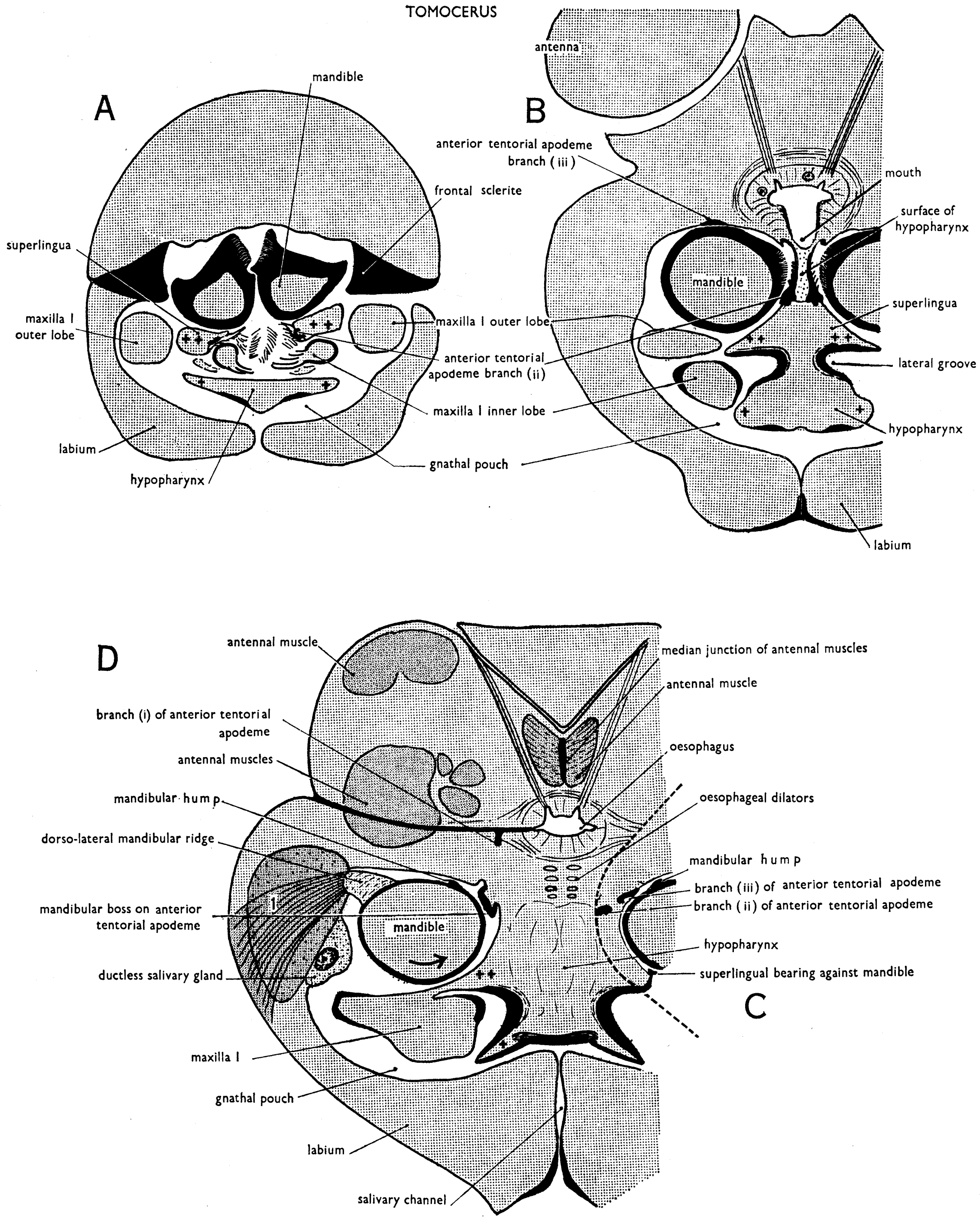


FIGURE 36. For legend see p. 158.

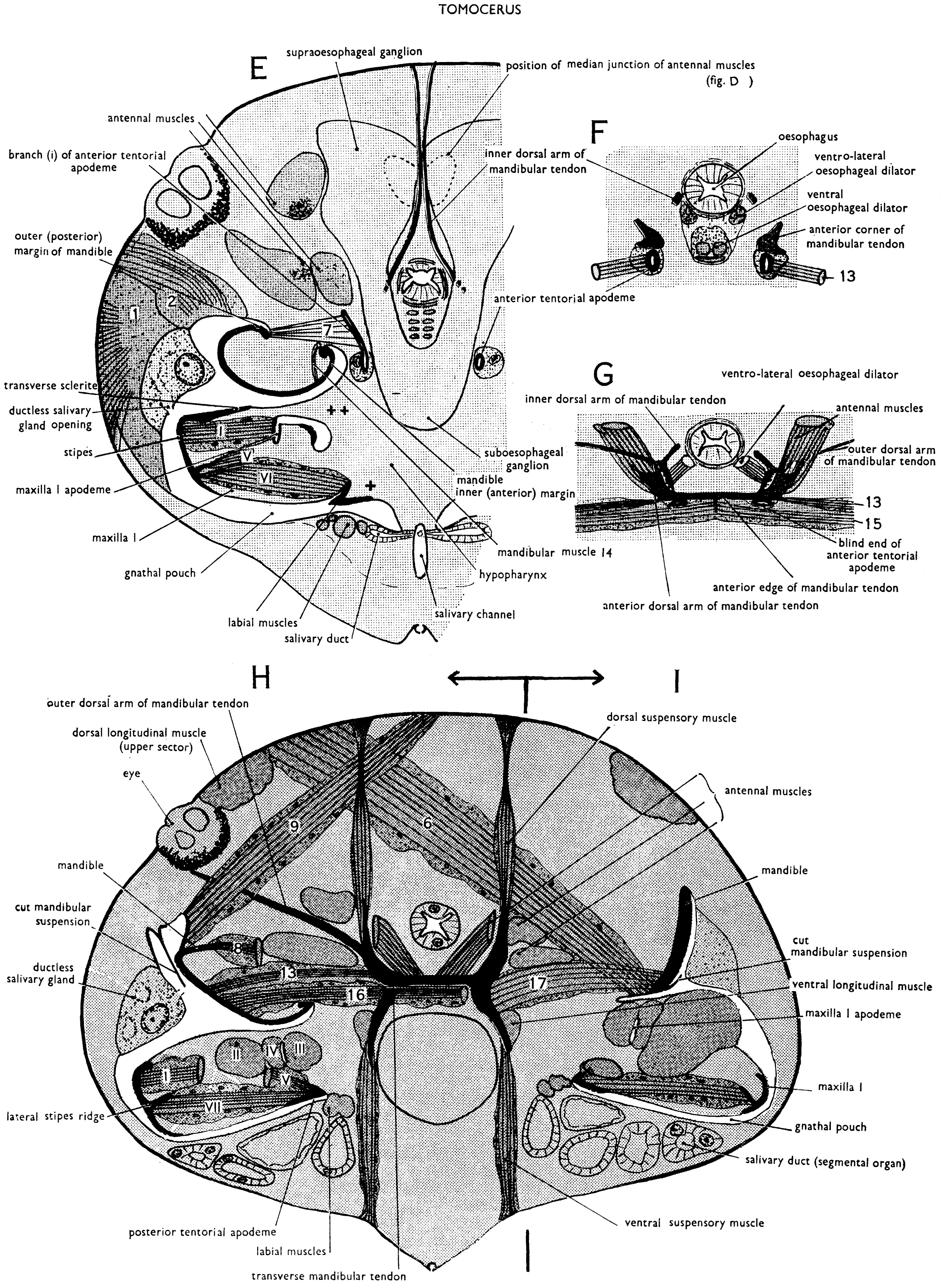


FIGURE 37. For legend see p. 159.

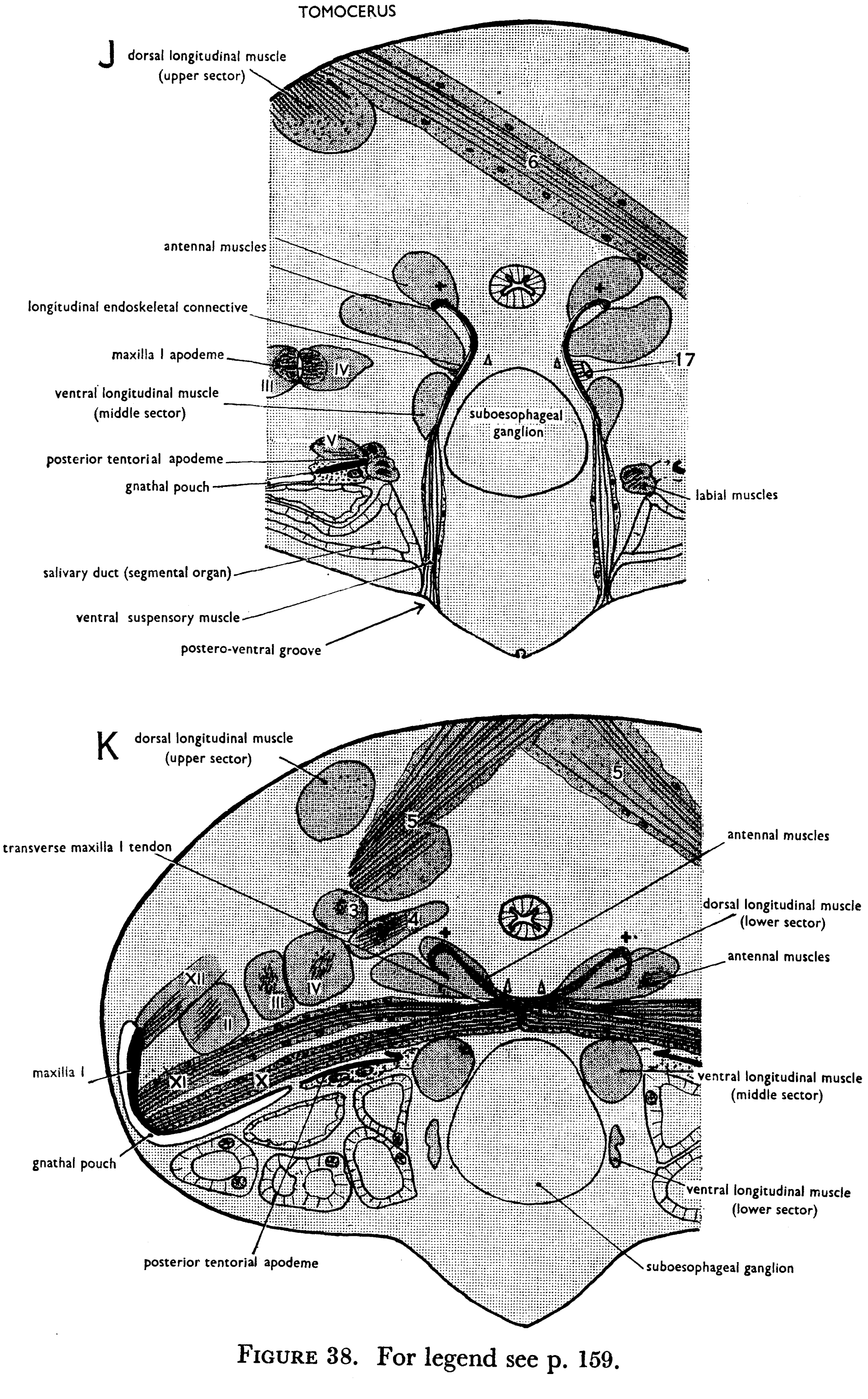


FIGURE 38. For legend see p. 159.

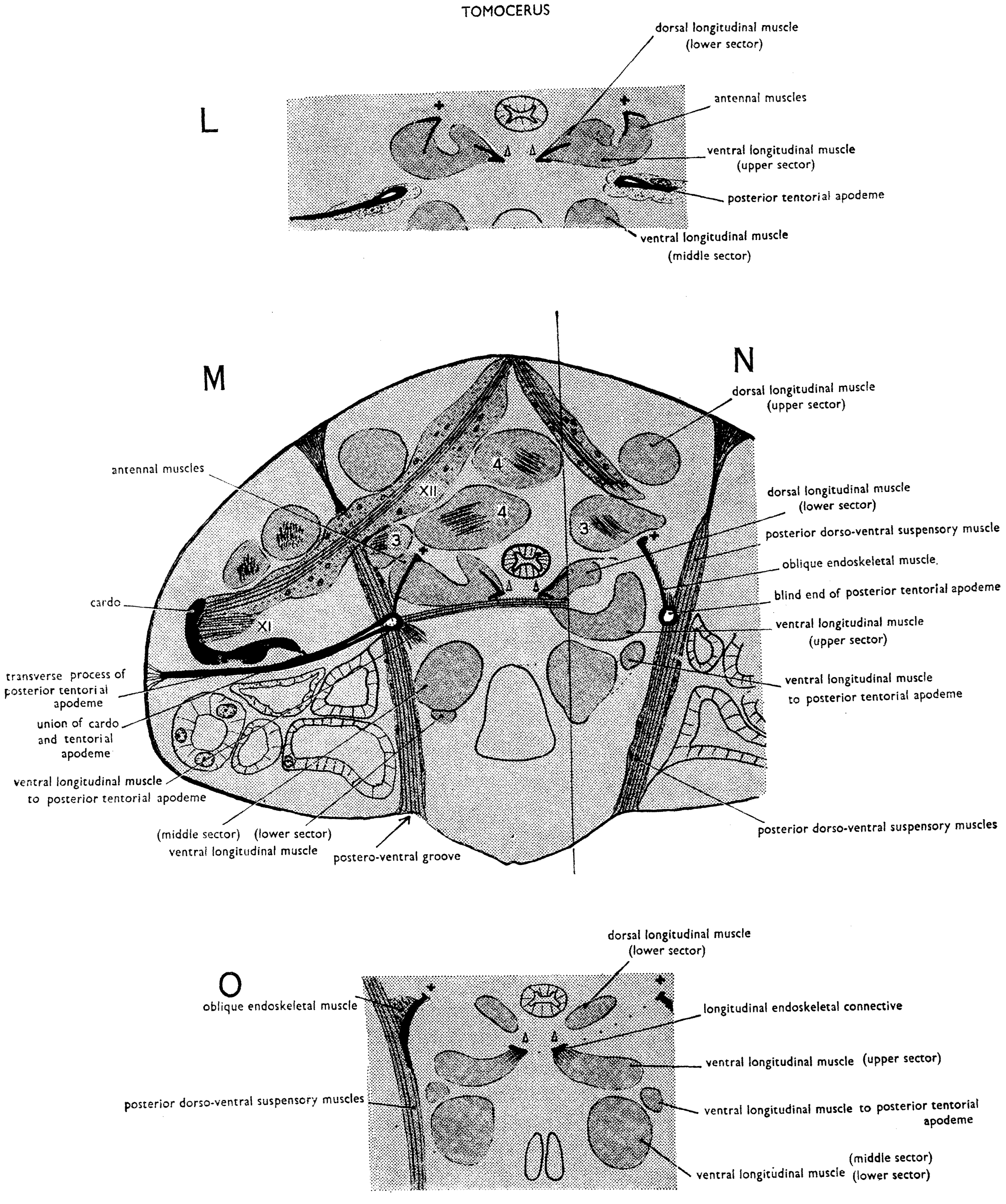


FIGURE 39. For legend see p. 160.

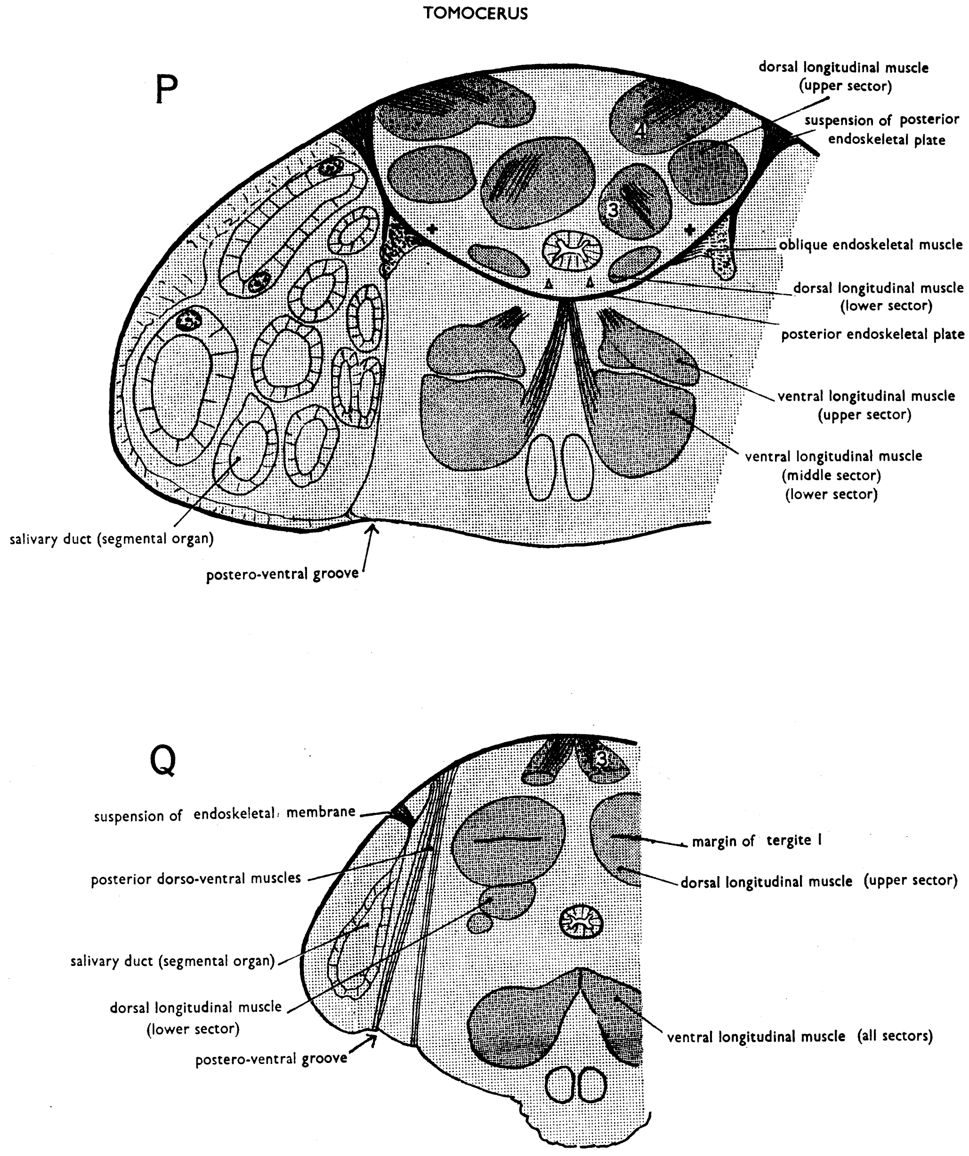


FIGURE 40. For legend see p. 160.

FIGURES 36 to 40. Diagrammatic anterior views of a series of thick transverse sections through the head of *Tomocerus longicornis* (Müller) at the levels A to Q marked in figures 32, 33 and 35. The planes of the transverse sections in the figures and of the frontal reconstructions in figures 32 to 34 are not exactly at right angles to one another. Highly sclerotized cuticle, appearing amber or red with Mallory's stain are shown in black. Tentorial apodemes are shown in red, transverse segmental tendons and their connectives are shown in blue. The thick ectoderm with vacuolated inner parts is omitted (see figure 41).

FIGURE 36. Level A anterior to the mouth through the free tips of the mandibles, maxillae 1, superlinguae and hypopharynx, and through the margins of the frontal sclerite.

Level B through the mouth where the hypopharynx becomes continuous with the oesophagus. The lateral margins of the hypopharynx and superlinguae are marked by one and two crosses respectively in order to facilitate locating the corresponding parts on levels D and E. The thick cuticle in the gully between hypopharynx and superlinguae 'lateral groove' forms a bearing for the movement of maxilla 1. Ventrally the labium closes the gnathal pouch. The anterior end of the anterior tentorial apodeme here lies on the surface of the hypopharynx supporting a row of spines.

Level C. Farther back to show the anterior tentorial apodeme lying in the lateral cuticle at the base of the hypopharynx.

Level D. A little farther back at the anterior margin of the antennal base. The anterior tentorial apodeme forms a boss against which the mandible is pressed when rotated by muscles 1 and 2, etc., in the direction of the arrow. Mandibular muscle 1 passes from the dorso-lateral mandibular ridge to the ventro-lateral head wall. Maxilla 1 is just united with the head by the superlingual edge, marked by two crosses, leaving a deep gulley on the mesial side of the maxilla which gives origin to the maxilla 1 apodeme (figures 34, 37E). The cut end of branch i from the anterior tentorial apodeme appears at this level and divides, passing inwards to the oesophagus and outwards to the head wall (see figure 32S). Ventrally the labium allows free access to the gnathal pouch in the middle line.

FIGURE 37 (continuation of figure 36). Level E. Through the anterior part of the eye, circum-oesophageal commissures, and the point of discharge of the salivary ducts (labial segmental organs). Giant ductless gland cells on the inner walls of the gnathal pouch discharge by irregular intracellular spaces. The upper face of the mandible is open to the body cavity and maxilla 1 is united on its mesial side to hypopharyngeal tissue, the superlingual tissue passing to the upper maxillary face (two crosses) and the hypopharyngeal tissue passing to the lower face (one cross). The maxilla 1 apodeme is here internal (cf. figure 36D). Laterally maxilla 1 cuticle is sclerotized and stiff; at this level a transversely directed sclerite passes on to the anterior upper face (see figure 34); a longitudinal ridge projects inwards 'lateral stipes ridge' marked in figure 37H and 'ventro-lateral maxilla 1 ridge' on figure 34, and the thick cuticle which formed the lateral angle to the hypopharynx now continues as the posterior tentorial apodeme. The anterior tentorial apodeme has sunk into the head as a hollow tube carrying with it a thick investment of ectodermal epithelium. The base of branch i of the anterior tentorial apodeme is shown on the left; its continuation is seen in figure 36D. The ventral oesophageal dilators are cut below the oesophagus (see figure 35).

Level F. Through the antero-lateral corners of the transverse mandibular tendon (blue) below which lies the anterior tentorial apodeme (red).

Level G. Close behind F, through the anterior edge of the transverse mandibular tendon where it gives rise to the antero-dorsal arms supporting the antennal muscles. Just in front arise the inner and outer dorsal arms of the transverse mandibular tendon (figures 32, 35), the forward course of the inner arm is seen in levels F and E. Below the transverse mandibular tendon the anterior ends of the anterior tentorial apodemes are attached to its ventral surface.

Level H. Through the posterior part of the eye and transverse mandibular tendon showing the outer dorsal arm and behind it the dorsal and ventral suspensory arms supporting the similarly named (and marked) muscles (see figure 41). A stiff cuticular flange gives origin to mandibular muscle 9. Maxilla 1 apodeme is clothed by muscles III and IV and the posterior tentorial apodeme is superficial.

Level I. Behind H, and through the proximal limit of the mandible where its posterior margin gives a strong cuticular process (homologous with the posterior mandibular apodeme of Thysanura, etc.) which bears rotator muscles (figure 32S), muscle 6 being shown. The origin of the suspensory sheet of cuticle from the base of the mandible (figures 32, 33) is seen in this section and its union with the upper lateral wall of the gnathal pouch in level H. The lateral stiff maxilla 1 cuticle is very limited in extent, leaving extensive arthrodial membranes on the upper (anterior) and lower (posterior) faces (cf. figures 33U, 34).

FIGURE 38 (continuation of figures 36, 37). Level J. Through the longitudinal endoskeletal connectives, shown in blue (staining blue with Mallory), which connect the transverse tendons of

(*Continued on p.* 160)

the mandible, maxilla 1 and posterior endoskeletal plate. The upper (anterior) edges of these connectives are marked by a cross and the mesial or lower (posterior) margins are marked by a triangle, as in levels K to O. The ventral suspensory arm is still present at this level and bears the middle sector of the ventral longitudinal muscle. The posterior tentorial apodeme has sunk into the head, surrounded by its own epithelium, forming a solid bar, and maxilla 1 apodeme has passed upwards and backwards.

Level K. Through the transverse maxilla 1 tendon which unites with the lower edges of the longitudinal connectives marked by triangles. The upper edges of these connectives, marked by crosses, are further apart, and their outer margins are incurled round the anterior end of the lower sector of the dorsal longitudinal muscle. Antennal muscles clothe the outer and upper surfaces of the longitudinal connectives. The posterior tentorial apodeme is further removed from the lower surface of the head, it is solid and is covered by its own epithelium.

FIGURE 39 (continuation of figures 36 to 38). Level L. Through the longitudinal endoskeletal connectives behind the maxilla 1 transverse tendon. Each has separated into upper and outer and a lower and mesial parts, marked by crosses and triangles, respectively; but both parts fade into fine sheets serving muscle insertions which cannot be drawn on this scale. The upper sector of the ventral longitudinal muscle inserts on this skeleton along with the remains of the antennal muscles and with the lower sector of the dorsal longitudinal muscle as shown. The posterior tentorial apodeme is becoming hollow.

Level M. Through the proximal limit of maxilla 1 showing its attachment to the posterior tentorial apodeme. The mesial part of this apodeme is now hollow, it extends a short distance farther back (level N) and ends blindly. The upper outer part of each longitudinal connective, marked by a cross, unites by an endoskeletal sheet with the internal end of the posterior tentorial apodeme (see left sides of levels L and M); this sheet bears the posterior extremity of the antennal muscles on the outer side and the lower sector of the dorsal longitudinal muscle on the inner side. The internal blind end of the posterior tentorial apodeme carries muscle fibres from the posterior dorso-ventral suspensory muscle and from the middle sector of the ventral longitudinal muscle, also a tough membrane from a loop of the segmental organ duct, and a transverse endoskeletal muscle to the posterior tentorial apodeme of the other side (drawn but not labelled here; see figure 34).

Level N. A little farther back through the internal end of the posterior tentorial apodeme. The skeletal sheet from this apodeme to the branch of the longitudinal connective marked by a cross is now bare both of antennal muscles and of the lower sector of the dorsal longitudinal muscle, and on its outer face it bears the oblique endoskeletal muscle. This muscle fans on to the posterior tentorial apodeme (figure 35) and some fibres pass forwards to fan over the posterior part of the transverse maxilla 1 tendon (figure 33U drawn but unlabelled). Tough membrane from the segmental organ joins the insertion on the ventral head wall of the posterior dorso-ventral suspensory muscle.

Level O. Just proximal to the posterior tentorial apodeme. The upper forks of the longitudinal endoskeletal connectives (marked by crosses) are now farthest from each other; they bear the oblique endoskeletal muscles on their outer faces, and the lower mesial parts of the longitudinal endoskeletal connectives (marked by triangles) are close together below the oesophagus, and bear part of the upper sector of the ventral longitudinal muscle as in level N. The arc of dots on the right between the triangle and the cross indicates the level of the posterior endoskeletal plate situated just behind (figure 40P).

FIGURE 40 (continuation of figures 36 to 38). Level P. Through the posterior endoskeletal plate, its dorsal suspension is a continuation of that of the posterior dorso-ventral suspensory muscles and the plate unites with both parts of the longitudinal endoskeletal connectives at the points marked by crosses and triangles. The posterior plate bears the oblique endoskeletal muscle on its lateral face (see figure 35), and gives origin to a dorso-ventral membrane boxing in the segmental organ. Strands from the middle sector of the ventral longitudinal muscle insert mid-ventrally on the posterior plate.

Level Q. Through the base of the head behind the posterior endoskeletal plate and cutting the anterior margin of tergite 1 where it gives origin to the upper sector of the dorsal longitudinal muscle (see figure 35). Posterior dorso-ventral muscles arise dorsally just behind the suspensory fibres of the endoskeletal plate and they pull on the postero-ventral groove at a point behind the insertions of the anterior and posterior suspensory muscles (figures 35, 34). One muscle in this group passes down the neck to the thorax (unlabelled in figure 35). Fibrils anchor investing membranes of the segmental organ to the dorso-lateral head wall.

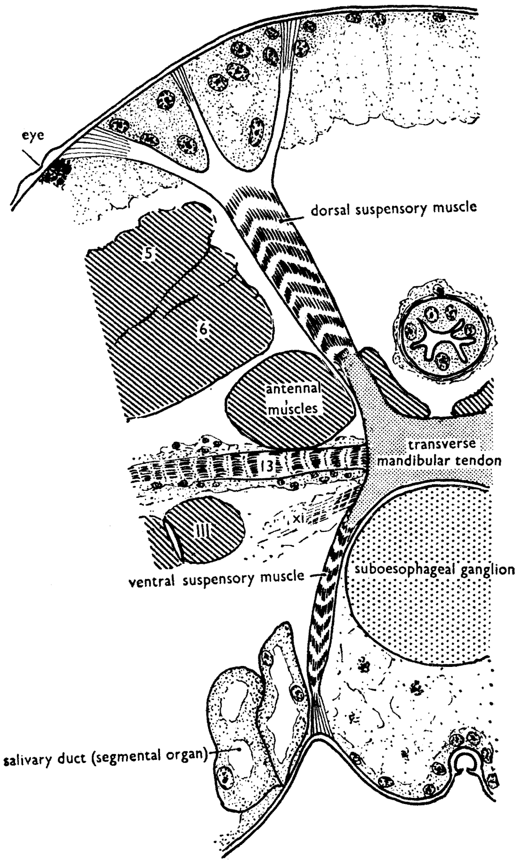


FIGURE 41. Transverse section through the head of *Orchesella villosa* (Geoffroy) at the level of the dorsal and ventral suspensory muscles from the transverse mandibular tendon, to show the endocuticle-like branched units situated between the dorsal suspensory muscle fibres and the unstriated fibrils linking the whole to the dorsal cuticle. Compare with the rod-like unbranched and probably elastic units in this position in *Tomocerus longicornis* in figures 37H, I.

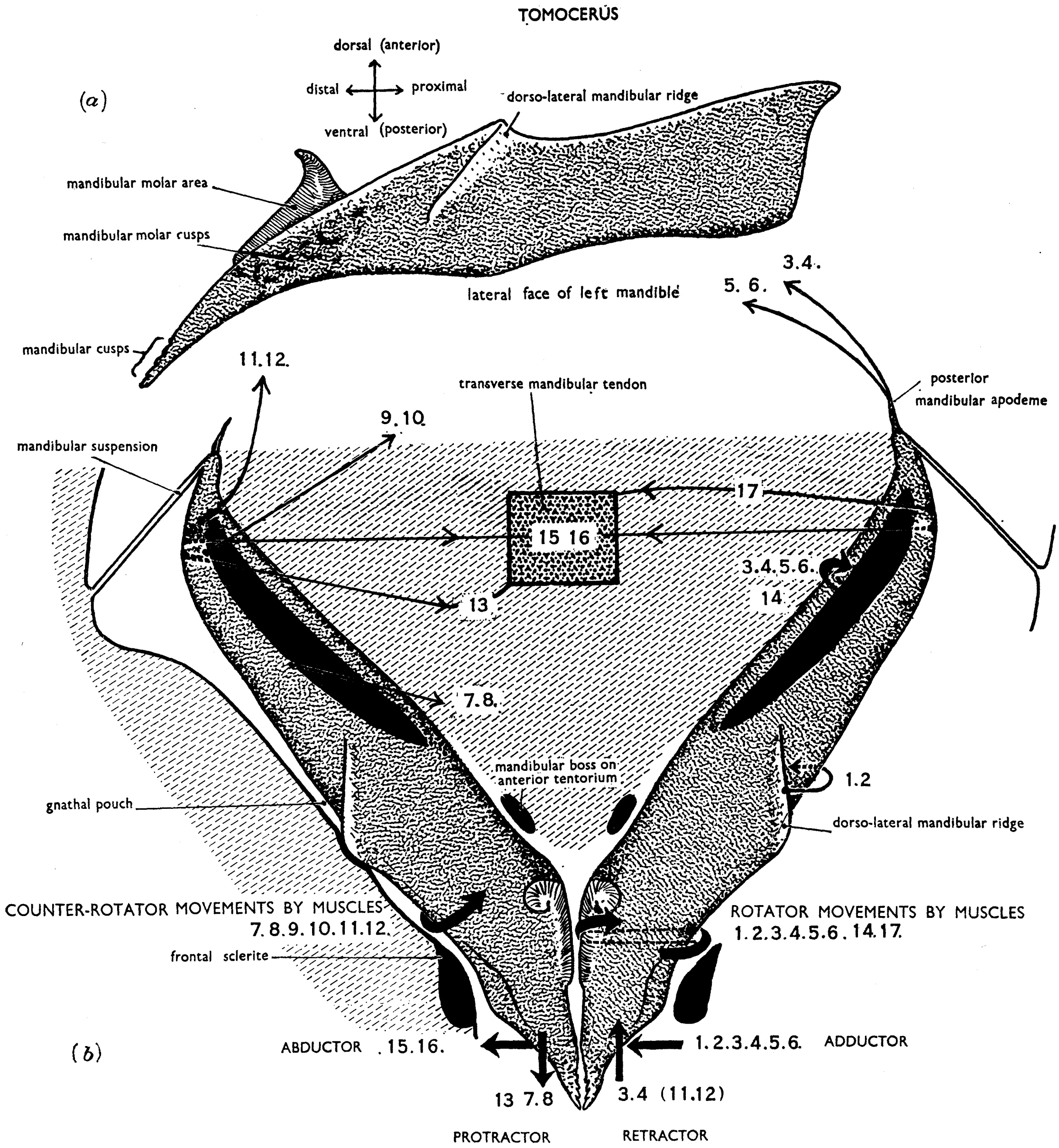


FIGURE 42. *Tomocerus longicornis* (Müller). (*a*) Shows the mandible in lateral view; the distal serrated lobe is downwardly directed and the grinding molar area projecting from the mesial face gives an upward process extending to the mouth. This process is foreshortened in (*b*) and is not shown in figures 32 and 33. The stout cusps on the posterior edge of the molar area are indicated as if the mandible was transparent.

(*b*) A diagram of the mandibles in their natural position in the head in antero-dorsal view to summarize the functions of the muscles. In using the diagram it must be remembered that no allowance can be made for foreshortening and for muscle pulls being exercised at an angle to the plane of the paper. The frontal sclerite and mandibular boss on the anterior tentorial apodeme, which limit the transverse range of movement of the tips of the mandibles, are shown in black. Rotator movements (curved arrow) and rotator muscles are shown on the right and counter-rotator movements (curved arrow) and muscles on the left. The muscles which can give predominantly protractor, retractor, adductor and abductor movements are listed. Different combinations of muscle contractions can give very many different kinds of small movements. Grinding by the molar areas is accomplished only on the rotator movement, but scratching by the distal cusps may be effected both by the rotator and counter-rotator movements. Protractor movements which may puncture food surfaces can take place alone or combined with abductor, counter-rotator movements. The effects of any one muscle depends on the action of other muscles.

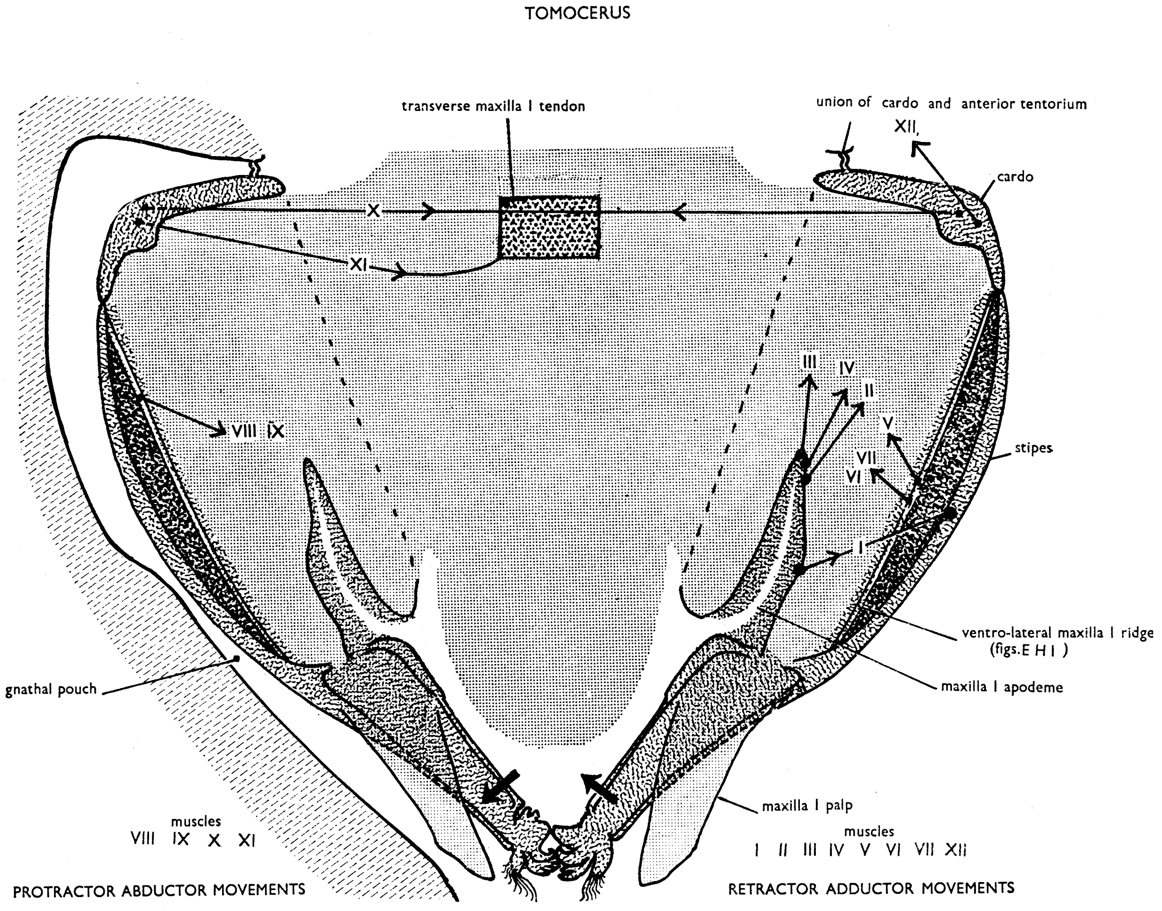


FIGURE 43. Diagram showing the maxilla 1 of *Tomocerus longicornis* to illustrate the muscles and movements controlling the distal armature of the inner lobe (cf. figure 34 for *Tomocerus* and figures 22, 27, 45 for other hexapods). The anterior margin of the maxilla is lightly tinted and bears muscle 1; the lateral ridge of the stipes, bearing muscles V to IX, lies deeper and is shown by a double line (cf. figure 37H) and a little beyond it arthrodial membrane extends as far as the dotted line.

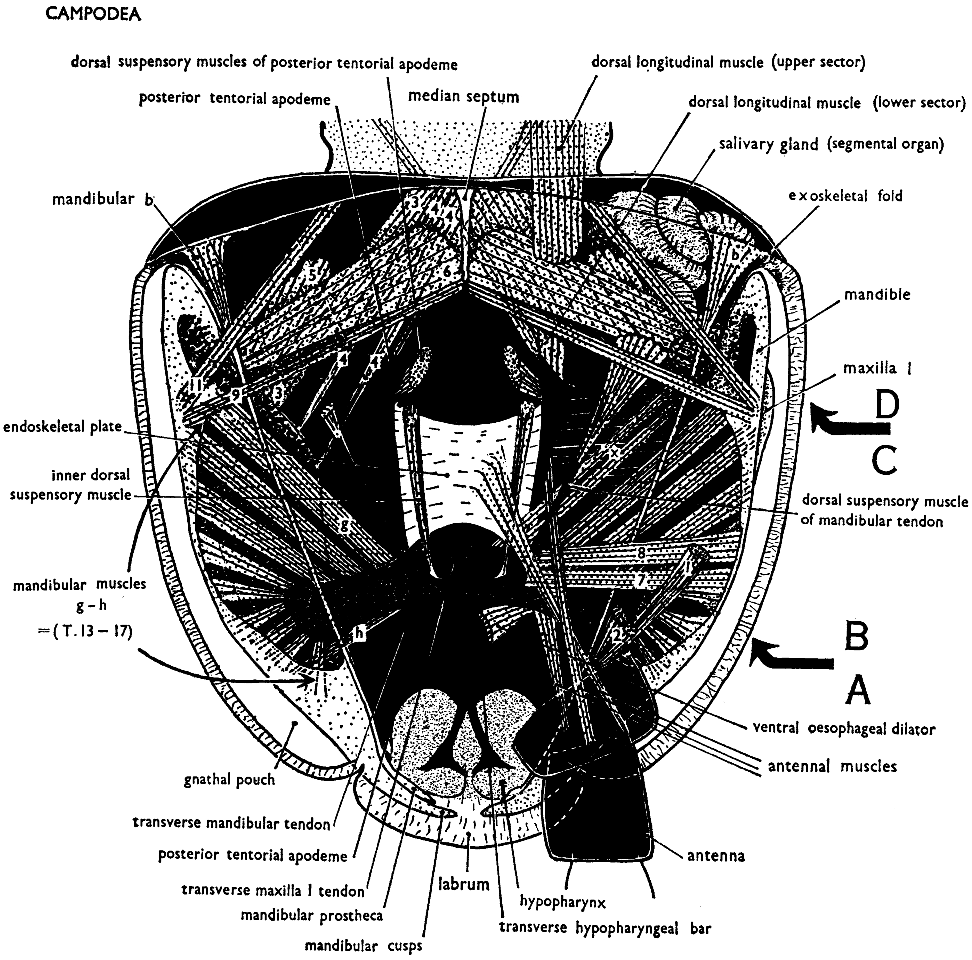


Figure 44. *Campodea staphylinus* West. Antero-dorsal reconstruction of the head, drawn as a transparent object. The antennal base, the antennal and superficial mandibular muscles, the unobscured muscles of maxilla 1, and some coils of the labial gland (segmental organ) are shown on the right, these structures being omitted on the left in order to display the mandible. Superficial mandibular muscles 7 and 8 are omitted on the left. Transverse segmental tendons are blue and the paired posterior tentorial apodeme and its processes are shown in red. The arrows indicate the levels and direction of view of the sectioned heads shown in figure 46. Mandibular muscles bear Arabic numerals and maxilla 1 muscles bear Roman numerals. The numbering suggests the homologies believed to exist between the muscles of *Tomocerus* and *Campodea*, figures 32 to 43, where similar numbering is employed. Mandibular muscles 1 and 2 are present in the Collembola and Diplura alone; muscles 3 to 11 here can be recognized also in *Petrobius* (see table of homologies between muscles of *Petrobius* and of *Tomocerus* in figure 21, which holds also for *Campodea* (muscles 3 to 11)). The muscles between the arrows on the left (between muscle fibres *g* and *h*) represent muscles 13 to 17 of *Tomocerus* but do not correspond in detail; they correspond more closely with *Petrobius* muscles 8 to 10, figure 21. Muscle fibres *g* and *h* are so marked by Tuxen (1959); the further relationship of his lettering with the numerals employed here is given on p. 65.

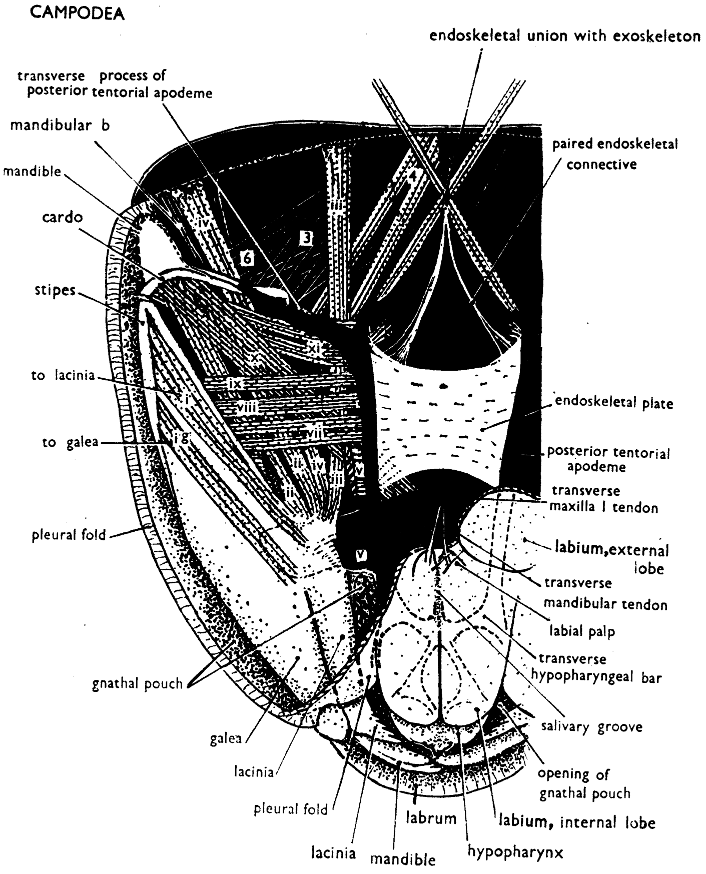


FIGURE 45. Reconstruction of the head of *Campodea staphylinus* in ventral view, drawn as if the surface cuticle and ectoderm on the right were cut away proximal to the external lobe of the labium and on the left uncovering the whole gnathal pouch, leaving only the distal part of the pleural fold (marked) forming the lip of the gnathal pouch. Cut edges are hatched. The stiff cuticle of maxilla 1 forms the postero-ventral face of the limb, here exposed in surface view (see figures 46A to C). Head endoskeleton is indicated as in figure 44 and muscle numbering is similar. The whole posterior tentorial apodeme is shown together with the short link of arthrodial membrane from the cardo to the apodeme. The posterior end of the mandible is visible above the maxilla. The correspondence between the maxilla 1 muscles, marked by Roman numerals, and the lettering of the muscles referred to by Tuxen (1959) is given in the footnote to p. 68.

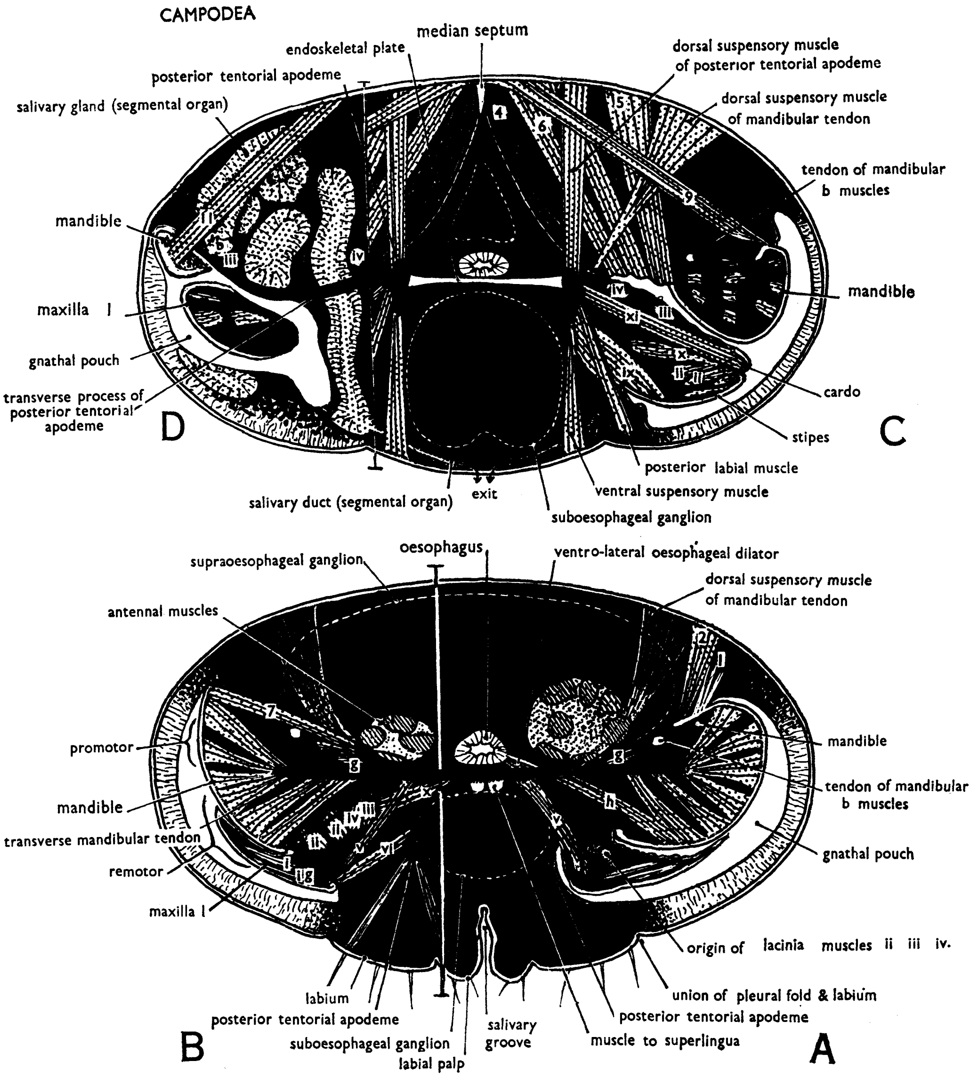


FIGURE 46. For legend see facing page.

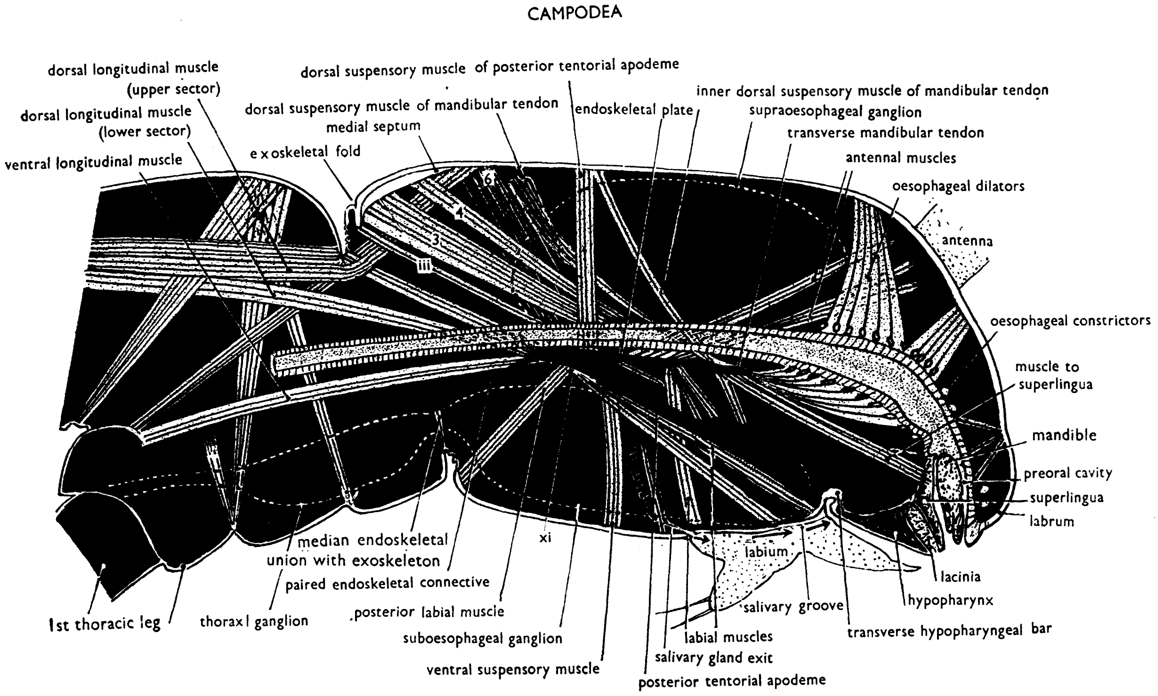


FIGURE 47. For legend see facing page.

FIGURE 46. Transverse portions of the head of *Campodea staphylinus* sectioned along the planes A to D indicated on figure 44 and observed from the distal face. Transverse segmental tendons and tentorial apodemes are shown in blue and red respectively. The limits of the supra- and sub-oesophageal ganglia are indicated by dotted lines (see also figure 47). The salivary ducts from the labial segmental organs open into a median labial groove, marked salivary groove, anterior to the level of section C. Cuticle but no ectoderm is shown. The brackets indicate the positions of promotor and remotor muscle fibres inserting in the transverse mandibular tendon.

FIGURE 47. Reconstruction of a sagittal half of the head of *Campodea staphylinus* to show the relationship of the transverse tendons with the posterior tentorial apodeme of the left side and with the muscles. The opening of the salivary duct into the posterior end of the median labial groove (salivary groove in figure 46A) is indicated and the direction of flow towards the mouth is shown by arrows. On the left the section is sub-median, passing through the coxa of the first thoracic leg. The positions of the ganglia of the nervous system are indicated by dotted lines.

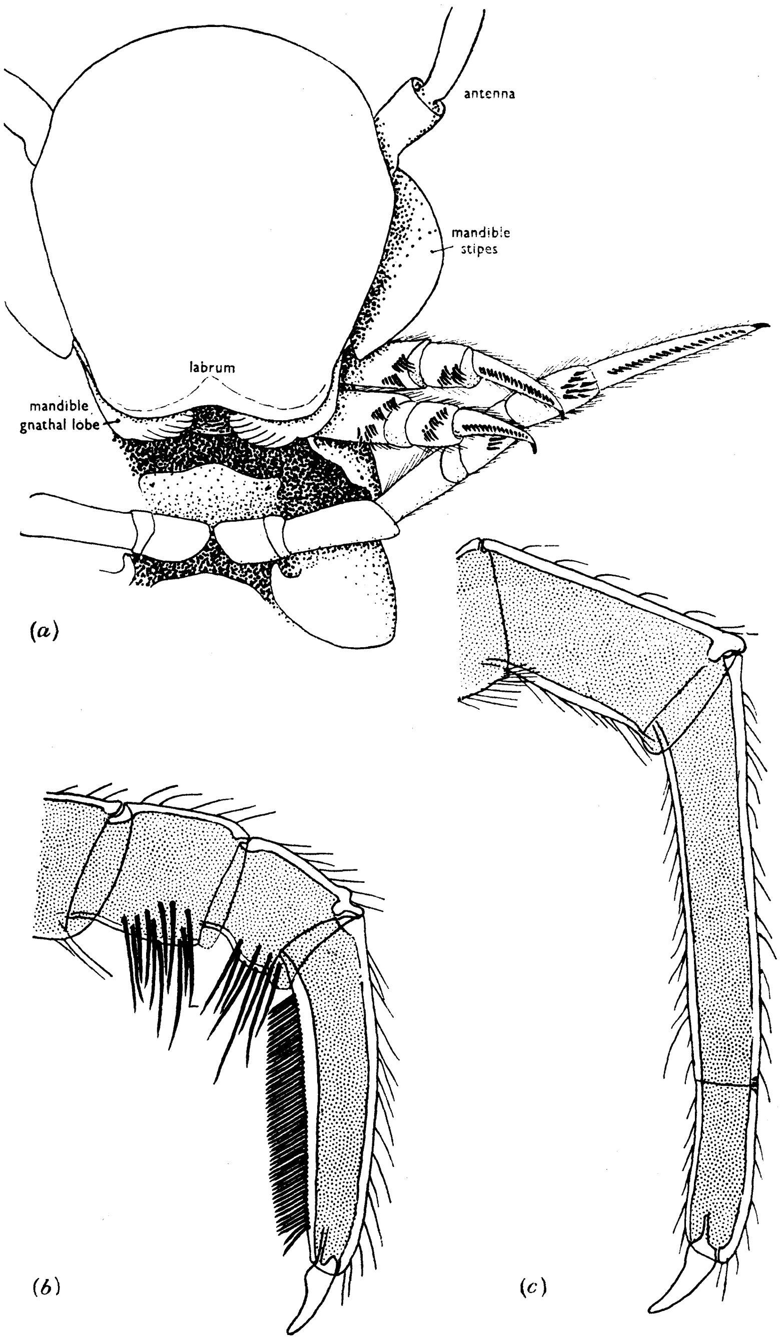


FIGURE 48. (*a*) Ventral view of the anterior end of the scavenging carnivorous diplopod *Callipus foetidissimus* (Savi), male, to show the three short spinous anterior pairs of legs which are used for holding food but not for walking. (*b*) and (*c*) anterior views of legs 2 and 30. The spines shown in heavy line are thick and highly sclerotized and are absent on the more posterior legs behind leg 3.

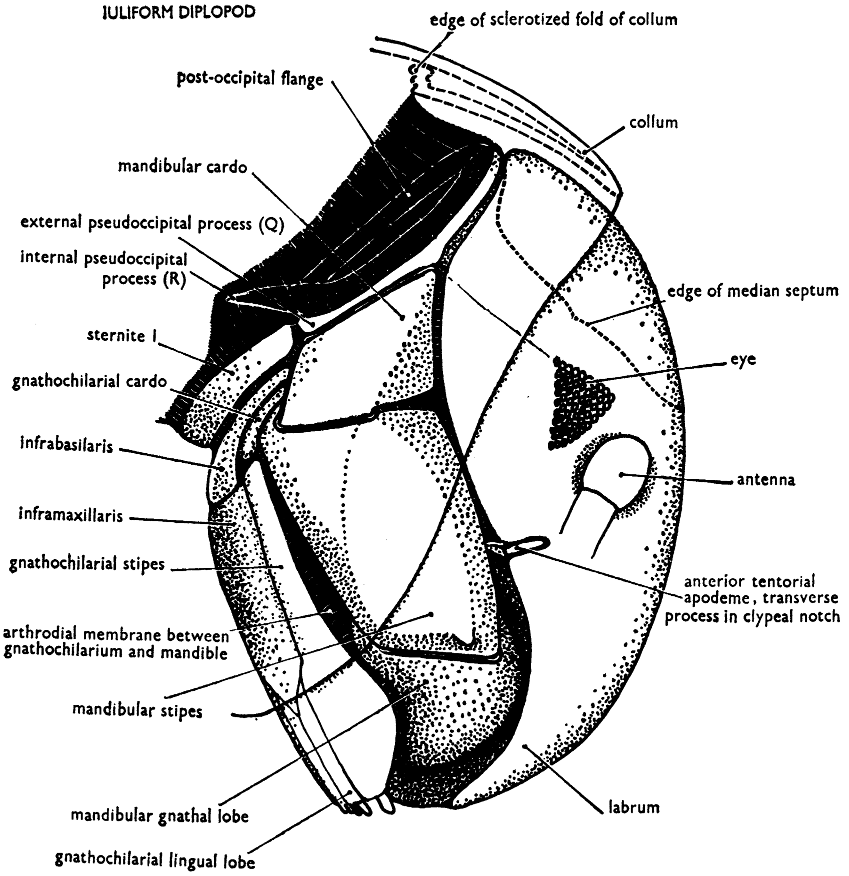


FIGURE 49. For legend see facing page.

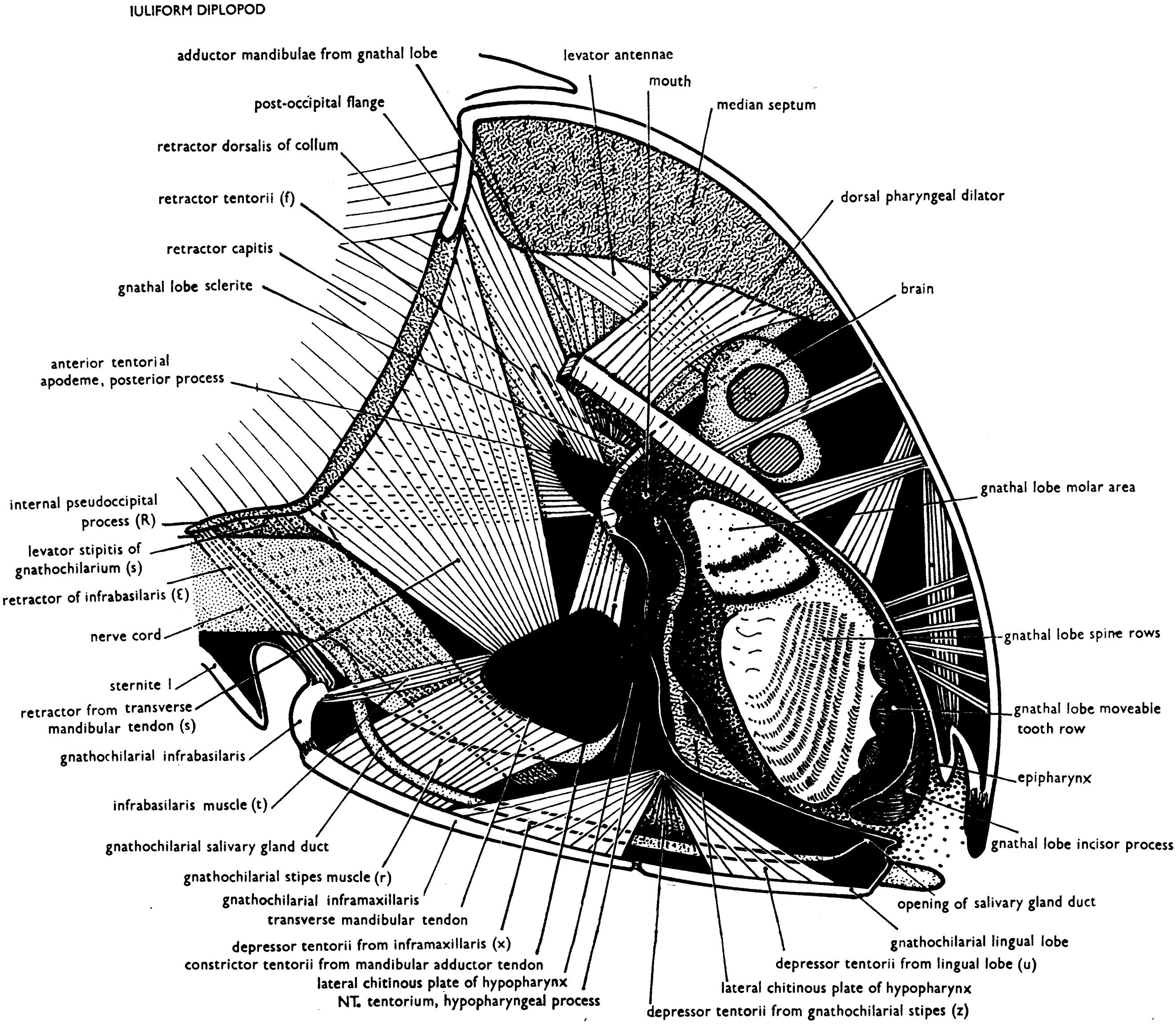


FIGURE 50. For legend see facing page.

FIGURE 49. Lateral view of the head of the spirostreptomorph diplopod *Poratophilus punctatus* Attems. The collum is drawn as if it were transparent and the antenna is cut short. Arthrodial membrane is indicated in black.

FIGURE 50. Sagittal half of the head of the diplopod *Poratophilus punctatus*. Most of the pharynx is cut away, leaving a dorsal section bearing the dorsal pharyngeal dilator muscle. The postero-dorsal pharyngeal dilator inserting on the post-occipital flange is cut away. The median part of the hypopharynx is also removed to display the lateral cuticular plate covering the hypopharyngeal process of the anterior tentorial apodeme (red). The distal part of this process, the 'Nebententorium', is jointed to the proximal part. The posterior process of the anterior tentorial apodeme curls round the sclerite in the gnathal lobe adductor tendon. Cut cuticle and ectoderm are white, uncut cuticular surfaces are mottled and the cut transverse mandibular tendon is blue and hatched. See footnote, p. 75.

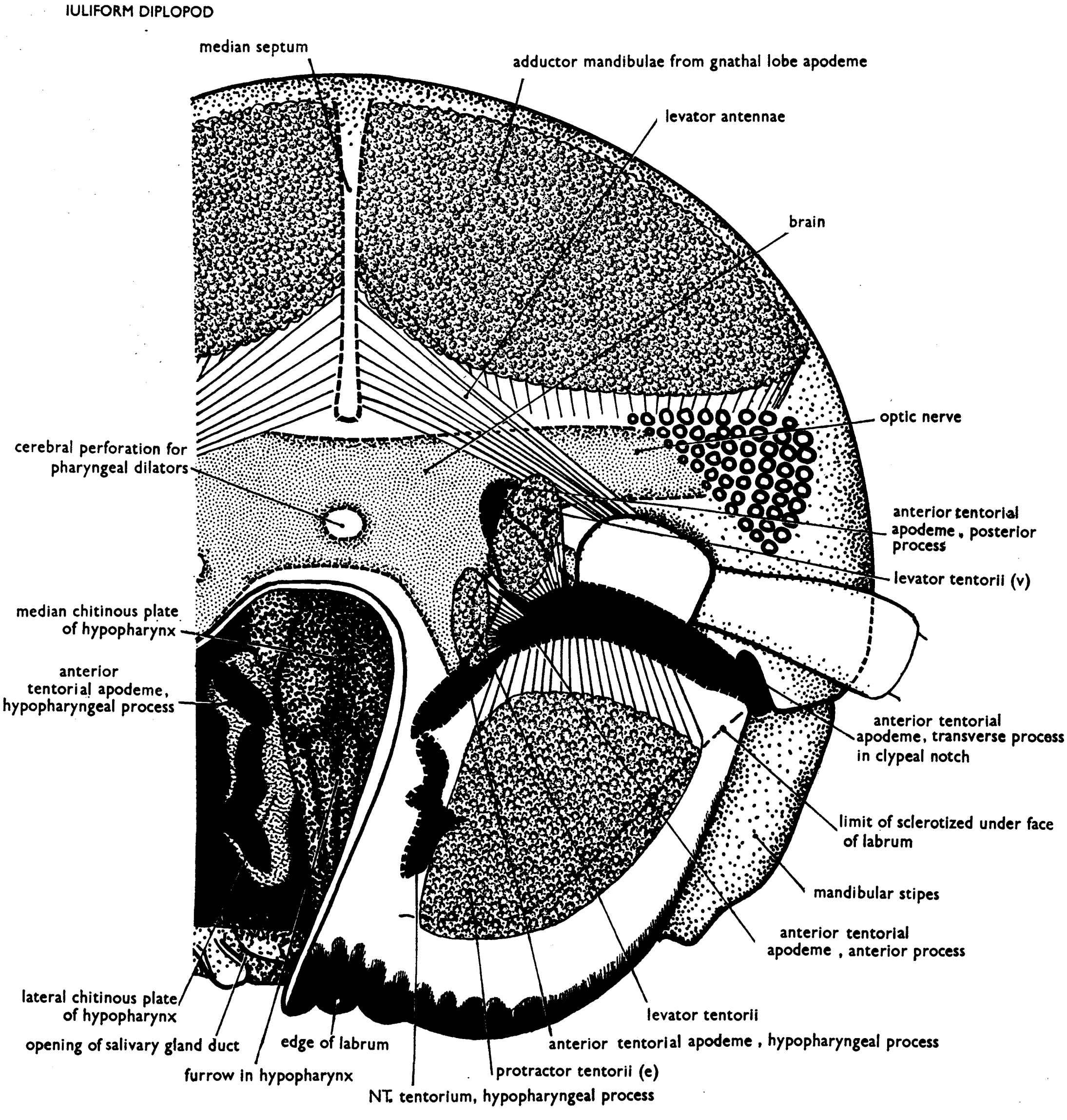


FIGURE 51. Anterior view of the head of the diplopod *Poratophilus punctatus* drawn as if the cuticle was transparent, with part of the labrum cut away to expose the hypopharynx, the gnathal lobe of the mandible being omitted. The position of the anterior tentorial apodeme and its processes is shown in red with black stipple and the heavy marginal sclerotization of the labrum is shown in black. The supraoesophageal ganglion is shown by fine stipple and a convention indicates muscle insertions on the cuticle.

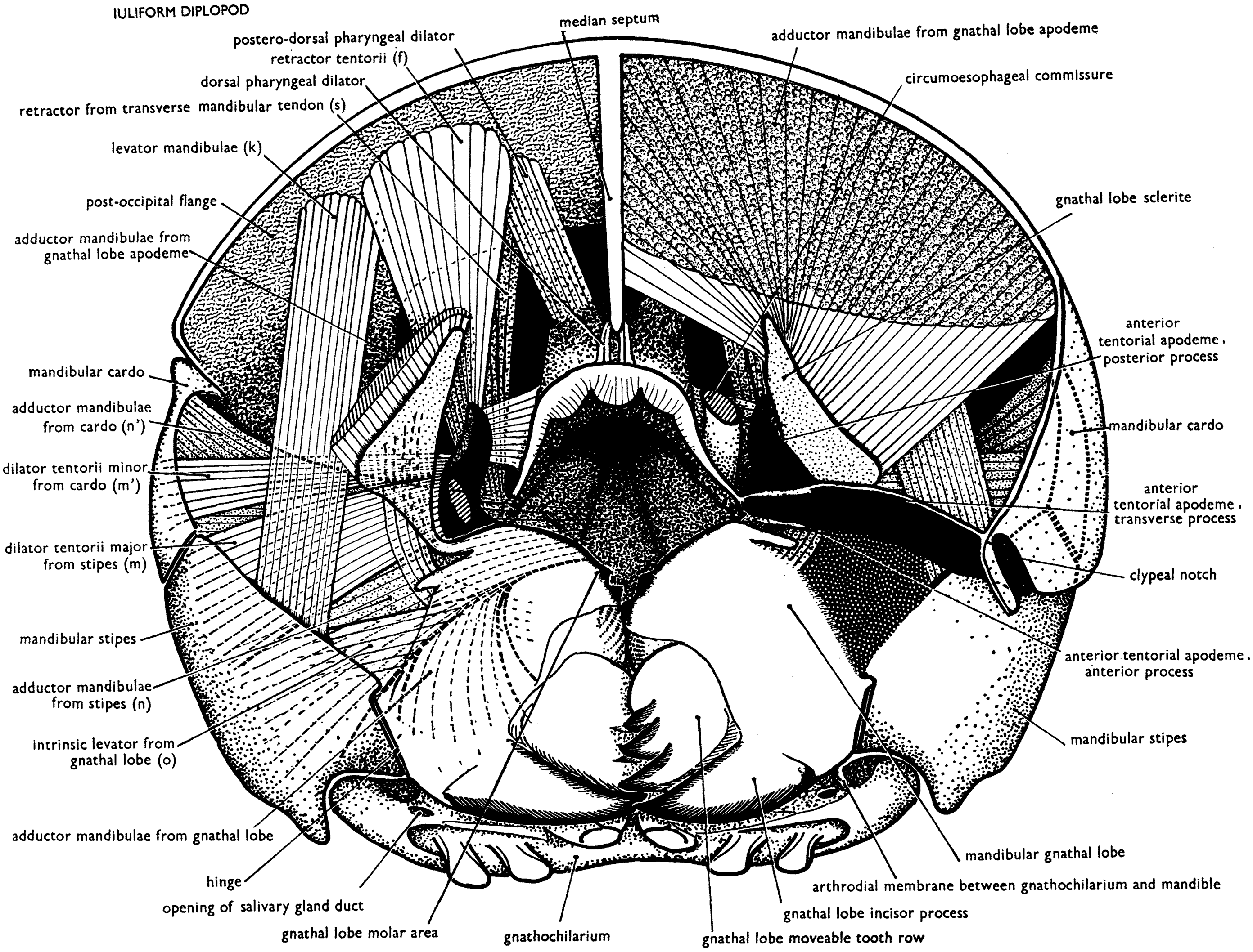


FIGURE 52. Anterior view of the head of the diplopod *Poratophilus punctatus* with the labrum cut away. The mandibular gnathal lobes are fully adducted. On the right: the preoral cavity is intact showing the transverse process of the anterior tentorial apodeme (red) lying in the arthrodial membrane (white stipple); the cranial roof has been cut away, leaving the clypeal notch; and the supraoesophageal ganglion has been removed. On the left: the transverse process of the anterior tentorial apodeme has been removed, its cut stump being hatched; the cranial wall is cut away entirely so as to expose the whole of the mandible; the gnathal lobe adductor muscle has been removed in order to show the deeper muscles and the post-occipital flange; and the circumoesophageal commissure is removed. See footnote p. 75.

FIGURE 54. View looking into the preoral cavity of the diplopod *Poratophilus punctatus*. The distal part of the gnathochilarium is lowered and consequently the mandibular gnathal lobes are widely abducted exposing the hypopharynx. The labrum is bent upward in an abnormal manner in order to show the epipharynx and the transverse process of the anterior tentorial apodeme (red). The whole of the anterior tentorial apodeme is shown, the posterior process being drawn as if the preoral cuticle was transparent and the 'Nebententorium' lies below the distal part of the lateral hypopharyngeal scutes. The paired arrows show the direction of thrust from the hypopharyngeal processes of the anterior tentorial apodemes against the gnathal lobes of the mandibles which causes mandibular abduction. The arrow on the right shows the level of abnormal bending back of the labrum and epipharynx. See footnote p. 75.

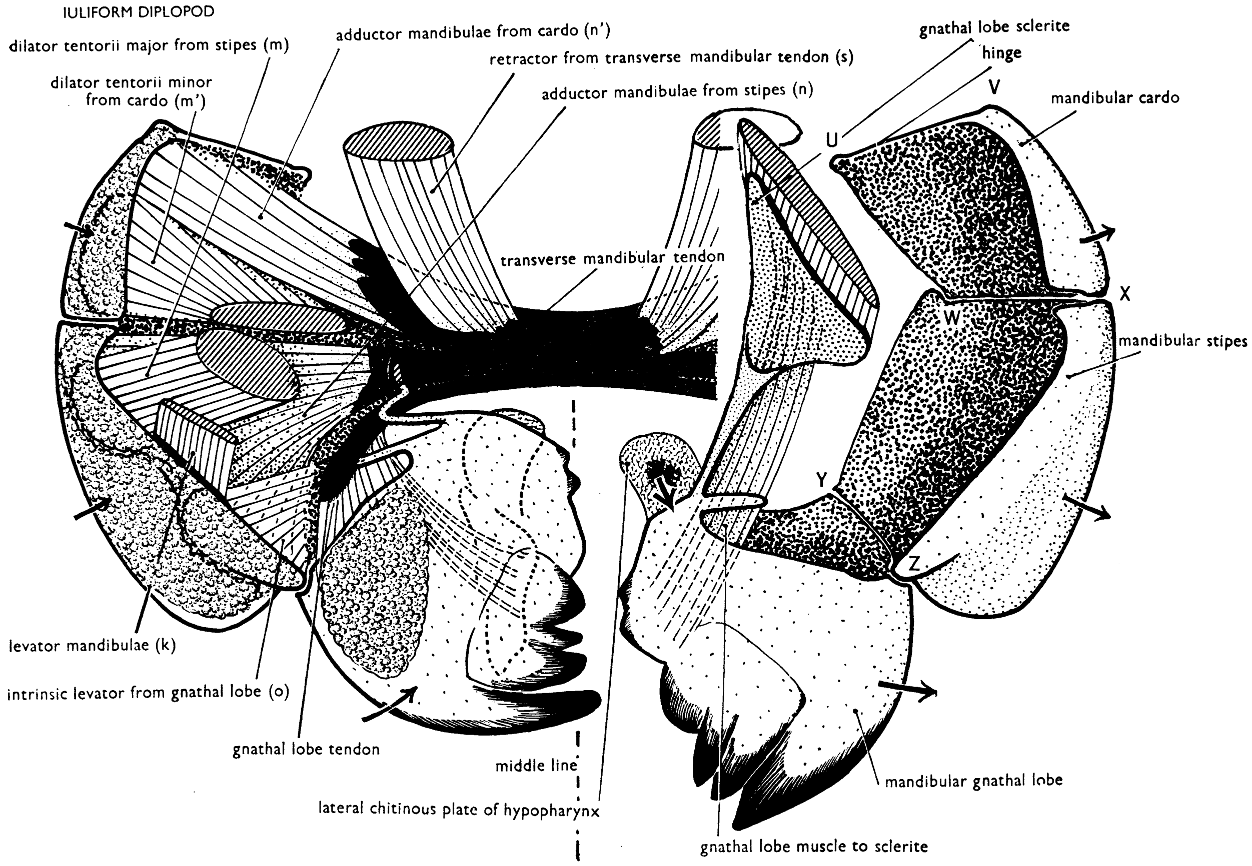


FIGURE 53. Anterior view of the isolated mandibles of the diplopod *Poratophilus punctatus*. On the left side the musculature is entire and the gnathal lobe and whole mandible is in a position of maximum adduction. On the right the muscles have been removed from the mandibular cuticle, with the exception of one intrinsic muscle, and the mandible and gnathal lobe are in a position of extreme abduction. The contrasting positions of the lateral hypopharyngeal scutes is also shown; the heavy arrow on the right indicates the direction of thrust of the anterior tentorial apodeme against the gnathal lobe.

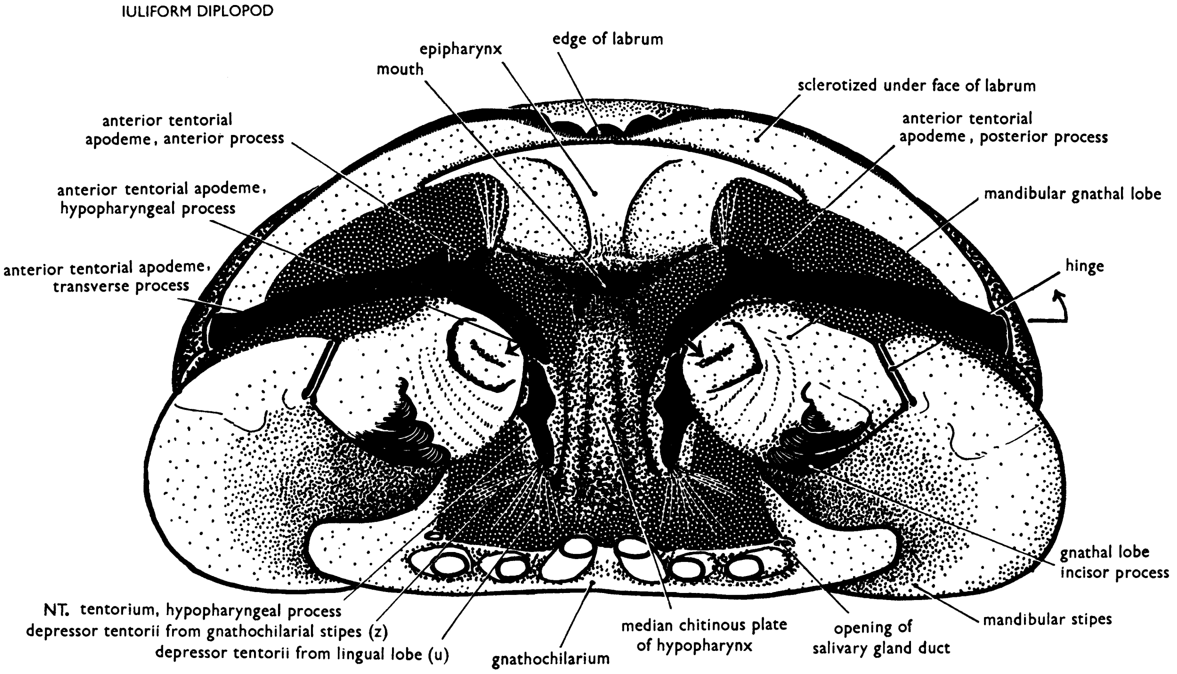


FIGURE 54. For legend see facing page.

FIGURE 55. Diagrams of a iuliform diplopod showing the participation of the tentorial, gnathochilarial and mandibular muscles in promoting mandibular adduction and abduction and the simultaneous closing and opening of the preoral cavity. Black indicates tension on a muscle, the mandible is coarsely mottled, the transverse mandibular tendon is blue, the anterior tentorial apodeme is red and the sclerite in the mandibular gnathal lobe tendon is white. The circle marks the point of thrust by the tentorial apodeme on the hypopharynx and gnathal lobe. For further description see text.

FIGURE 56. Lateral view of the head of the symphylan *Scutigerella immaculata* Newport drawn as a transparent object to show the position and component parts of the mandible. The muscles situated in the basal segment are shown and the gnathal lobe and its apodemes are finely ruled. Mandibular muscles 1 and 8 to the cranium are shown. The lateral knob-like process from the distal part of the basal mandibular segment is shown lying outside the galea in a strengthened concavity of the latter; the combine forms part of the mandibular abductor mechanism. The arrows D to K mark the levels of transverse sections shown in figure 59. For mandibular muscles 2 and 3 see figure 57 B.

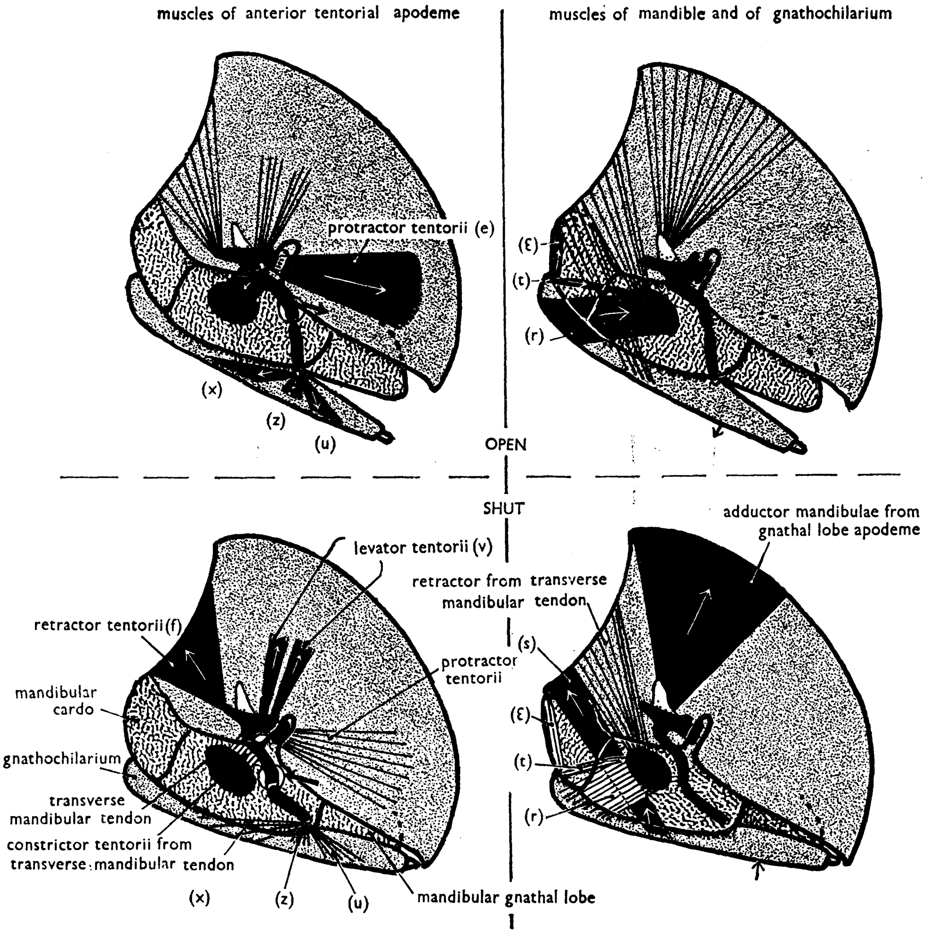


FIGURE 55. For legend see facing page.

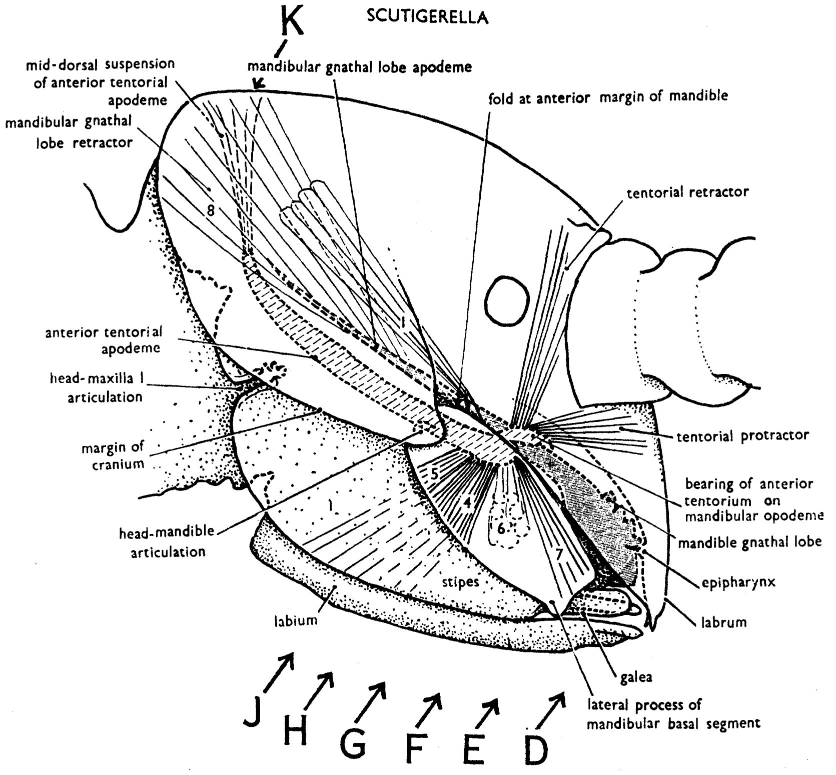


FIGURE 56. For legend see facing page.

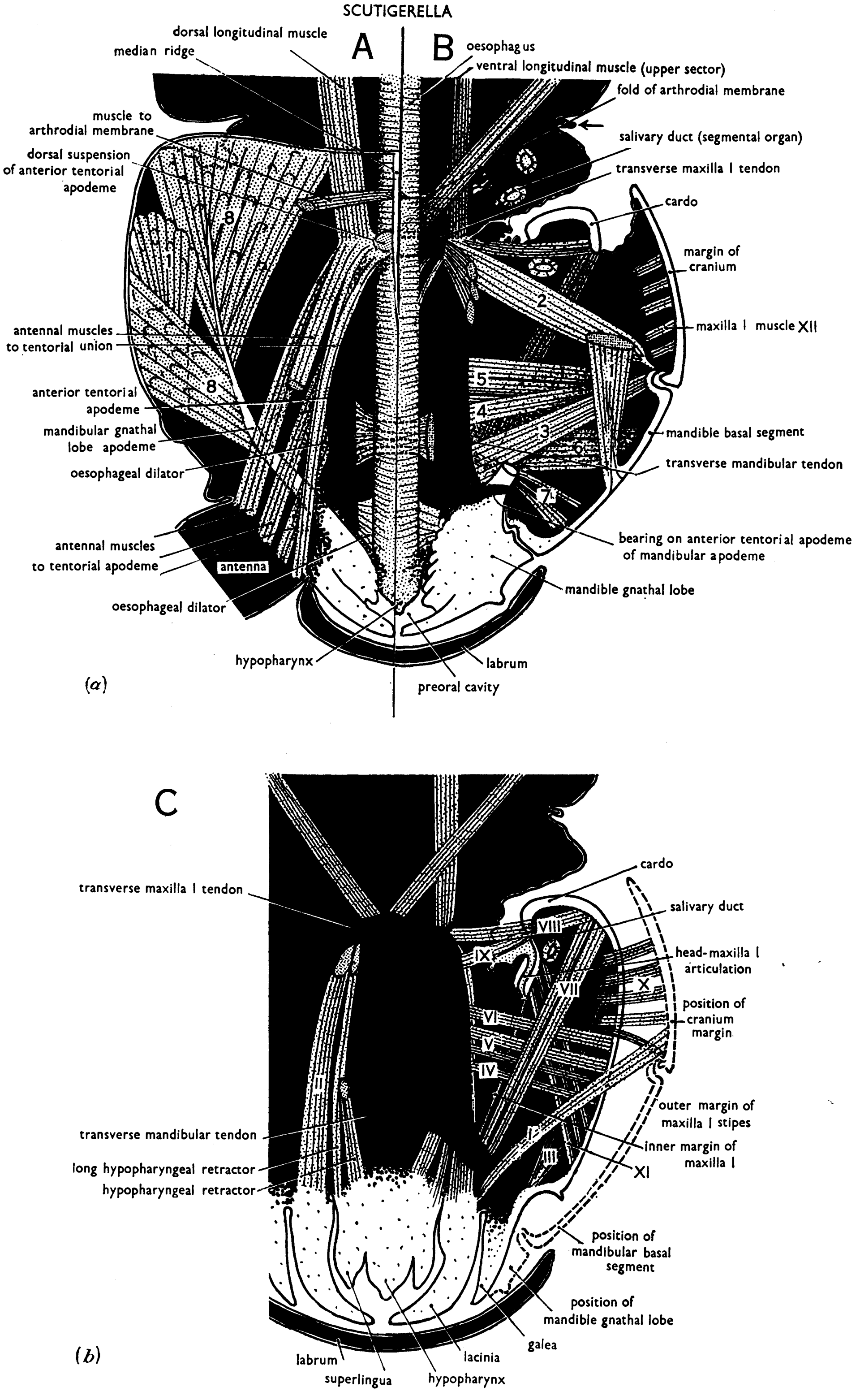


Figure 57. Dorsal reconstructions of the head of *Scutigerella immaculata* Newport to show the muscular ture, the mandibles, the maxillae and the endoskeleton. The transverse segmental tendons are blue and the tentorial apodeme is red.

Level A. Upper level showing the most superficial of the antennal muscles, the adductor muscle 8 to the gnathal lobe, the insertion of muscle 1 and the supra-oesophageal bridge with the tentorial suspension, see also figure 59K.

Level B. A lower level, the postero-dorsal overhanging part of the cranium is sliced off leaving the lateral lobe above the maxilla 1 (see figure 56). The junction of head and trunk is shown by the arrow. The antenna together with the gnathal lobe apodeme and muscle 8 is sliced away so displaying the whole of the mandible. An oesophageal dilator muscle inserting on the anterior tentorial apodeme has been cut, so displaying the transverse mandibular tendon.

Level C. Deeper level, in dorsal view, to show maxilla 1 and the endoskeleton. The positions above of the edges of the mandible and overhanging cranial lobe bearing muscles I and X are shown by dotted lines. The finely stippled area marks the inner part of the space between head wall and the cardo region of the maxilla, and is so marked in order to show up the articular facets of the maxilla 1-head joint.

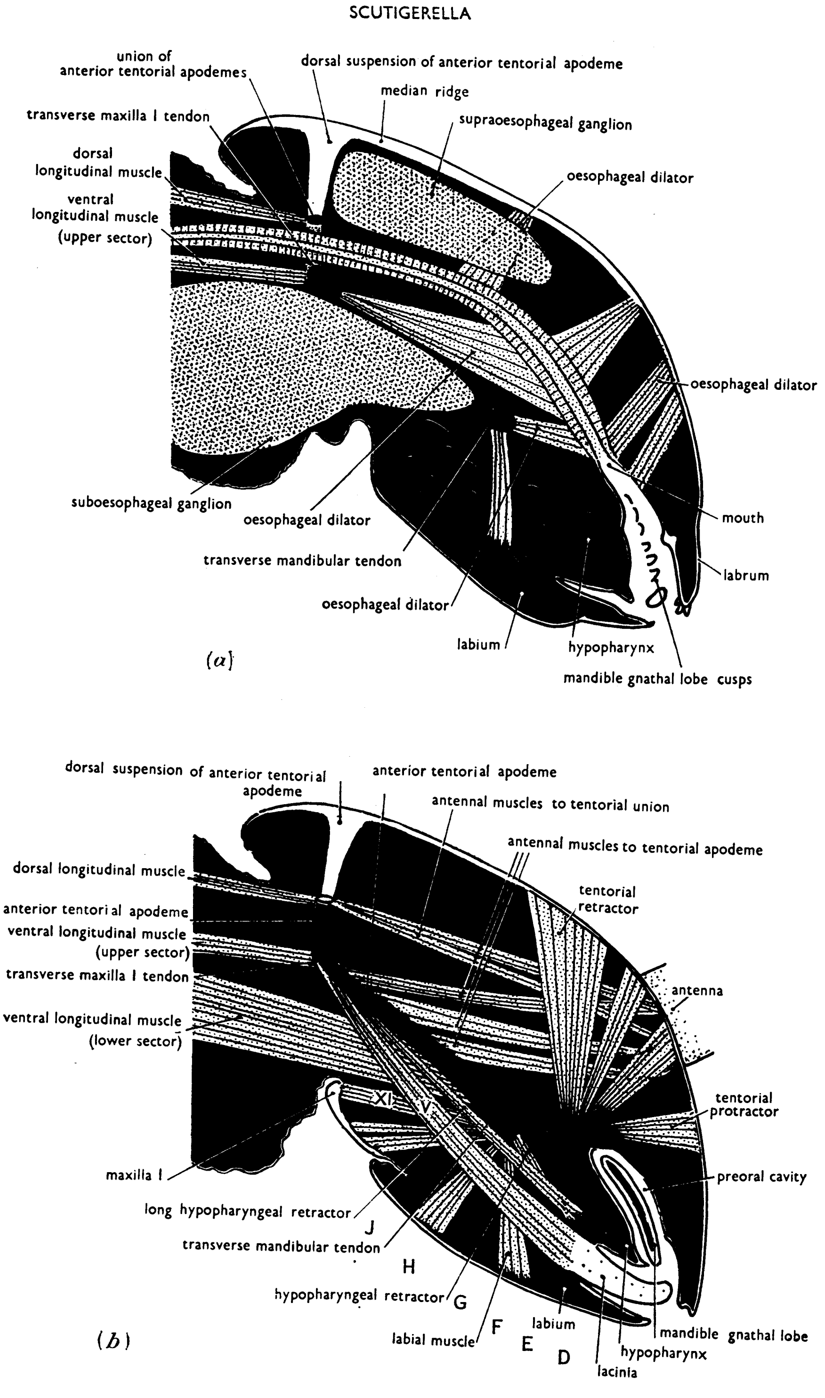


FIGURE 58. Sagittal half of the head of *Scutigerella immaculata*. Cuticle but not ectoderm is drawn. (*a*) Shows the most median structures and (*b*) shows parasagittal structures after removal of the alimentary canal and nerve ganglia. The whole of the anterior tentorial apodeme is exposed together with the muscles to which it gives attachments.

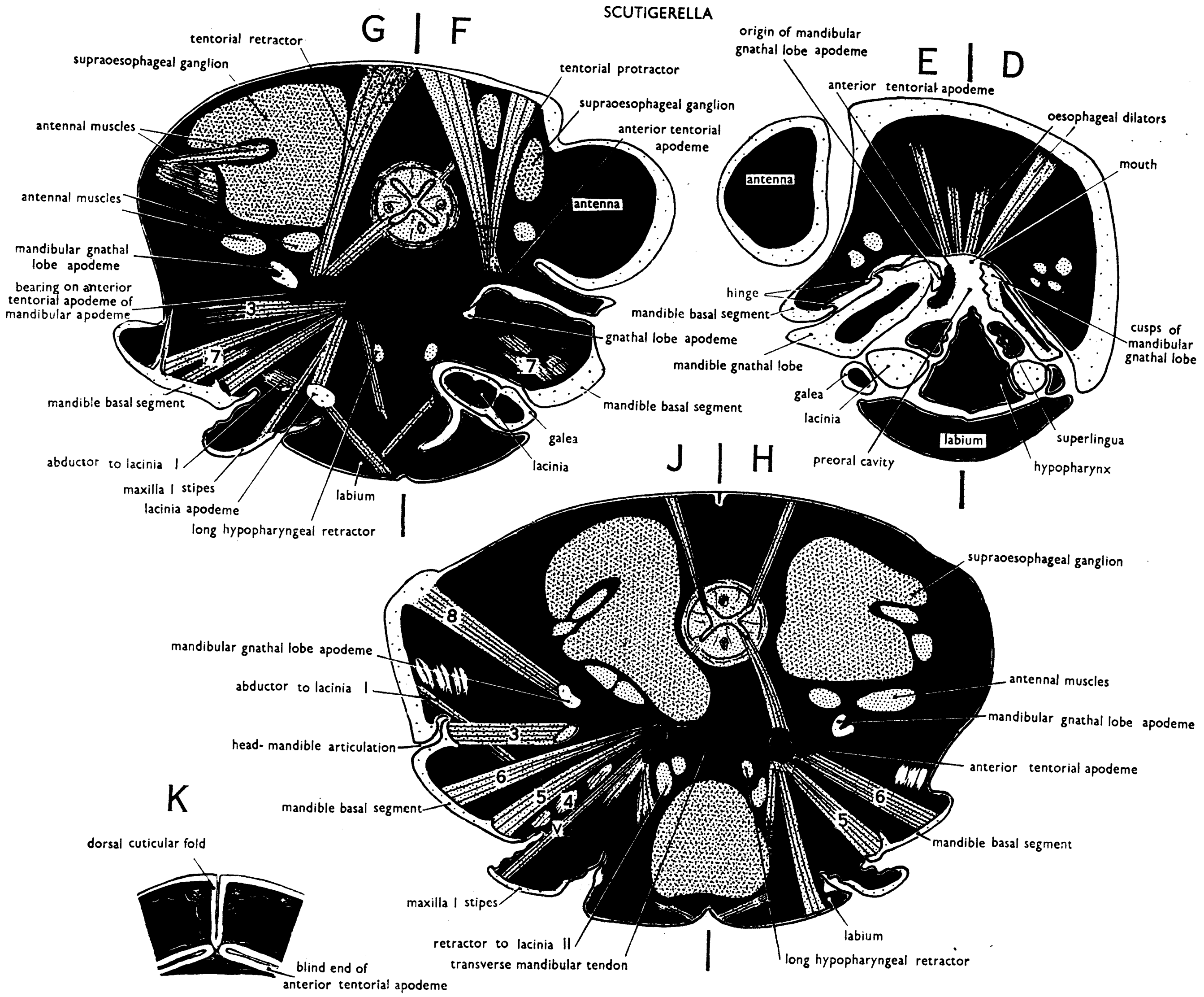


Figure 59. Diagrams of the head of *Scutigerella immaculata* cut transversely at the levels indicated by the letters D to K in figure 56, and viewed from in front. The diagrams include structures lying behind the plane of section. Cuticle but not ectoderm is drawn.

Level D. Through the distal part of the preoral cavity.

Level E. Through the hinge between the gnathal lobe and the basal mandibular segment, cutting the origin of the gnathal lobe apodeme and ensheathing flange from the anterior tentorial apodeme.

Level F. Through the transverse process of the anterior tentorial apodeme and origin of the galea and lacinia of maxilla 1.

Level G. Through the bearing of the anterior tentorial apodeme which grips the gnathal lobe apodeme.

Level H. The anterior tentorial apodeme, hollow and concave ventrally, is sunk into the transverse mandibular tendon. The concave face of the apodeme is largely filled by its own epithelium, not drawn.

Level J. Through the articulation between the basal segment of the mandible and the cranium.

Level K. Through the cuticular dorsal suspension of the anterior tentorial apodemes.

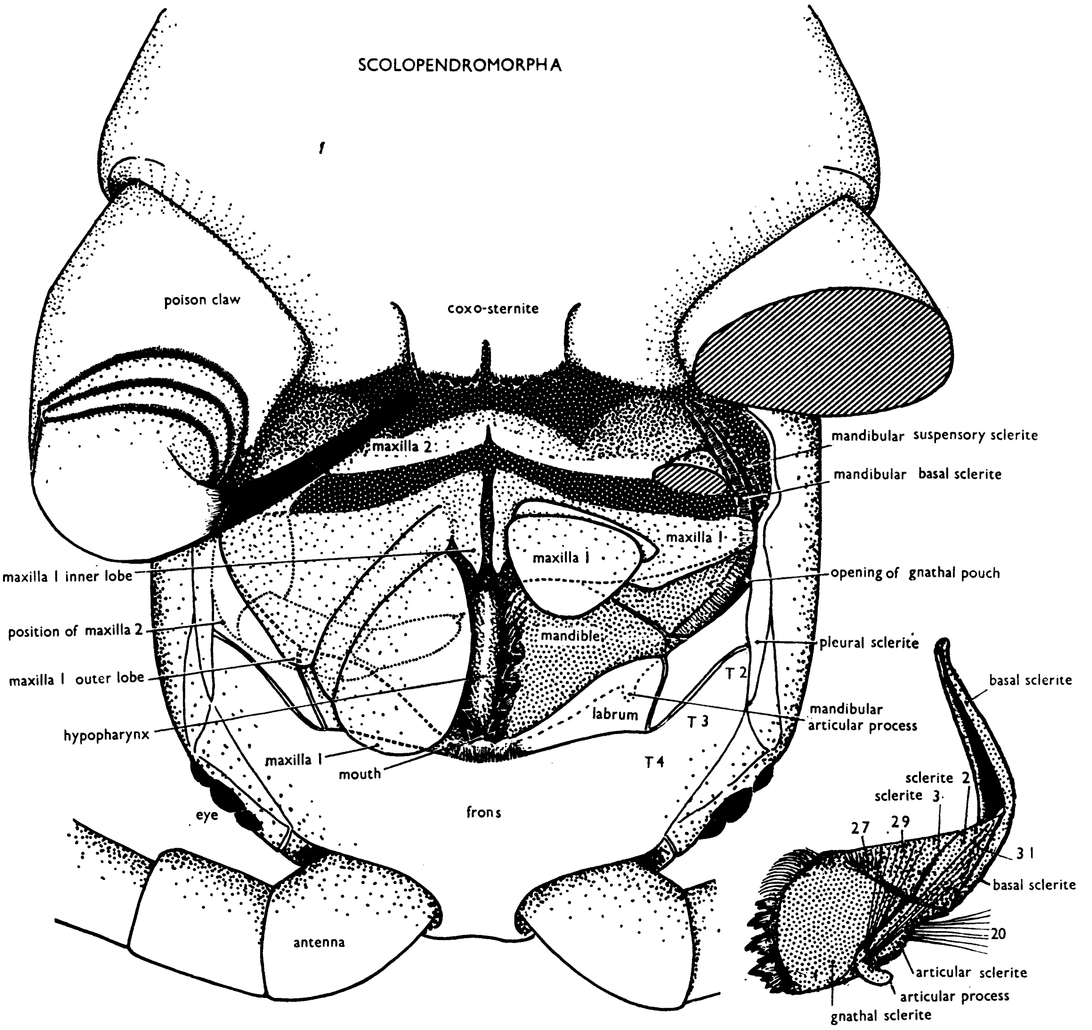


FIGURE 60. Ventral view of the head of the scolopendromorph centipede *Cormocephalus nitidosus* Por. On the left-hand side the poison claw is depressed away from the mouth and foreshortened and the position of maxilla 2 telopodite is shown by a close dotted line. The whole of the maxilla 1 is thus seen, together with its manner of overlap of the labrum and closure of the gnathal pouch. On the right-hand side the poison claw and maxilla 2 telopodite are cut away and the distal part of maxilla 1 is abnormally pulled back to expose the mandible (stippled). The whole mandible in a similar position is drawn at the side. Arthrodial membrane is stippled in white. T. 2 to T. 4 indicate the areas of insertion of tentorial muscles 2 to 4. The 5 mandibular sclerites are drawn (but see figure 64*b* for numbers), the plain numbers refer to mandibular muscles.

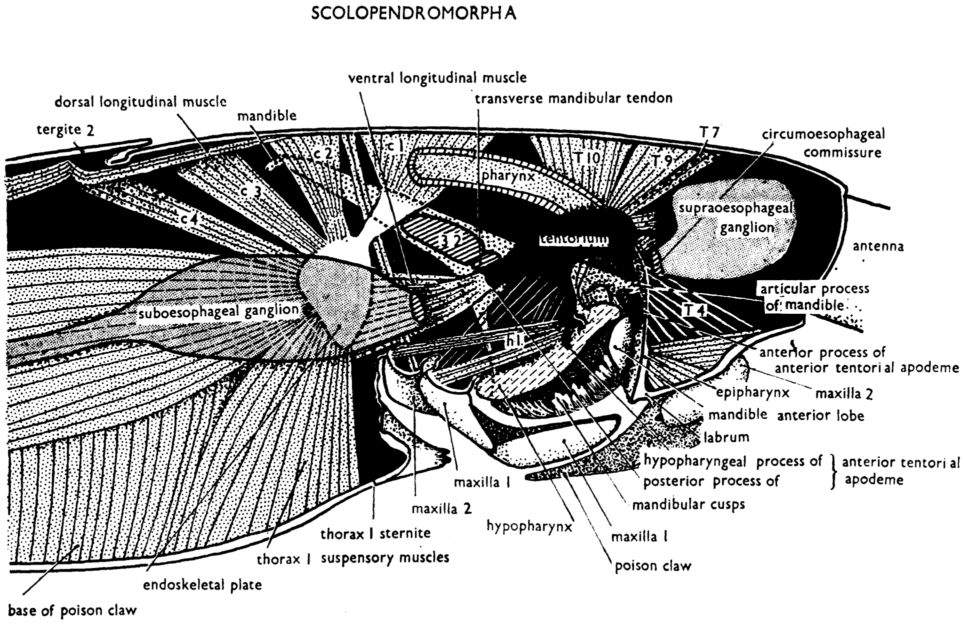
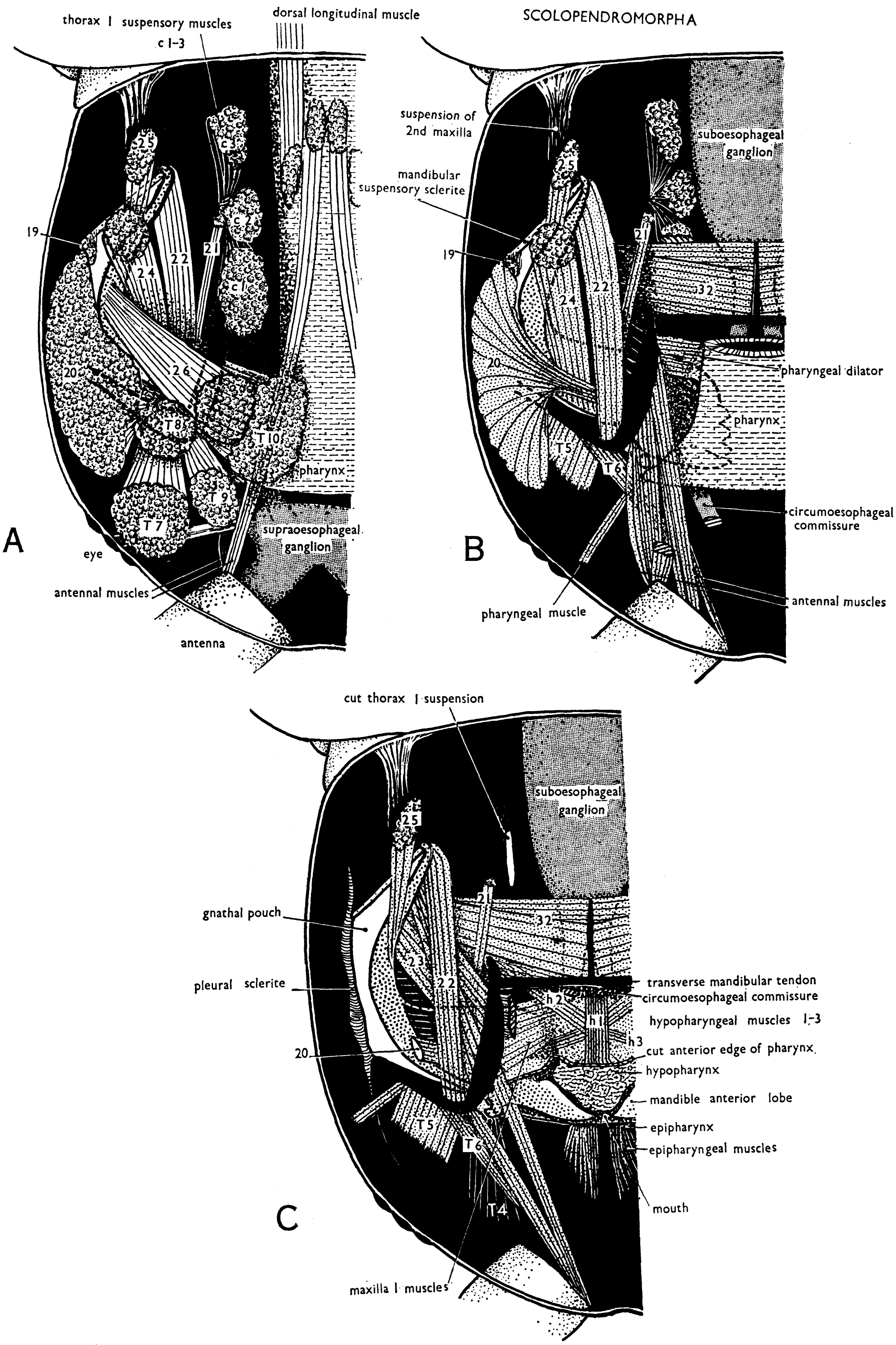


Figure 61. Sagittal half of the head of *Cormocephalus nitidosus* Por. The circumoesophageal commissure is cut away and the pharynx cut short; cuticle, but no glandular tissue or ectoderm is drawn. The preoral cavity passes into the pharynx at a level near the articulation of the mandible with the anterior process of the anterior tentorial apodeme (red). A vertical tendinous endoskeletal plate (white) bears dorsal (c. 1. to c. 4) and ventral suspensory muscles from the cranium and poison claw, and the ventral longitudinal muscles to the posterior process of the anterior tentorial apodeme; among other functions this complex raises the poison claws and retracts the tentorial apodeme (Manton 1964). The cut hypopharynx is marked by interrupted hatching, and the lateral lobe (probably homologous with a superlingua) is uncut and unlabelled, and projects into the angle of the preoral cavity near the articular process of the mandible; the whole forms a mobile tongue. The gnathal margin of the mandible is foreshortened, the soft anterior lobe of the mandible projects upwards to meet the edge of the hypopharynx, the cusp row forms the middle and the spine row the posterior parts of the free edge, which can be kept close against the hypopharynx, so retaining the food. The articular process of the mandible hooks round the anterior process of the anterior tentorial apodeme. The rest of the mandible is indicated by dotted lines and the transverse muscle 32 and transverse mandibular tendon are cut. The thick sclerotized epipharyngeal cuticle bears a muscle complex to the frons (protractor labri, d. 1 of Meinert). The muscles attached to the anterior tentorial apodeme which are here visible are: T. 4 from the anterior process to the frons; above it lies the long protractor to the pharynx (d. 12 and d. 13 of Meinert, figure 62B, unlabelled); above this lies the insertion of the antennal muscle on the tentorial apodeme, unlabelled; and dorsally muscles T. 7, T. 9 and T. 10 are labelled. Two muscles lying deep in the body are shown by white lines on black below the posterior process of the posterior tentorial apodeme, the longer and more posterior are muscles from maxilla 1 to the tentorial apodeme and the shorter and more anterior are part of muscle 27 to the mandible (figures 62C, 63D, E). The two sub-median paired hypopharyngeal muscles, h. 1, insert upon the sternites of maxilla 1 and maxilla 2 (retractor linguae duplex, d. 19 of Meinert who shows also two hypopharyngeal levators).



FIGURES 62, 63. Dorsal view of the head of *Cormocephalus nitidosus* showing structures at progressively deeper levels. Ectoderm and glandular tissue are omitted and no detail is shown of maxilla 1 and maxilla 2 muscles or of the musculature from the trunk. The diagrams show the mandible, its associated muscles, the gnathal pouch, tentorial apodemes and organs surrounding the preoral cavity. The apodemes are marked in red and the transverse mandibular tendon in blue.

The numerals mark mandibular muscles and correspond with the numbering of Meinert but prefixed by him with 'c', Meinert's descriptive terms for each muscle are not repeated here. Muscles c. 1 to c. 3 of Meinert, and so marked here, pass to the vertical tendinous plate of the first trunk segment. Muscles T. 2 to T. 10 of Meinert, and so marked here, arise from the anterior

(*Continued on p.* 180)

tentorial apodeme. The whole anterior tentorial apodeme and mandible are drawn on the same scale separately on figure 63, bottom left and right, in order to facilitate recognition of the parts shown at higher levels. Mandibular muscle origins are more clearly seen in figure 64, and a brief diagnosis of the mandibular muscles is given in the legend to figure 64.

Level A. Superficial view of intact mandibular and tentorial muscles, dorsal pharyngeal dilators and glandular tissue being removed. The optic nerve is shown but unlabelled.

Level B. The pharynx and superficial antennal muscles are cut short, supra-oesophageal ganglia are removed, and the tentorial muscles T. 7 to T. 10 are removed but their origins are indicated by a row of crosses on the anterior tentorial apodeme. The more dorsal part of muscle 20 is cut away.

Level C. Mandibular muscles 20 and 24, the more superficial of the antennal muscles inserting on the tentorial apodeme, and the pharynx are removed. The free dorsal surface of the hypopharynx is mottled and the hypopharyngeal muscles are exposed. The whole of the anterior tentorial apodeme, visible in dorsal view, is here exposed. The preoral cavity, which lies between the hypopharynx and the anterior lobe of the mandible (unlabelled), continues laterally into the gnathal pouch.

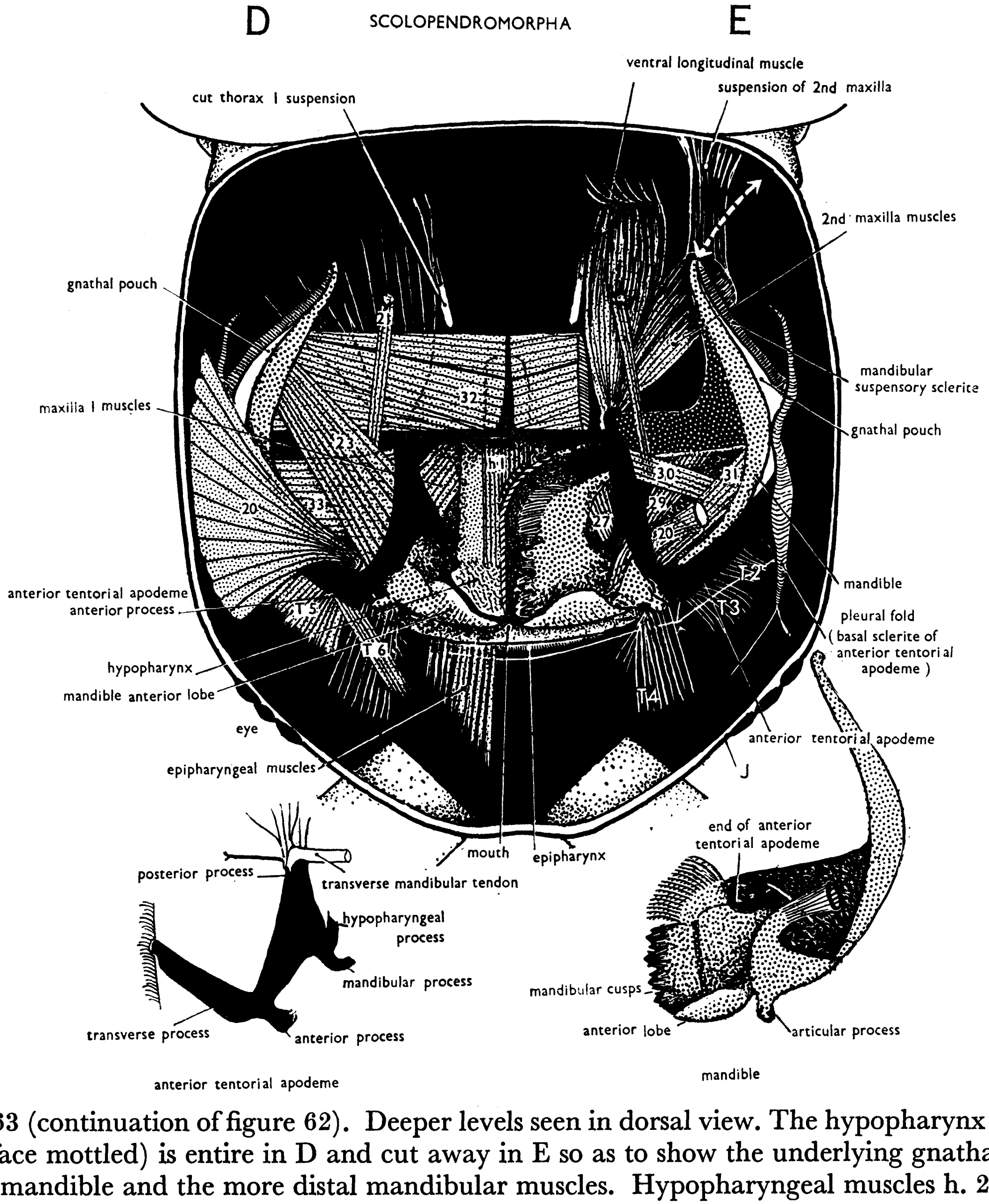


Figure 63 (continuation of figure 62). Deeper levels seen in dorsal view. The hypopharynx (exposed surface mottled) is entire in D and cut away in E so as to show the underlying gnathal edge of the mandible and the more distal mandibular muscles. Hypopharyngeal muscles h. 2 and h. 3 are cut away, the superimposed paired muscles h. 1 (see figure 61) are in place in D and cut back in E, the dotted line below muscle 32 showing the extent of muscles h. 1 which insert on the sternites of maxillae 1 and 2.

Level D. Mandibular muscle 22 is removed but muscle 20 is in part left in position.

Level E. Mandibular muscles 20, 23, 33 are removed and muscle 32 is cut short so exposing muscles 27 and 30, the origin of muscle 21 (muscle labelled on level D) and intrinsic muscles 29 and 31.

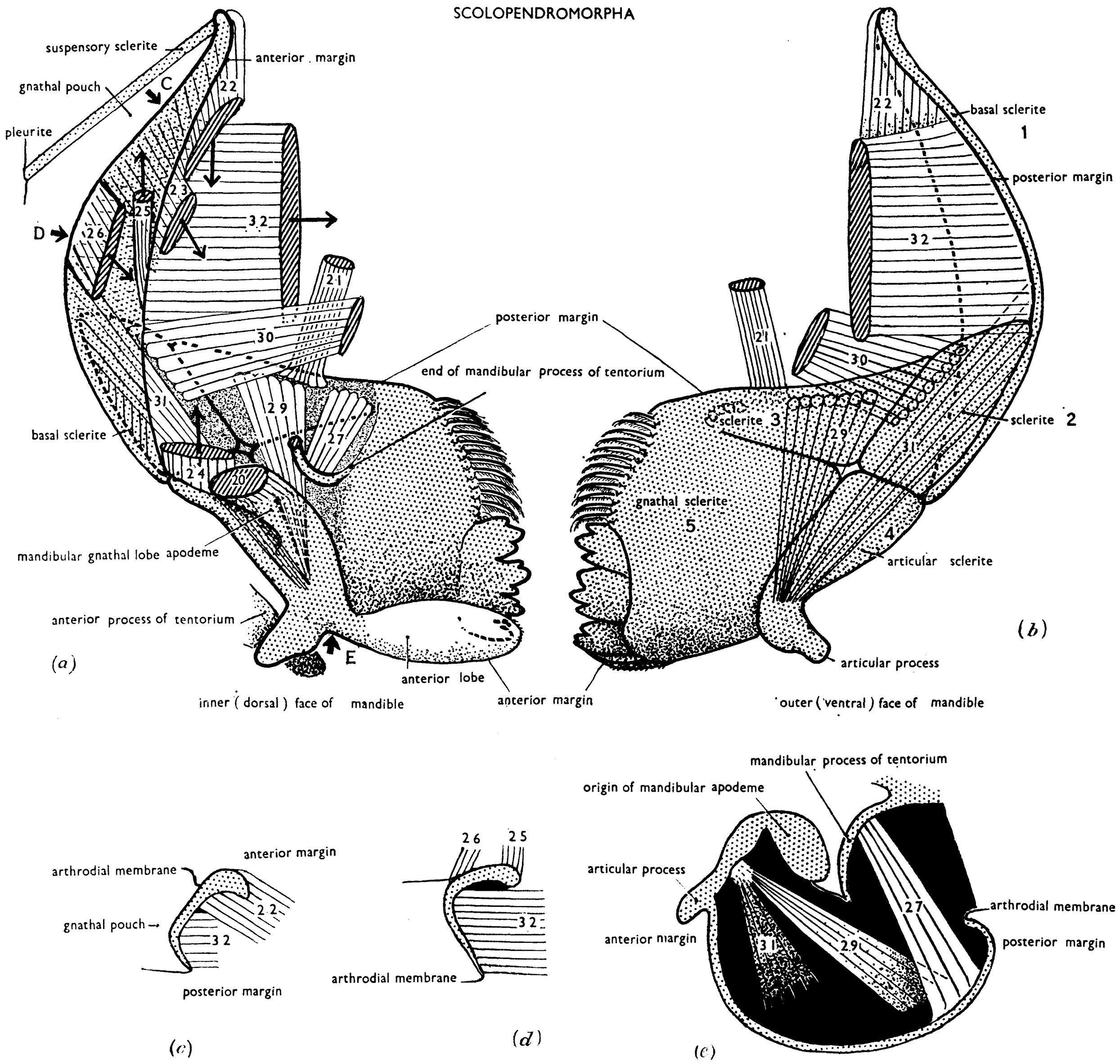


Figure 64. Diagrammatic views of the mandibles of *Cormocephalus nitidosus* to show the component sclerites and muscle origins. Sclerotized stiff cuticular surfaces are stippled, the flexible anterior lobe is white, the exposed internal cavity of the mandible is shaded in (*a*) and black in figs. (*c*) to (*e*). Muscle 33 is omitted (see figure 63D).

(*a*) Dorsal view of the right mandible. (*b*) Ventral view of right mandible (*c*) to (*e*) sections across the mandible at the levels shown by arrows C, D and E on (*a*).

Diagnose of mandibular muscles of Cormocephalus nitidosus

The terms adductor, abductor, levator and depressor refer to the distal gnathal edge of the mandible, not to the proximal basal end of the mandible whose movements are opposite.

19 is not strictly a mandibular muscle, arising from the mandibular suspensory rod and inserting on the cranium (depressor to mandible) (see level A).

20 from the apodeme on sclerite 4 to the dorso-lateral cranium (adductor-levator) (see figures 62A and 63D).

(*Continued on p.* 182)

21 a narrow long muscle from sclerite 3 to the dorsal cranium (levator) (see figure 63 levels D and E).

22 from the proximal anterior edge and concavity of sclerite 1 to the origin of the transverse process of the tentorial apodeme (protractor) (see figure 62 level B).

23 from the anterior margin and concavity of sclerite 1 to the posterior process of the anterior tentorial apodeme (protractor) (see figure 63 level D).

24 from the proximal antero-dorsal edge of sclerite 4 to the cranium (retractor) (see figure 62 level B).

25 from the outer surface of the anterior margin of sclerite 1 to the cranium (retractor) (see figure 62 level C).

26 from the outer surface of sclerite 1 (figures 64 (*a*), (*d*)) to the cranium (abductor-depressor) (see figure 62 level A).

27 from the proximal postero-ventral part of sclerite 5 passing upwards to the curved edge of the mandibular process of the anterior tentorial apodeme (levator) (see figure 63 level E where it is foreshortened, figure 61 unlabelled see legend, and figure 64 (*a*), (*e*)).

29 intrinsic muscle from sclerite 4 near the articular process to the posterior part of sclerite 3 (flexor) (see figures 63 level E and 64 (*b*) and (*e*)).

30 from the posterior part of sclerite 2 upwards and backwards to the posterior process of the anterior tentorial apodeme (levator-adductor) (see figures 63 level E and 64 (*b*)).

31 intrinsic muscle from sclerite 4 near the articular process to sclerite 1 (flexor) (see figures 63 level E and 64 (*b*) and (*e*)).

32 from the concavity of sclerite 1 to the transverse mandibular tendon, inserting in several layers both on the transverse bar and median flange (stabilizer) (see figure 63 level D and 64 (*a*) to (*d*)).

33 from the anterior margin and concavity of sclerite 1 to the posterior process of the anterior tentorial apodeme (adductor) see figure 63 level D.

The above diagnoses correspond with those given by Meinert (1883) for *Scolopendra subspinipes* Leach with the exception of his small muscles c. 28 and c. 29. Meinert records his difficulty in ascertaining the connexions of these and of neighbouring small muscles. Modern equipment has failed to substantiate the presence in *Cormocephalus nitidosus* of a separate muscle 28, and muscle 29 clearly does not insert on the anterior tentorial apodeme but on sclerite 4.

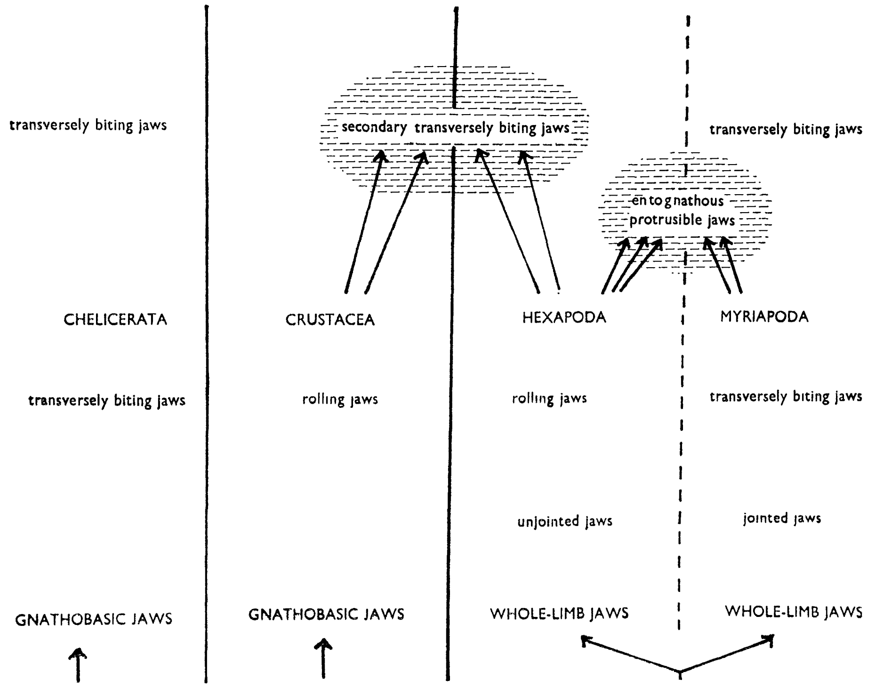


Figure 65. Diagram showing the conclusions reached concerning the distribution of the principal types of mandibles or jaws (below) and the derivation of the jaw mechanisms (above). The heavy vertical lines indicate an entire absence of common ancestry between the jaws referred to on either side; an interrupted vertical line indicates separate evolutions of the jaw mechanisms of Hexapoda and Myriapoda which probably had a common origin; and the shaded areas indicate mandibular mechanisms showing convergent similarities derived from unlike origins.

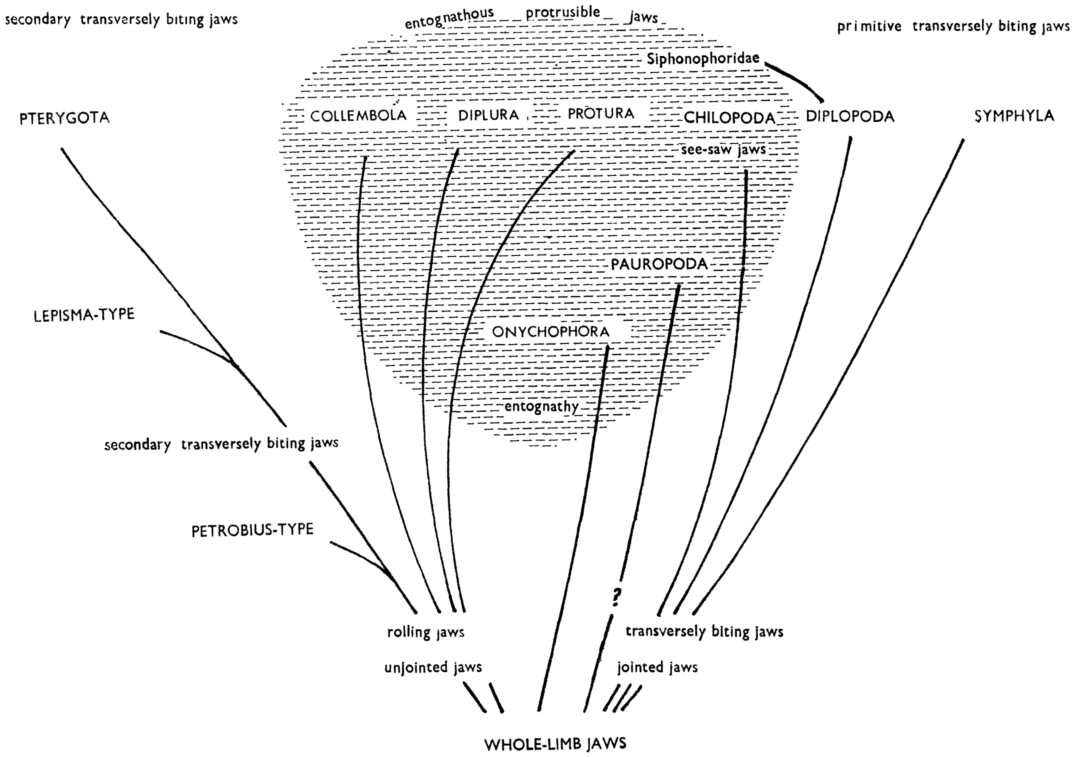
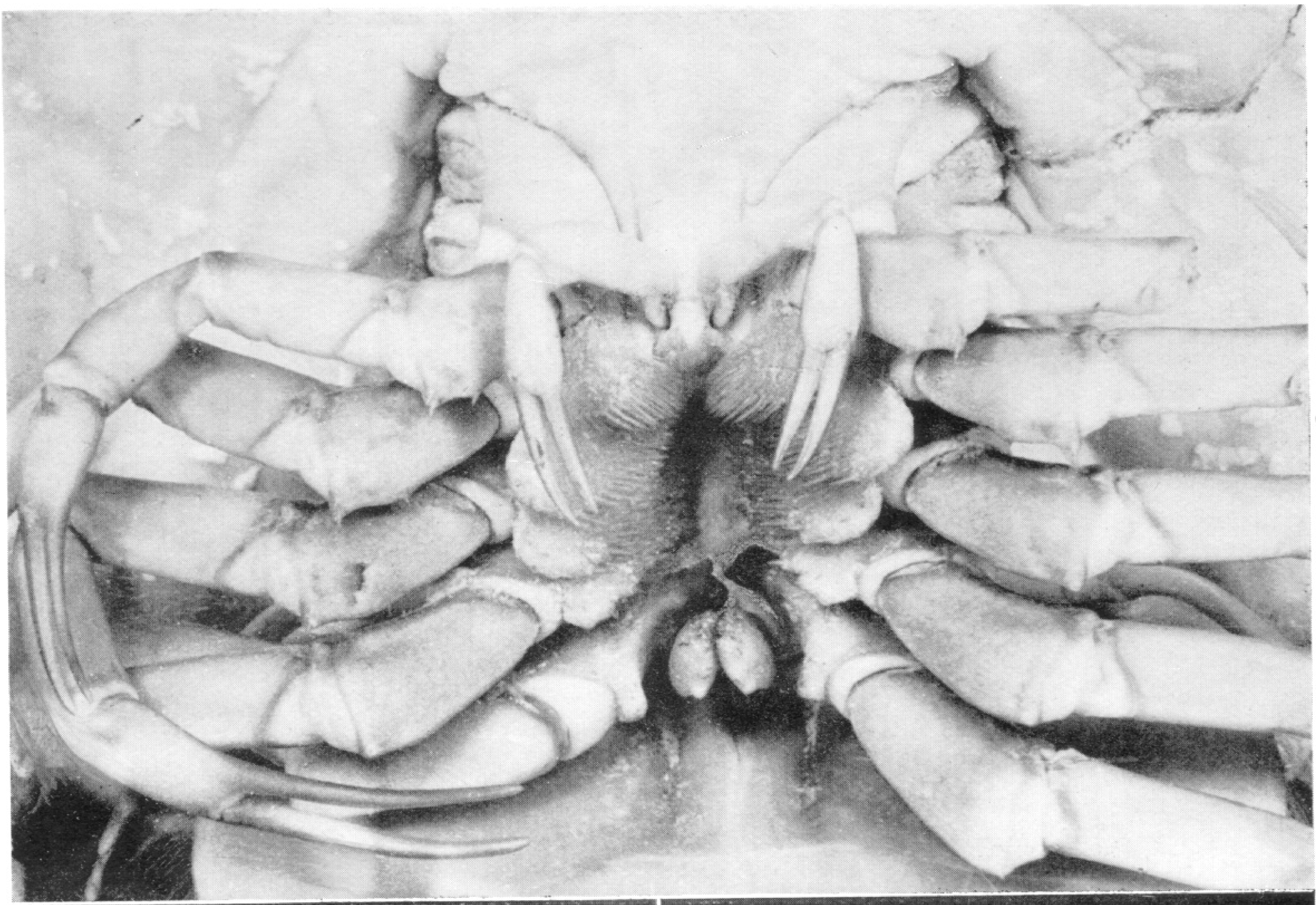


Figure 66. Diagram showing the conclusions reached concerning the interrelationships and evolution of the jaw mechanisms of Onychophora, Myriapoda, Apterygota and Pterygota. The shaded area indicates convergent evolution of entognathy and protrusible mandibles. The Pauropoda possess an unsegmented mandible, but there is no evidence as to whether this has been derived from a primitively segmented or unsegmented mandible.



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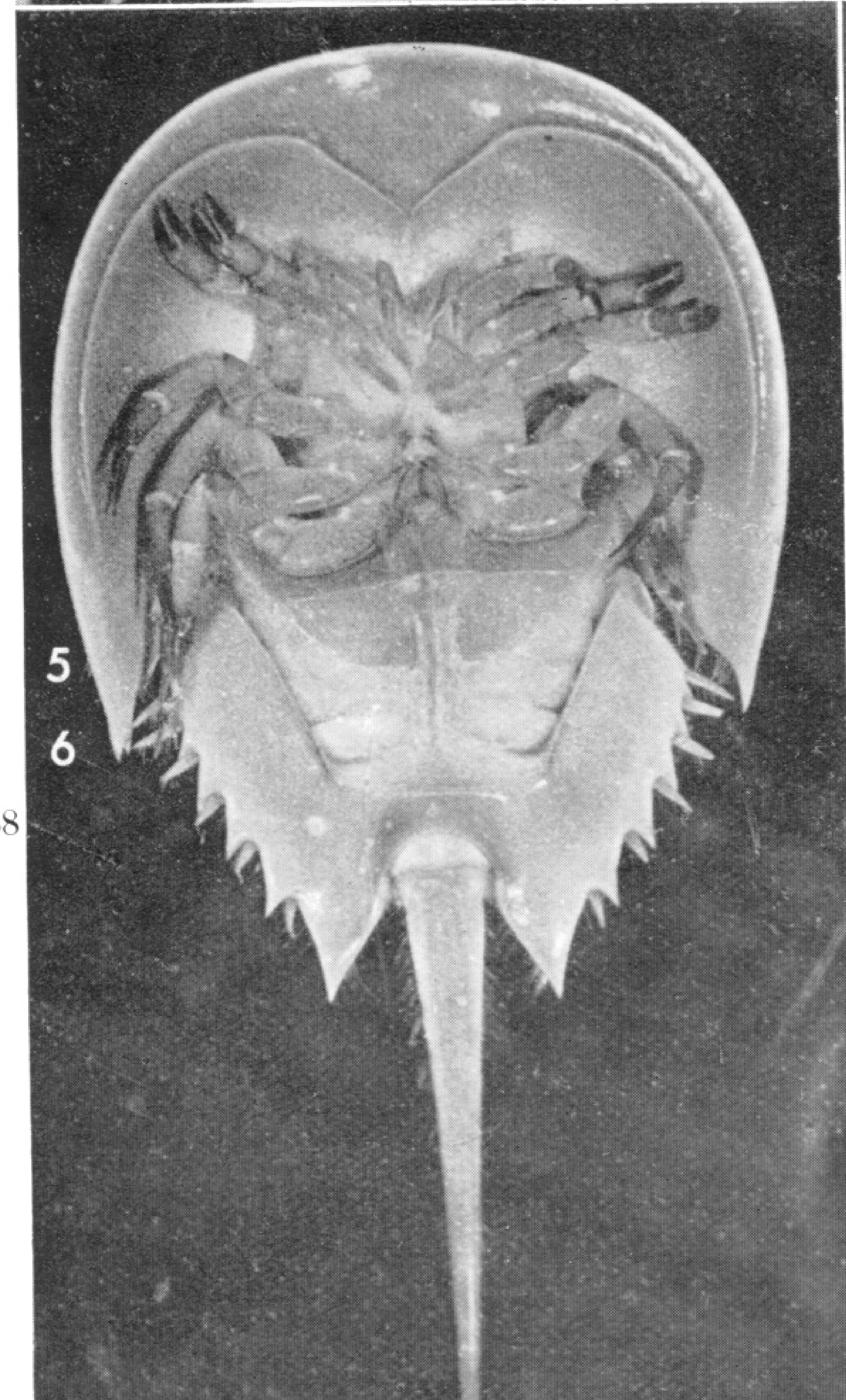

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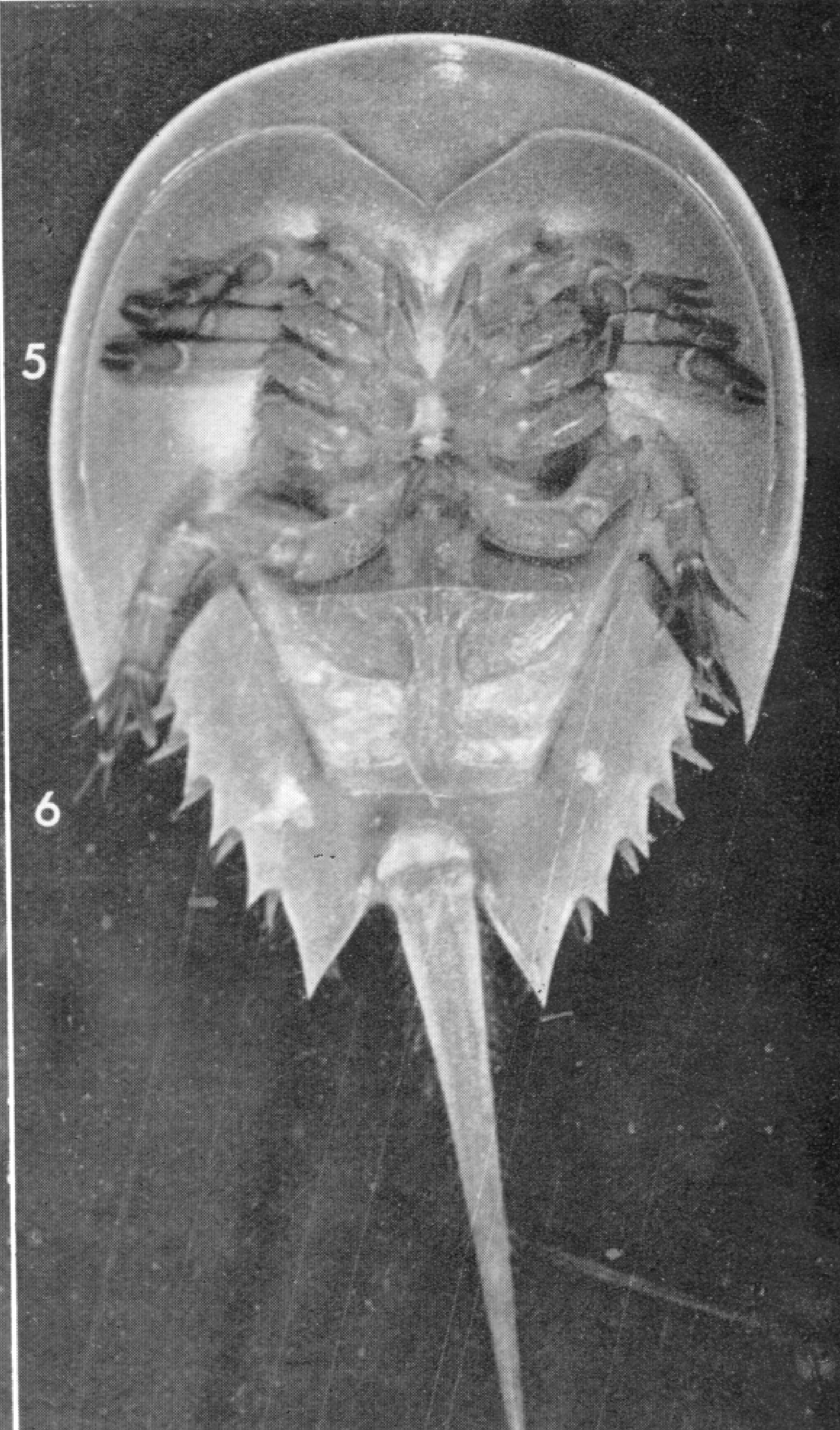

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FIGURE 3. For legend see facing page.

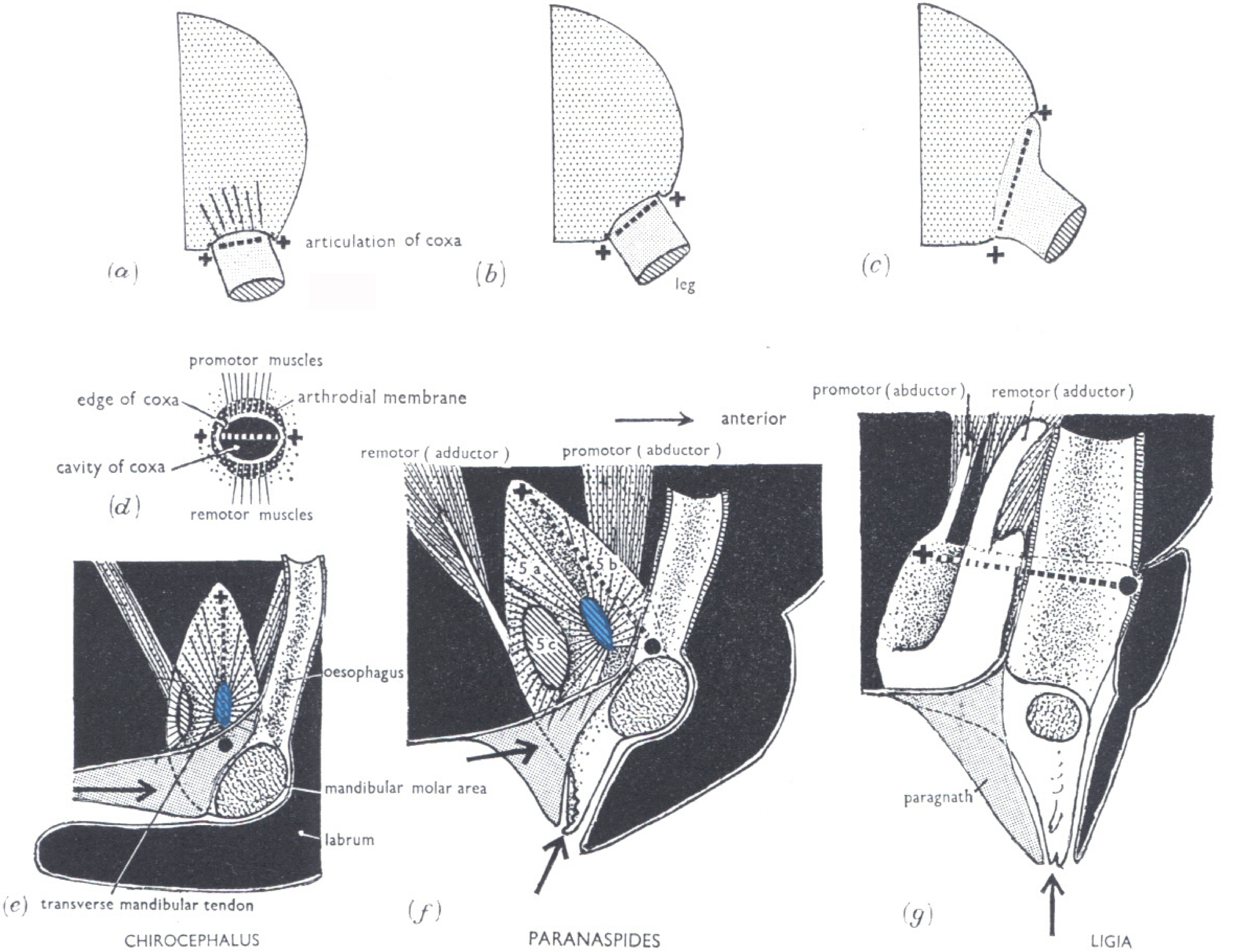


FIGURE 5. (*a*) to (*c*) Diagrammatic transverse views of half of the body of an arthropod to show the several positions of the axis of swing of the coxa on the body, dotted line between the crosses. In each case the axis lies in the transverse plane of the body, (*a*) as in Crustacea and Diplopoda, (*b*) as in Symphyla, (*c*) as in Chilopoda.

(*d*) Represents an end-on view of a typical coxa-body joint, the axis of swing being marked as in (*a*) to (*c*). This axis passes through the points where the arthrodial membrane (white stipple) between coxa and body is shortest (see Manton 1958*b*).

(*e*) to (*g*). Diagrammatic views of sagittal halves of the heads of *Chirocephalus diaphanus*, *Paranaspides lacustris* and *Ligia oceanica* to show the positions of the axis of the mandibular roll which is indicated by the interrupted line between the dorsal union of the mandible and cranium (marked by a cross) and the black spot; the positions of the molar areas and incisor processes with respect to this axis; and the routes to the mouth of fine food (upper arrows) and of large food (lower arrows). The direct transverse mandibular muscle 5*c* and the transverse mandibular tendon are cut. Promotor and remotor (abductor and adductor) muscles are homologous in the three animals, muscles 3 and 4 both possess apodemes in *Ligia* and a posterior remotor (adductor) apodeme is present in *Paranaspides*. Further details are shown in figures 1 to 3, 7 and 8, 10 and 11.

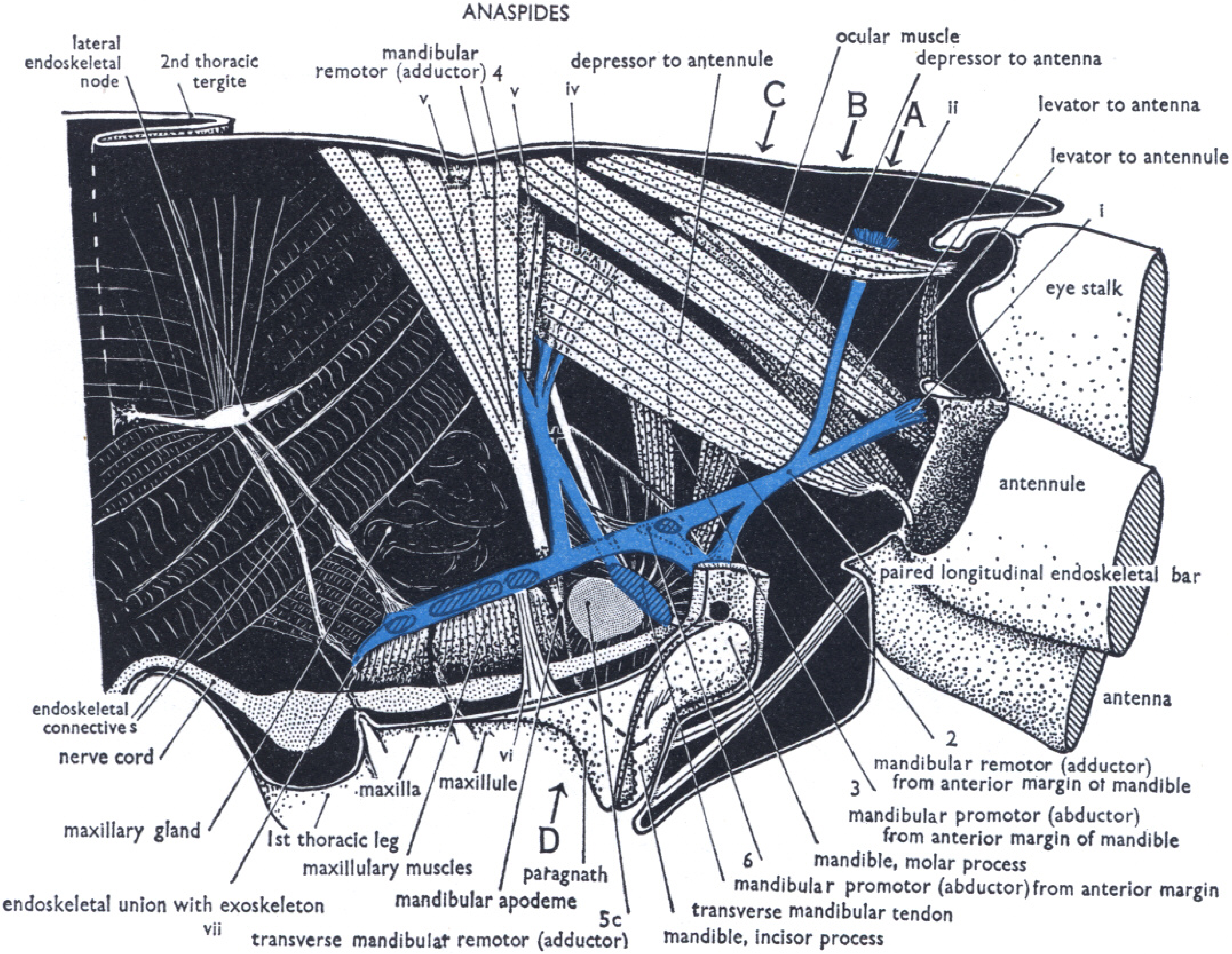


Figure 8. Sagittal half of the head of *Anaspides tasmaniae* Thomson with the alimentary canal and digestive gland removed to display the cephalic endoskeleton and mandibular musculature. The posterior mandibular apodeme is shown in white, and the transverse segmental tendons and their connectives are blue, the median endoskeletal bridges cut in the sagittal plane are hatched. The positions of the mandibular margins and of the axis of movement between the dorsal union with the head (a cross) and the black spot are indicated. The web of fibrous connexions between the transverse mandibular tendon, the lateral longitudinal tendinous bars and the three dorso-lateral struts is more complex than shown. The levels A to D mark the planes of sections shown in figure 9. For further descriptions see text.

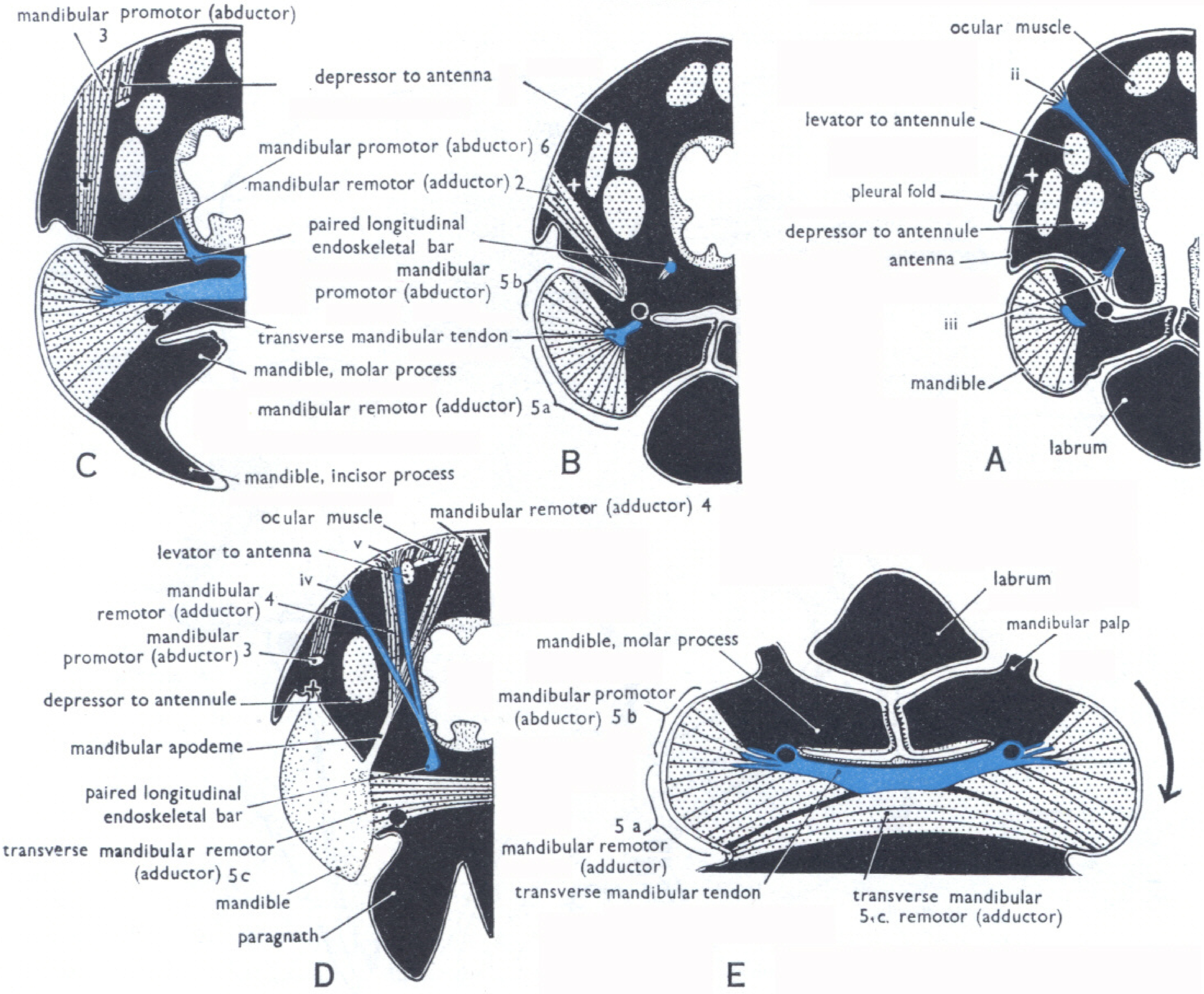


FIGURE 9. *Paranaspides lacustris* Smith. Thick diagrammatic transverse sections of the head at the levels indicated on figure 8 at A to D, to show the mandibular muscles and cephalic endoskeleton. The position of the axis of movement passing from the dorsal union of the mandible and head, marked by a cross in D, to the black spot in A is projected on to the other figures which show only part of the obliquely situated mandible. The designations (adductor) and (abductor) to the muscles shown is made in the sense described in the text; it does not signify a basic adduction and abduction in the transverse plane, but a remotor-promotor roll.

Level A shows the cuticular unions ii and iii of the paired longitudinal tendinous bars, iii being close to the oral angle braced by the termination of the transverse mandibular tendon shown in level B.

Level B shows the lateral longitudinal tendinous bar; the anterior dorso-lateral mandibular remotor (adductor) 2; and the anterior extension of the transverse mandibular tendon.

Level C shows the transverse mandibular tendon bearing remotor (adductor) and promotor (abductor) fibres (see labelling on level B); the transverse union of the paired longitudinal endoskeletal bars at the level where they bear abductor 6 (see the unlabelled dotted outline of the origin of muscle 6 in figure 8); and promotor (abductor) 3 arising mainly from the arthrodial membrane below the carapace fold. Level D shows the longitudinal endoskeletal bar and its tendinous suspensions iv and v; the hollow posterior mandibular apodeme with its dorsolateral remotor (adductor) 4; and the transverse mandibular remotor (adductor) 5*c* lying behind and independent from the mandibular tendon.

Level E. Oblique horizontal section just below the mouth to show the mandibles and their molar processes at the end of the remotor roll; the transverse mandibular tendon, which supports the lower end of the axis of movement (black spot); and the transverse muscles.

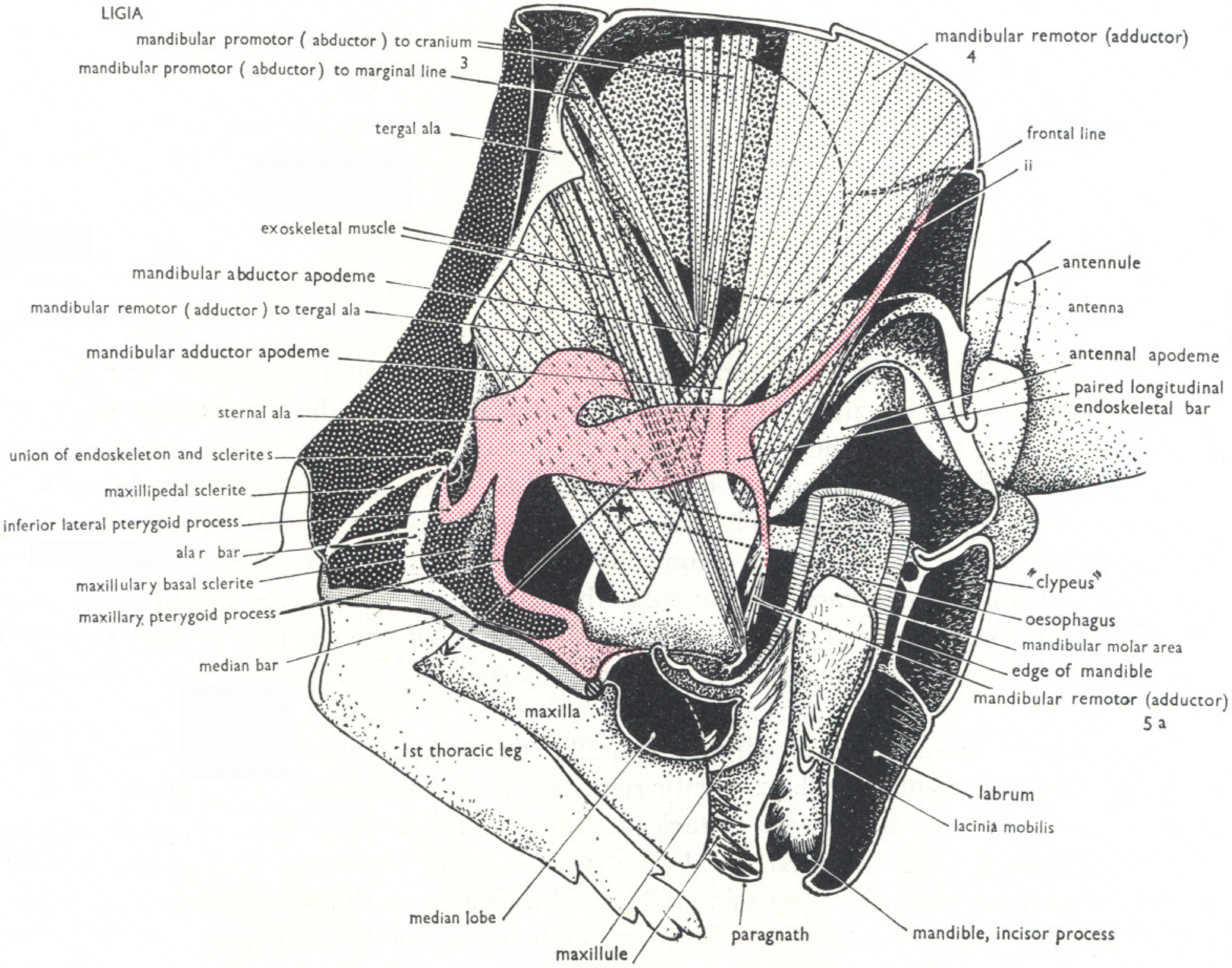


FIGURE 11. *Ligia oceanica* Roux. Sagittal view of left half of the head to show the longitudinal apodemal endoskeleton (red), the mandible and mandibular muscles. The mandibular cuticle is drawn alone in figure 12*b* from the same aspect. The cut through the ventral cuticle of the head passes along the 'median bar', a superficial scute, and one arm is shown of its anterior bifurcation which ends on the paragnath; the cut end of the other arm is hatched. The antennal muscles passing to the genal fossa region of the cranium (between the circle and cross in figure 10) are removed; they pass between the mandibular adductor and abductor muscles. The extrinsic muscles of the maxillule and maxilla to the tergal ala and sternal ala (see dotted arrow) and the maxillipedal muscles to the maxillipedal sclerite and alar bar are also omitted. The mandibular hinge on the head lies between the cross and black spot. The broad mandibular adductor apodeme leaves the parasagittal edge of the mandible and passes directly upwards (see figure 12*a*). The narrow posterior mandibular abductor apodeme leaves the antero-dorsal edge of the mandible close above the hinge and passes outwards and upwards (see left side of figure 12*a*). The mandibular remotor (adductor) muscle forms three main sectors, a posterior sheet passes from the proximal posterior edge of the apodeme upwards and backwards to the tergal ala; the most bulky sector fans out from the apex of the apodeme to the whole dorsal and antero-dorsal face of the cranium above the 'frontal line' (half of it is cut away to expose the abductor muscles); and an anterior sector arises from a tuft of fibres half way along the anterior edge of the apodeme and inserts on and around the 'supra-antennal line' (see figure 10) of the cranium. The mandibular promotor (abductor) comprises 4 sectors: two pass to the dorsal cranial wall just median to the eye; one passes to the 'marginal line' (see figure 10) behind the eye; and another to the anterior face of the tergal ala. The principal head apodeme the 'sternal ala' is shown in red. It arises from a maxilla 1–2 intucking (white stipple) bearing the inferior lateral pterygoid process and the maxillary pterygoid process in its outer and inner angles respectively. The maxillulary basal sclerite is attached laterally to the maxillary pterygoid process and can be seen through the membranous part of the apodemal intucking. The circle marks the union of the superficial scutes with the inferior lateral pterygoid process, a point also supported by the end of the tergal ala. Setae of maxilla 2 are drawn as if the median lobe was transparent.

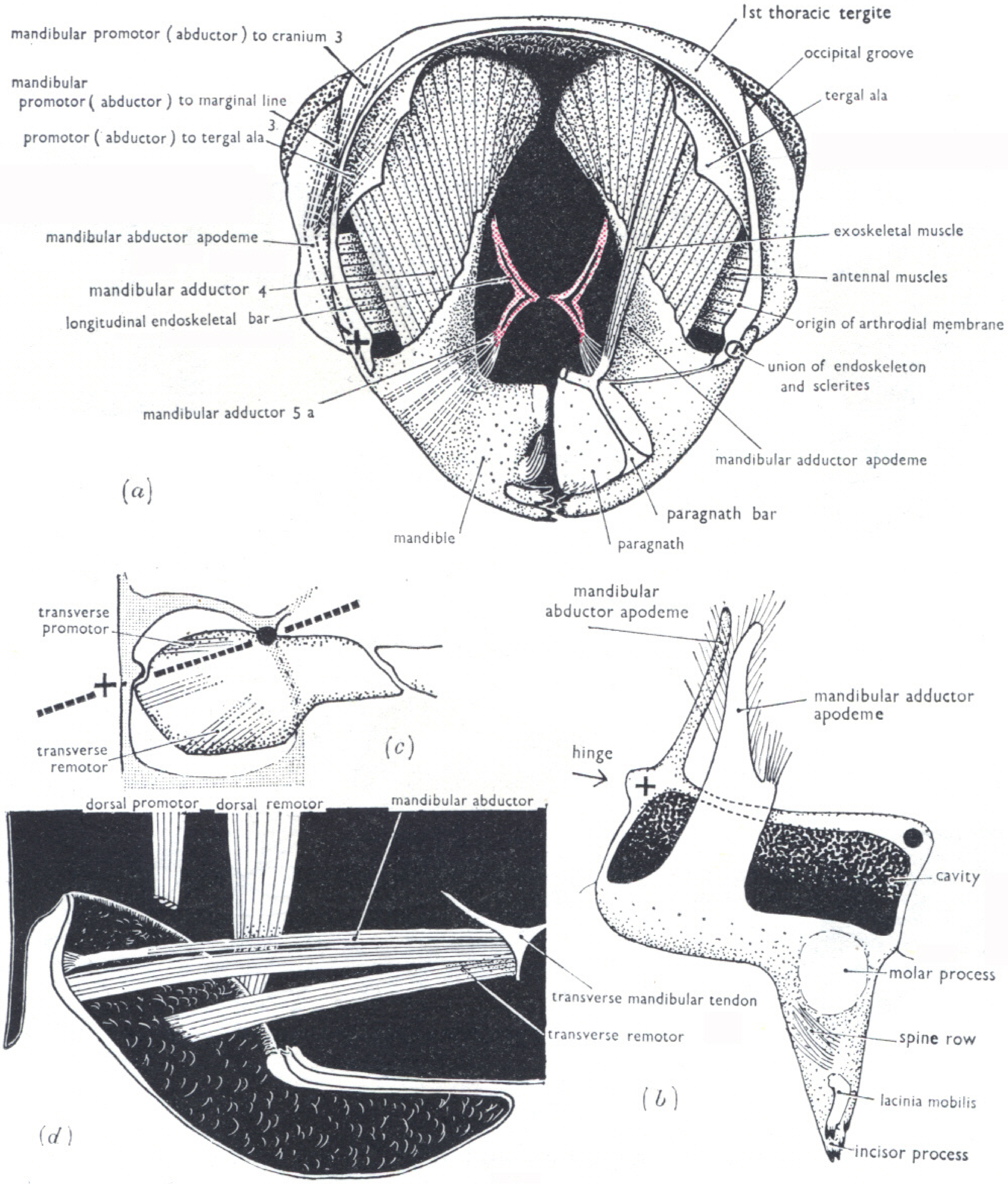


FIGURE 12. (*a*) Posterior view of the head of *Ligia oceanica* Roux, intact dorsally and laterally as far as the notch surrounded by the circle, marked as in figures 10 and 11. Ventrally the mouth parts are removed leaving the left mandible and the right paragnath and mandible. The principal head apodeme, the sternal ala, is cut and shown in red, and its process bears the small remains of mandibular remotor (adductor) 5*a* (cf. figures 7, 9).

(*b*) Sagittal view of the mandibular cuticle of *Ligia oceanica* devoid of muscles seen from the same aspect as in figure 11.

(*c*) *Calanus finmarchicus* Gunner, ventral view of right mandible. The interrupted line marks the axis of roll, the easiest movement elicited by micro-manipulation of a cuticle preparation devoid of muscles. The cross marks the loose lateral articulation with the head and the black spot the region of close hinge-like union with a transverse sclerite of the head. One arm of this sclerite curves posteriorly to form the inner margin of the mandibular socket.

(*d*) Diagrammatic thick transverse section through the right mandible of *C. finmarchicus* viewed from in front. The cut lies just behind the lateral articulation and through two of the three transverse muscle fibres (probably abductor) arising in this position (see (*c*)). The anterior (promotor) transverse fibres are cut away with the anterior part of the mandible and the origin of the dorsal promotor muscles, and the larger posterior (remotor) transverse muscle fibres are shown arising from the posterior shoulder of the mandible (see (*c*)). More anteriorly the transverse mandibular tendon is wider, the dorsal suspensory arms are cut. For further consideration see p. 98.

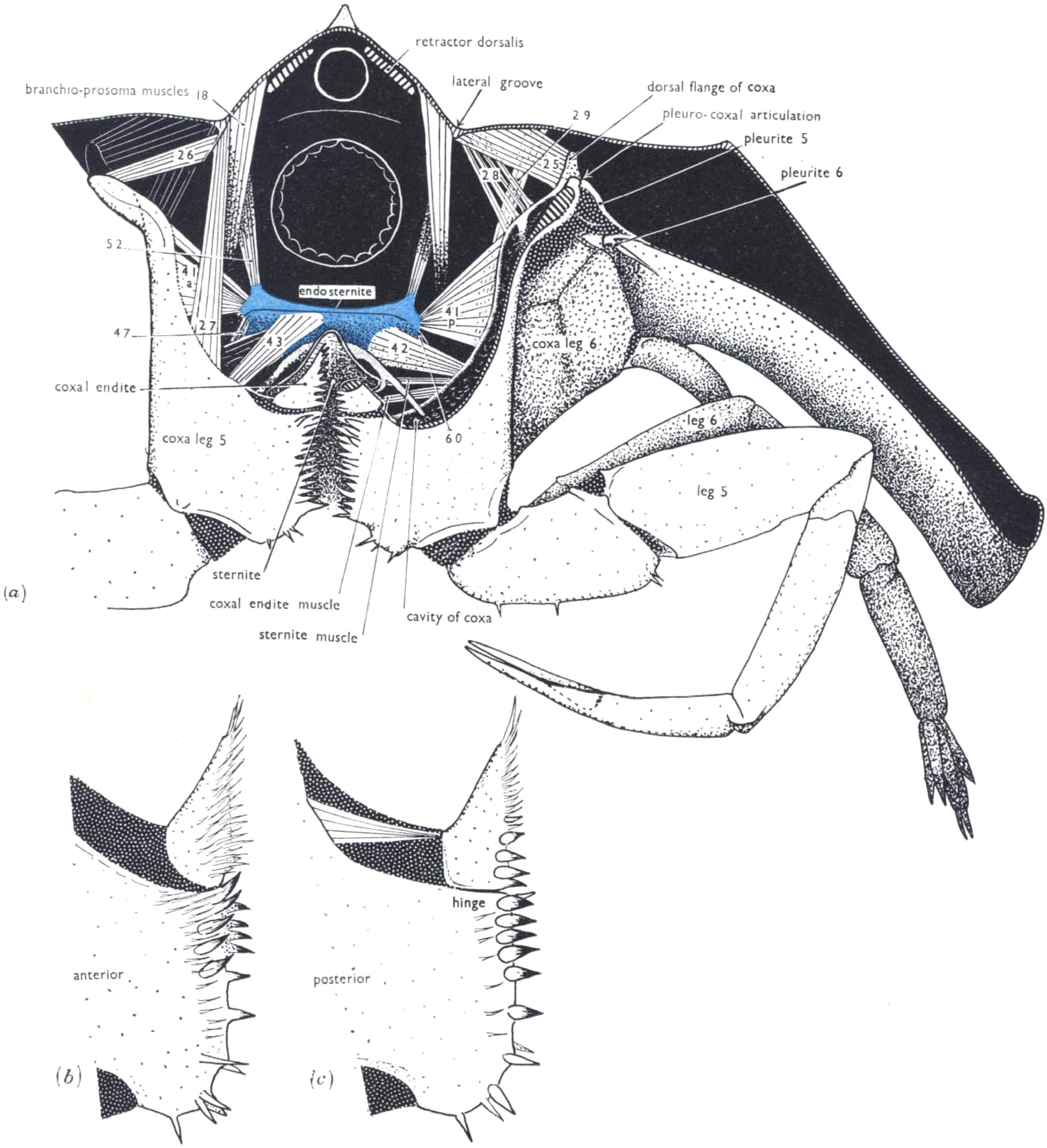


Figure 14. (*a*) The prosoma of *Tachypleus tridentatus* Leach cut transversely in front of legs 5 and viewed from in front to show the extrinsic limb muscles. The digestive gland is omitted; portions of the heart, pericardial floor and intestine are indicated but unlabelled; pedal nerves are stippled and arthrodial membranes are shown by white dots. Ventrally the anterior end of the sternite is passing upwards towards the oesophagus (see figure 16). The endosternite (blue) is cut transversely, its ventral surface and that of the ventral (pleural) surface of the carapace are foreshortened. Muscle numbers are those of Benham (Lankester, Benham & Beck 1885). Muscles 52 attach the dorsal cornua of the endosternite to the carapace and 18 comprise the branchio-thoracic muscles which pass forwards from the branchial limbs to the prosomal carapace.

The coxa of leg 5 is entire on the left and on the right it is cut away as far as its articulation with the pleurite, disclosing the 'dorsal flange' (marked) which is covered by a fold of arthrodial membrane (see figure 17*a*). On the right one limb of the Y-shaped pleurite, with which leg 5 articulates, and the entire pleurite articulating with leg 6, are shown. The extrinsic muscles attached to the anterior thickened rim of the coxa are indicated in white on the left, some of the more posterior muscles being indicated in black. The extrinsic muscles attached to the posterior thickened rim of the coxa are shown on the right where the anterior rim and its muscles are cut away. The coxal endite is cut short on the right to show the sternite.

(*b*) Anterior view of the mesial part of the gnathobase of leg 5 to show the heavy spines (with black tips) and the endite set in ample arthrodial membrane which allows the proximal rim of the endite to tip into the rest of the gnathobase on forward flexure of the endite (see figure 16*b*).

(*c*) Posterior view of the same to show the straight hinge between the endite and the rest of the gnathobase and the muscle extending from the endite to the posterior rim of the coxa. Contraction of this muscle returns the endite into line with the rest of the gnathobase after the endite has been pushed forwards by adductor movements of the coxa which press the endite against food or against the roof of the food basin (see also figure 16*b*).

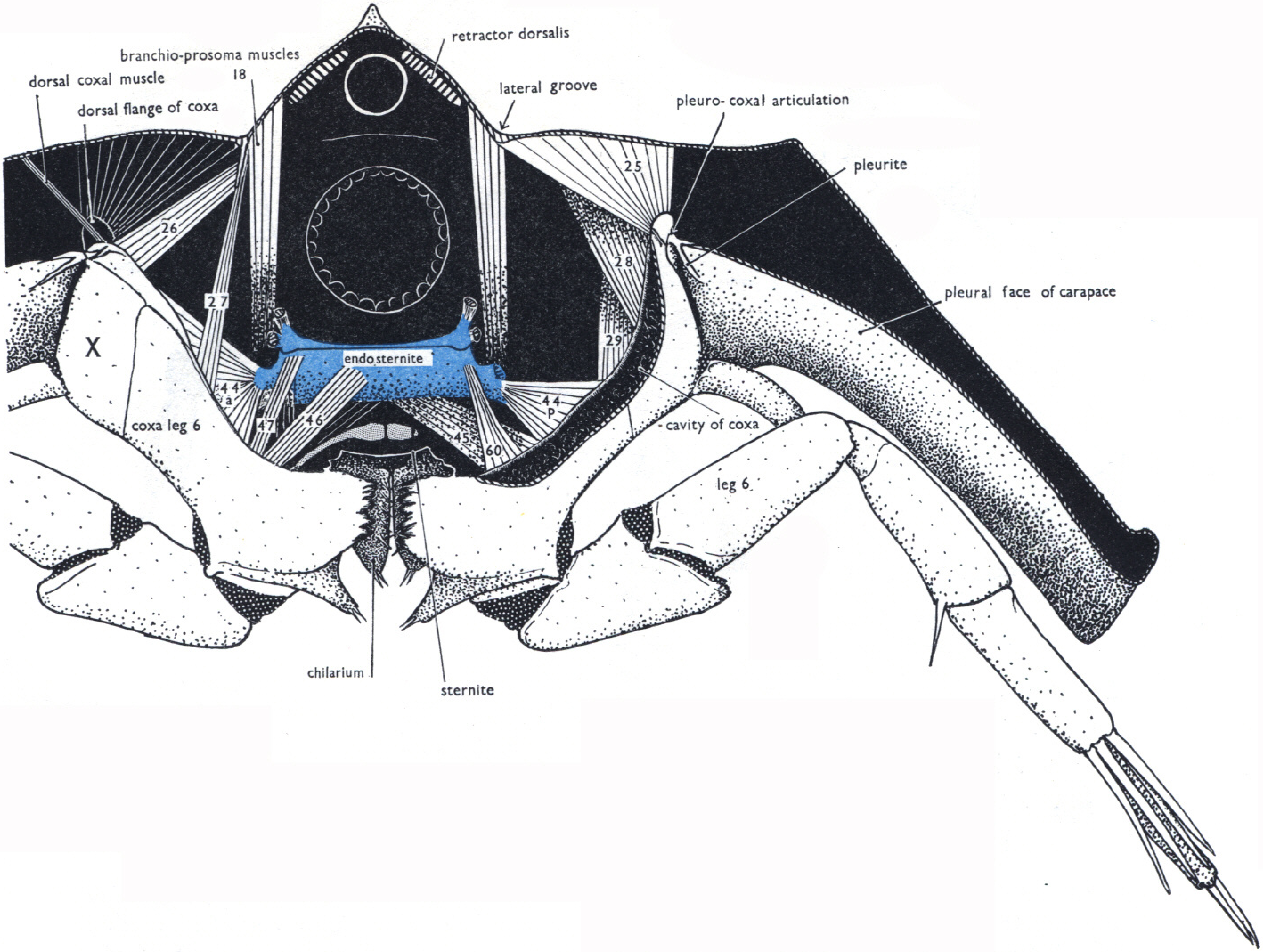


FIGURE 15. The prosoma of *Tachypleus tridentatus* Leach cut transversely as in figure 14 but the 5th limb pair and its muscles are cut away, the bases of muscles 52 and 41 (unlabelled, see figure 14) remaining on the endosternite (blue) which expands posteriorly to form the posterior cornua bearing muscles 44*a* and 44*p*. The thickened anterior coxal rim of leg 6, with its muscles, are shown on the left and are cut away on the right to disclose the muscles attached to the posterior rim of the coxa. Muscles 46 and 60 arise from the endosternite anterior to leg 6 and pass backwards to the anterior and posterior margins of coxa 6 (see figure 17*b*). Muscle 29 passes backwards from coxa 6 to insert laterally near the posterior margin of the carapace. A small muscle, marked dorsal coxal muscle, passes from the antero-dorsal margin of the coxa outwards and upwards to the carapace. It is not present on leg 5. The muscles 18 from the branchial limbs are shown in part. The area '*X*' marked on the coxa is similarly marked in the 5th and 6th coxae in figure 17*a* and *b* and has been claimed to be part of a precoxal segment (see text).

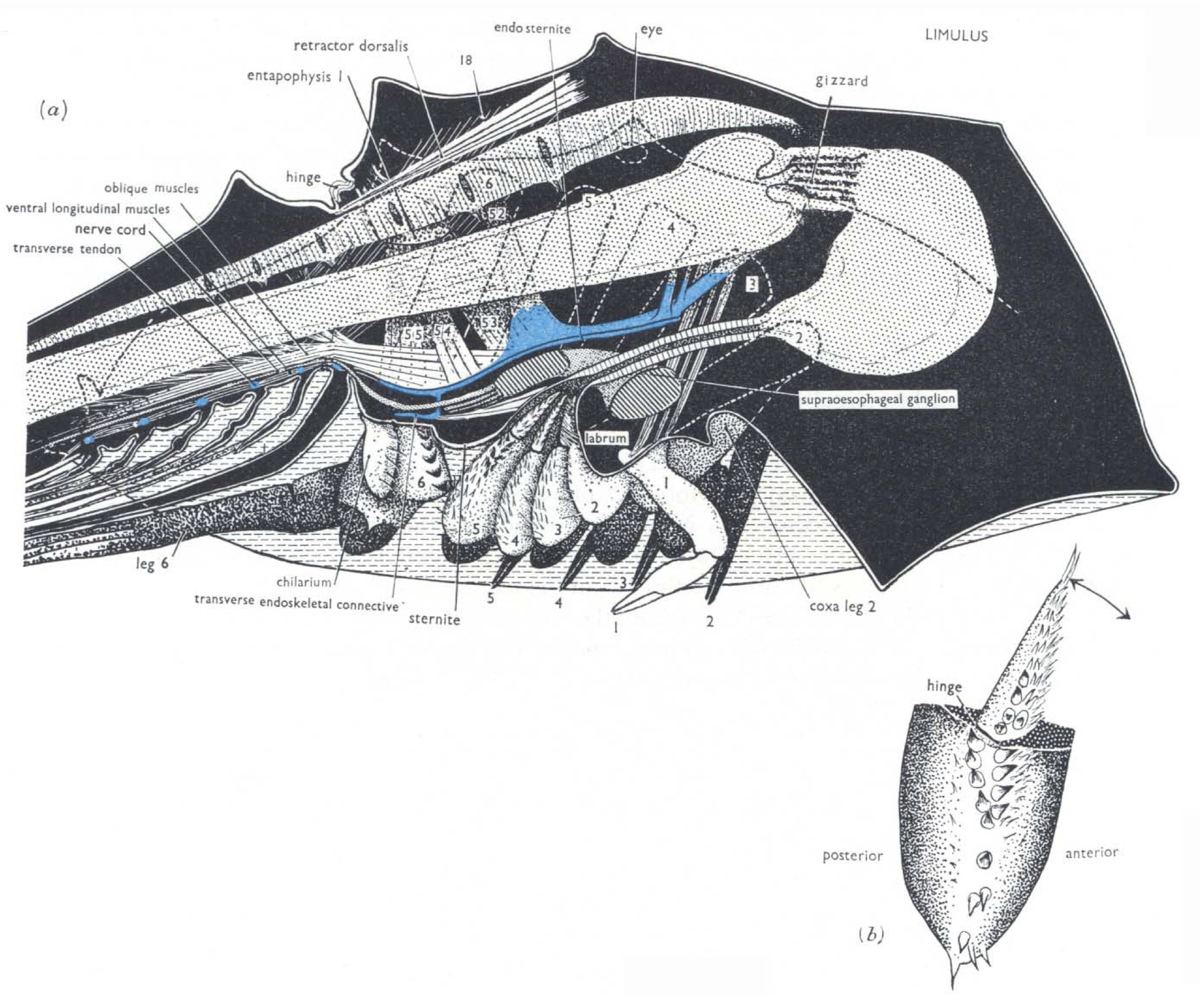


FIGURE 16. (*a*) Sagittal half of the prosoma of *Tachypleus tridentatus* Leach to show the form and positions of the gnathobases, the mouth and the endoskeleton with its attachments. The lateral prosomal ridge and the postero-lateral margin of the carapace are shown by a dotted line. Muscle numbers are those used by Benham (Lankester, Benham & Beck 1885). The heart, oesophagus, proventriculus and intestine are not labelled. Numbers 2 to 6 mark the gnathobases of legs 2 to 6; the movable coxal endites of legs 3 to 5, which are directed towards the mouth, are not labelled. The positions of the coxal margins of legs 2 to 6, which are attached by arthrodial membrane to the flanks of the animal, are indicated by dotted lines and marked 2 to 6. The anterior face of coxa 2 is visible lateral to leg 1. The supra- and suboesophageal ganglia are cut. The cut endosternite and its foreshortened dorsal face are shown in blue, the anterior cornu and two lateral cornua are attached by muscles (now shown) to the antero-lateral part of the carapace, the dorsal cornu is attached by muscle 52 to the carapace and by muscles 53 from the base of the dorsal cornu and muscles 54 and 55 from the dorsal face of the endosternite pass to entapophysis 1. A small 'transverse endoskeletal connective' lies below the nerve cord above the gnathobase of leg 6; this skeletal bridge is united laterally with the endosternite and carries a muscle to the anterior part of the sternite as shown (the occipital ring of Patten & Redenbaugh). The oblique and ventral longitudinal muscles are shown diagrammatically (for details see Benham (Lankester, Benham & Beck 1885, pl. 74–5, figs. 1–3) and Patten & Redenbaugh (1900, pl. 8, fig. 4)). Two large superimposed 'oblique muscles' comparable with oblique trunk muscles of other arthropods (see Manton 1961, and future publications), pass from the posterior dorsal face of the endosternite and branch to entapophyses 3 to 7 of the opisthosomal dorsal shield; these apodemes are not drawn but they lie in line with entapophysis 1, and arise from the opisthosomal cuticle on either side of the mid-dorsal line. These muscles are the dorsal and ventral entapophysio-plastral muscles of Benham, and they form part of the longitudinal abdominal muscles of Patten & Redenbaugh. The ventral longitudinal muscles form two series: one arising from the dorsal face of the endosternite and sending branches to (i) transverse segmental tendons 2 to 6 in the opisthosoma (the mesosomatic entochondrites of Benham, which also bear the muscles to the branchial limbs), and to (ii) entapophyses 4 to 7, and the muscle ends on the opisthosomal sternite; and the other forms a series of fibres linking one transverse tendon with the next and also ends on the opisthosomal sternite. The dorsal longitudinal 'retractor dorsalis' muscles comprise the large submedian arthro-tergal muscles of Benham, but in *L. longispinus* this muscle arises from the anterior border of the opisthosomal dorsal shield and passes forwards to the prosomal carapace. The series of muscles which extend from entapophysis 1 to entapophyses 2 to 5 as a fan of almost parallel strands (not drawn) are probably comparable with the lateral longitudinal or paratergal muscles of other arthropods. Muscles 18 extend from the branchial limbs to the prosomal carapace (see also figures 14 and 15). Three extrinsic cheliceral muscles insert on the carapace; the largest and most posterior is the flexor and the most anterior is the extensor.

(*b*) View of the gnathobase of leg 5 from the sagittal plane to show the free anterior and tight posterior union of the endite with the stiff cuticle of the rest of the gnathobase, and the range of movement of the endite in the parasagittal plane (see also figures 14*b*, *c*).

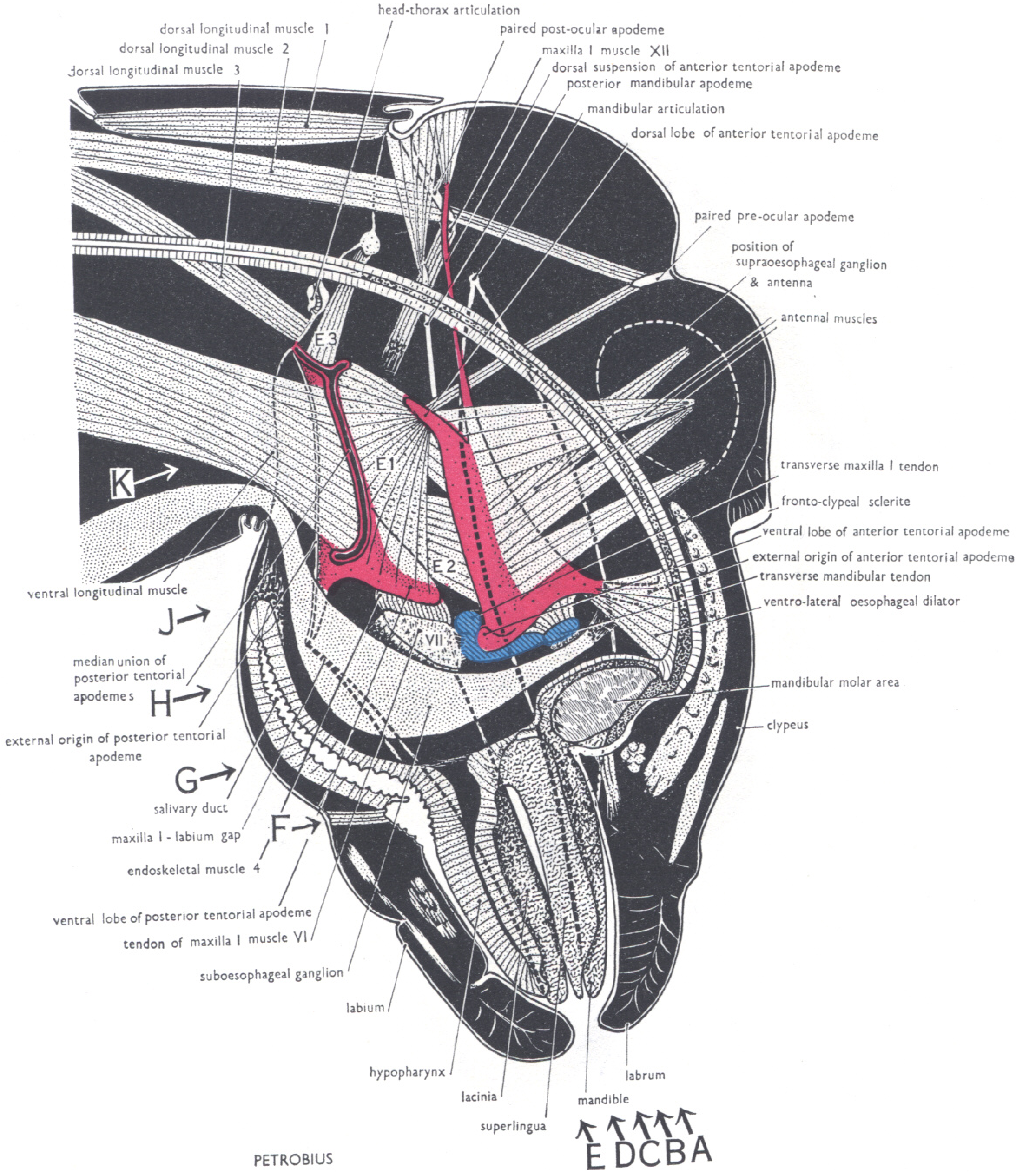


FIGURE 20. Sagittal half of the head of *Petrobius brevistylis* Carpenter. The suboesophageal ganglion and circumoesophageal commissures are in position but the cerebral ganglion has been removed to display the antennal muscles, the ganglion outline in this view is superimposed on the base of the antenna marked by a dotted line. The edge of the whole mandible is shown as if the head was transparent; only the distal part of maxilla 1 is marked by dotted lines. The median bridge formed by the union of the posterior tentorial apodemes is cut, its cavity passes anteriorly into the paired ventral lobes and the long slit-like external opening is shown by dotted lines at the maxilla 1-labium intersegment. Endoskeletal muscles E1 to E3 are shown and maxilla 1 muscle VII is marked, no distinction being shown between muscles VI and VII, see figure 22E. Clypeo-labral muscles are only roughly indicated. The arrows show the positions of transverse sections A to E and frontal sections F to K in figures 21 to 24. The three sectors of the dorsal longitudinal muscles are drawn but the ventral longitudinal muscle is more complex than shown. The lateral parts of the labium, labrum and the galea, which neatly close in the sides of the mouth part cone, are omitted in order to indicate the boundaries between the structures shown, which are closely packed together. For further description see text.

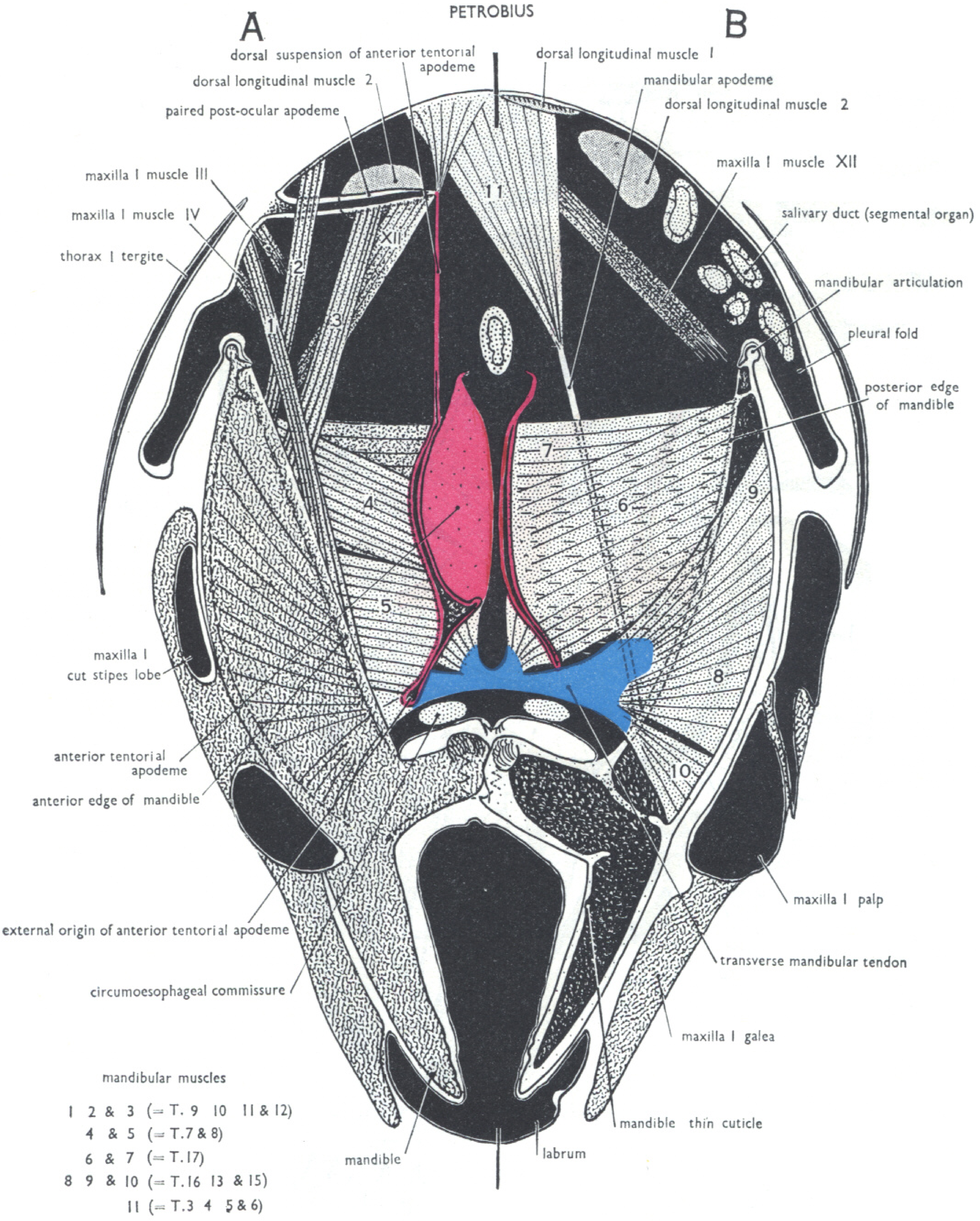


Figure 21. Transverse view from in front of the head of *Petrobius brevistylis* at the levels indicated in figures 19 and 20 to show the mandible, endoskeleton, muscles and general anatomy. The anterior face of the mandibular cuticle is seen in level A and a section through the mandible in level B. The insertion of sector 1 of the dorsal longitudinal muscle lies posterior to mandibular muscle 11 (see figure 20). The insertion of sector 2 of the dorsal longitudinal muscle on to the postocular apodeme is shown in A. A larger scale diagram of the dorsal mandibular articulation is given in figure 4*a*; the cusps on the molar lobe lie across its posterior edge (see figure 20). The suggested homologies between the mandibular muscles of *Petrobius* and *Tomocerus* are listed below on the left, the muscle numbers of *Tomocerus* being given in brackets (see figures 32 to 40). The dorsal end of promotor muscle XII to the maxilla 1 cardo is shown, the rest of the muscle being drawn in figure 22C (see also figure 19*b*).

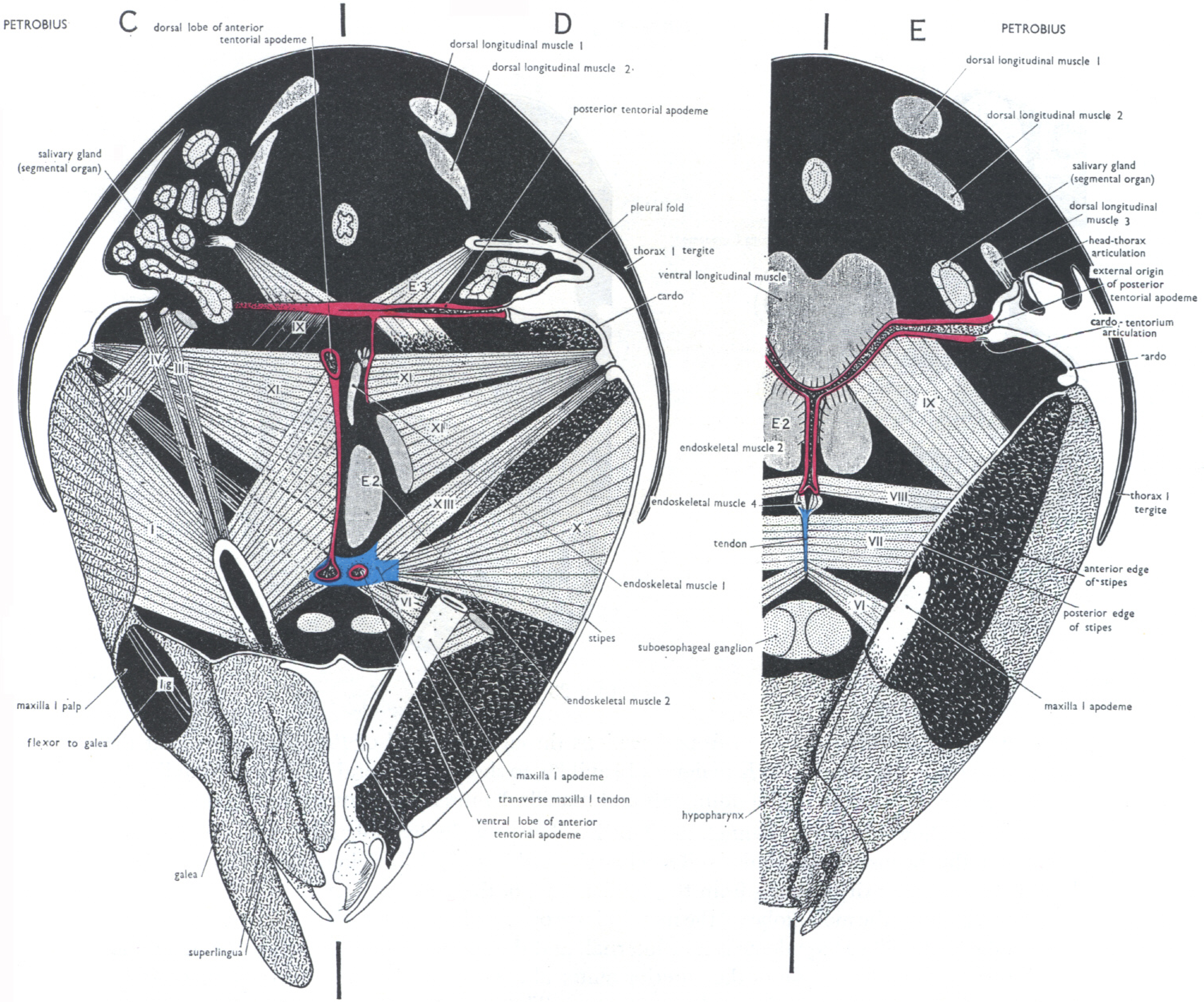


FIGURE 22. Transverse views from in front of the head of *Petrobius brevistylis* at the levels shown by the arrows C, D and E in figures 19 and 20 to show the maxilla 1 and its muscles, the anterior and posterior tentorial apodemes and transverse maxilla 1 tendon. The cuticle on the anterior face of the maxilla 1 stipes is seen in C and a section through the stipes and cardo in D, in E the whole anterior stipes cuticle above and below the palp base is intact but the muscles in the stipes cavity are omitted in order to show the muscles extending from the posterior rim of the stipes (see also figures 24H and J which show the antero-posterior thickness of these muscles). The shape of the cut posterior tentorium in E is due to the curvature of the transverse bridge (see figure 20); the ventral lobes pass forwards from the small ventral bifurcation seen here. Muscle E. 3 from the posterior tentorial bridge inserts on the most anterior part of the prothoracic section of the head-thorax articulation. The union of the circumoesophageal commissures with the suboesophageal ganglion is indicated.

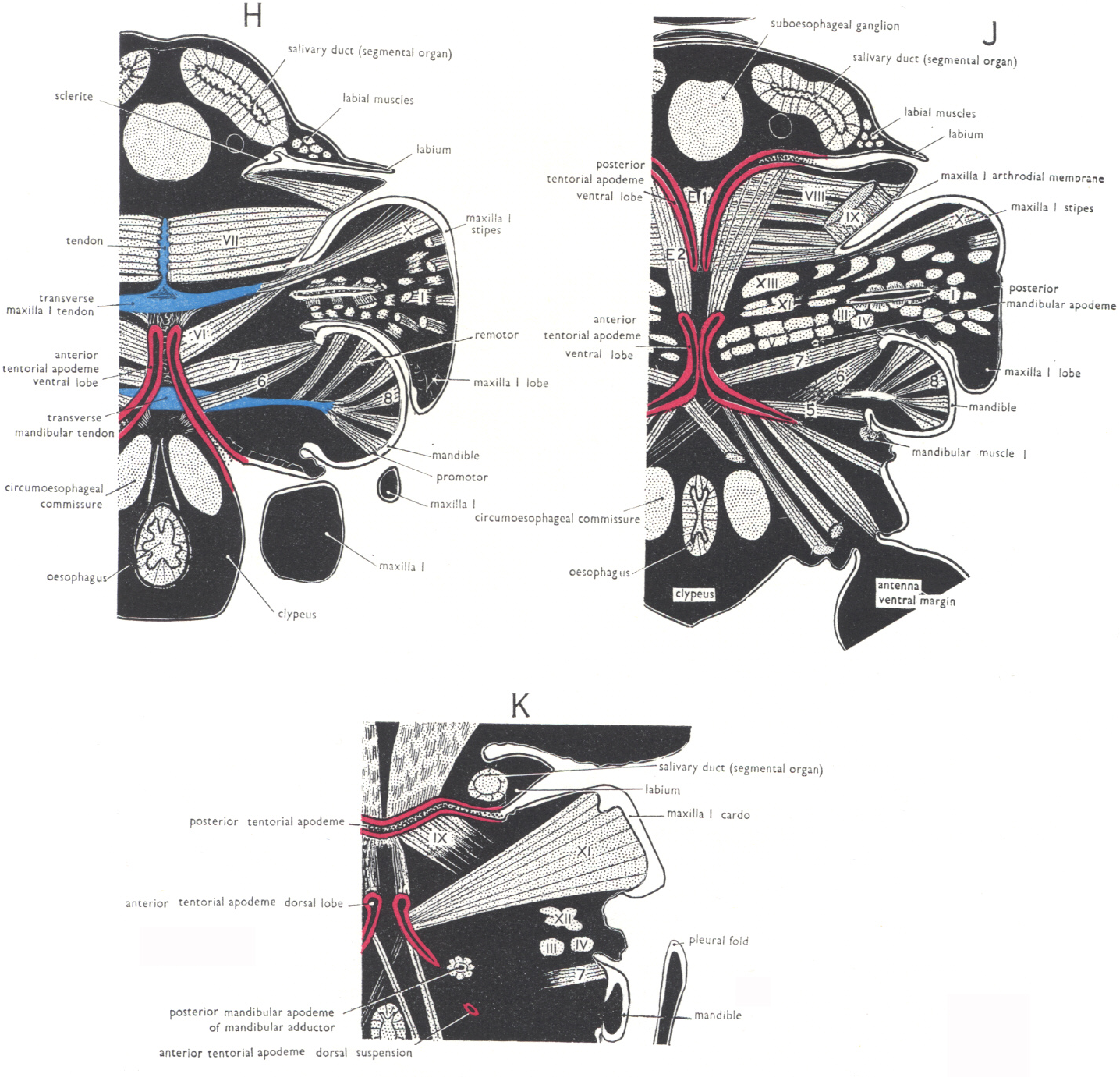

H
salivary duct (segmental organ)
sclerite
labial muscles
labium
maxilla I stipes
tendon
VII
X
I
transverse maxilla I tendon
VI
remotor
anterior tentorial apodeme ventral lobe
7
6
8
maxilla I lobe
transverse mandibular tendon
mandible
promotor
circumoesophageal commissure
maxilla I
maxilla I
oesophagus
clypeus
J
suboesophageal ganglion
salivary duct (segmental organ)
labial muscles
labium
posterior tentorial apodeme ventral lobe
E1
VIII
IX
maxilla I arthrodial membrane
maxilla I stipes
X
E2
XIII
XI
I
III
IV
V
posterior mandibular apodeme
anterior tentorial apodeme ventral lobe
7
6
8
5
maxilla I lobe
mandible
mandibular muscle I
circumoesophageal commissure
oesophagus
clypeus
antenna ventral margin
K
salivary duct (segmental organ)
labium
maxilla I cardo
posterior tentorial apodeme
IX
XI
anterior tentorial apodeme dorsal lobe
XII
III
IV
pleural fold
7
posterior mandibular apodeme of mandibular adductor
mandible
anterior tentorial apodeme dorsal suspension

Figure 24

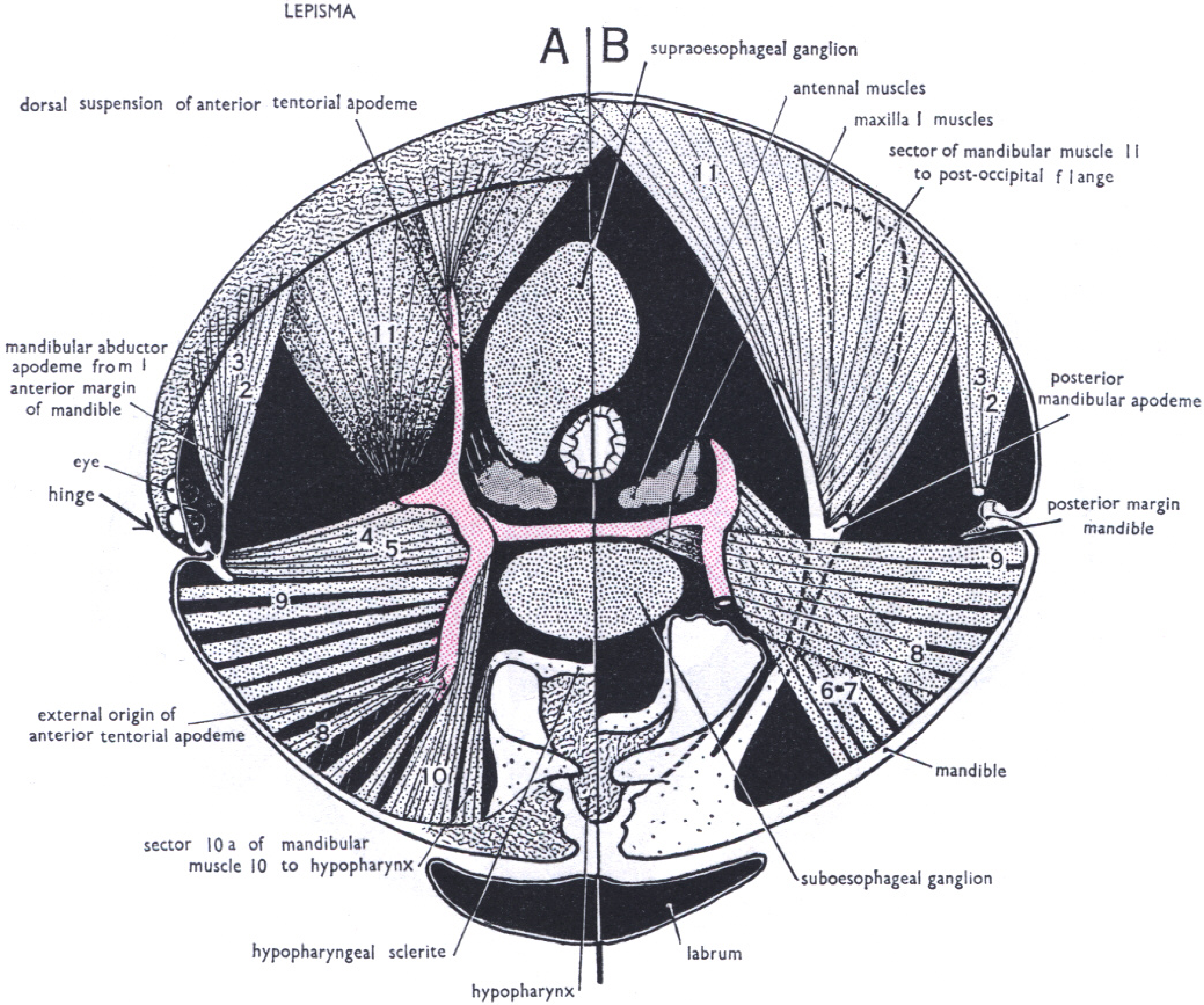


FIGURE 26. Thick transverse sections of the head of *Ctenolepisma ciliata* Dufour passing through the mandible and viewed from in front. The levels A and B are indicated in figure 25*a*, A being anterior to B. The external origin of the anterior tentorial apodeme is shown in A but the anterior face of the mandible has been removed to display the muscles. The transverse bridge formed by union of the anterior tentorial apodemes is shown in both levels. Muscle numbering corresponds with that of *Petrobius*. Mandibular abductor 5 is shown and abductor 4 lies just behind it. The apodeme bearing mandibular abductor 2 plus 3 (corresponding with the separate muscles 2 and 3 in *Petrobius*), is entire in A and cut short in B; the long cranial insertion of these muscles is also seen in figure 27C. Muscles 2 plus 3, 4 and 5 pull on the very short pre-axial border of the mandible (cf. muscles 3 and 6 in *Paranaspides* passing to the cranial wall and to the endoskeleton in figure 9C). The fan of adductor fibres 8, 9 and 10 from the inner face of the whole mandible to the anterior tentorial apodeme is entire in A and cut away ventrally in B to display the more posterior adductor muscle corresponding with 6 and 7 of *Petrobius*, Adductor muscle 11 is more complex than shown, one large and some small sectors passing behind to the post-occipital flange.

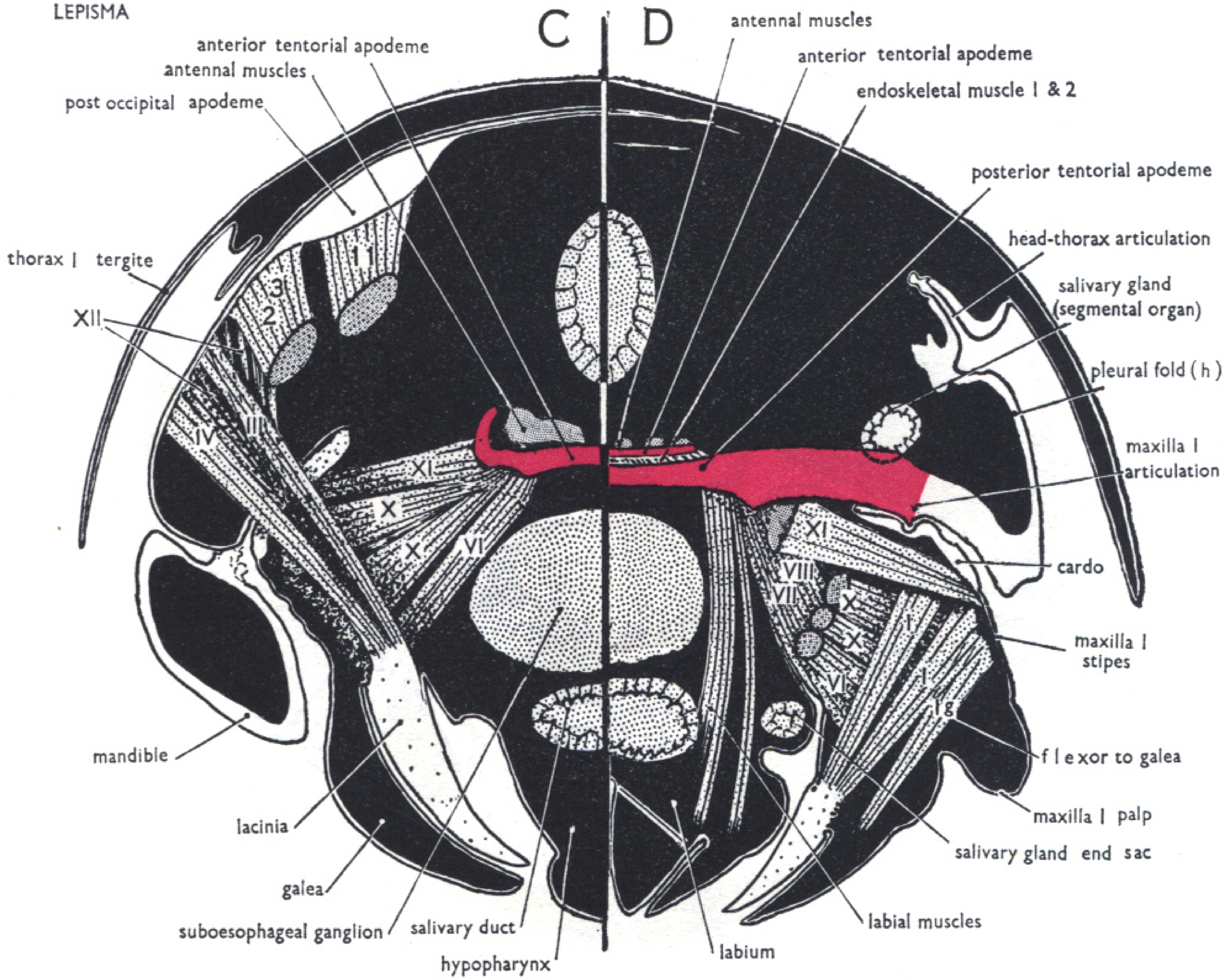


FIGURE 27. Thick transverse sections of the head of *Ctenolepisma ciliata* Dufour passing through the maxilla 1 and viewed from in front, level C being anterior to level D; the planes are indicated on figure 25*a*. Muscle numbering corresponds with that of *Petrobius*. Muscle XI, the protractor-depressor to the cardo-stipes hinge, and the stipes muscles VI and X are shown inserting on to the anterior tentorial plate in C; muscles VI and X are cut in D so displaying the more posterior stipes muscles VII and VIII which insert on the posterior tentorial plate. Muscle X runs in several sectors. The cranial retractors of the lacinia, muscles III and IV, are shown in C and the promotor of the cardo, muscle XII, in two sectors, lies immediately behind muscles III and IV; the sectors of muscle XII resemble those drawn more clearly for *Thermobia* by Chaudonneret (1950, fig. 42 *rl*, *rm*). The labial segmental organ is cut showing the end sac (marked) from which a duct passes up to the pleural fold and down to the median exit duct.

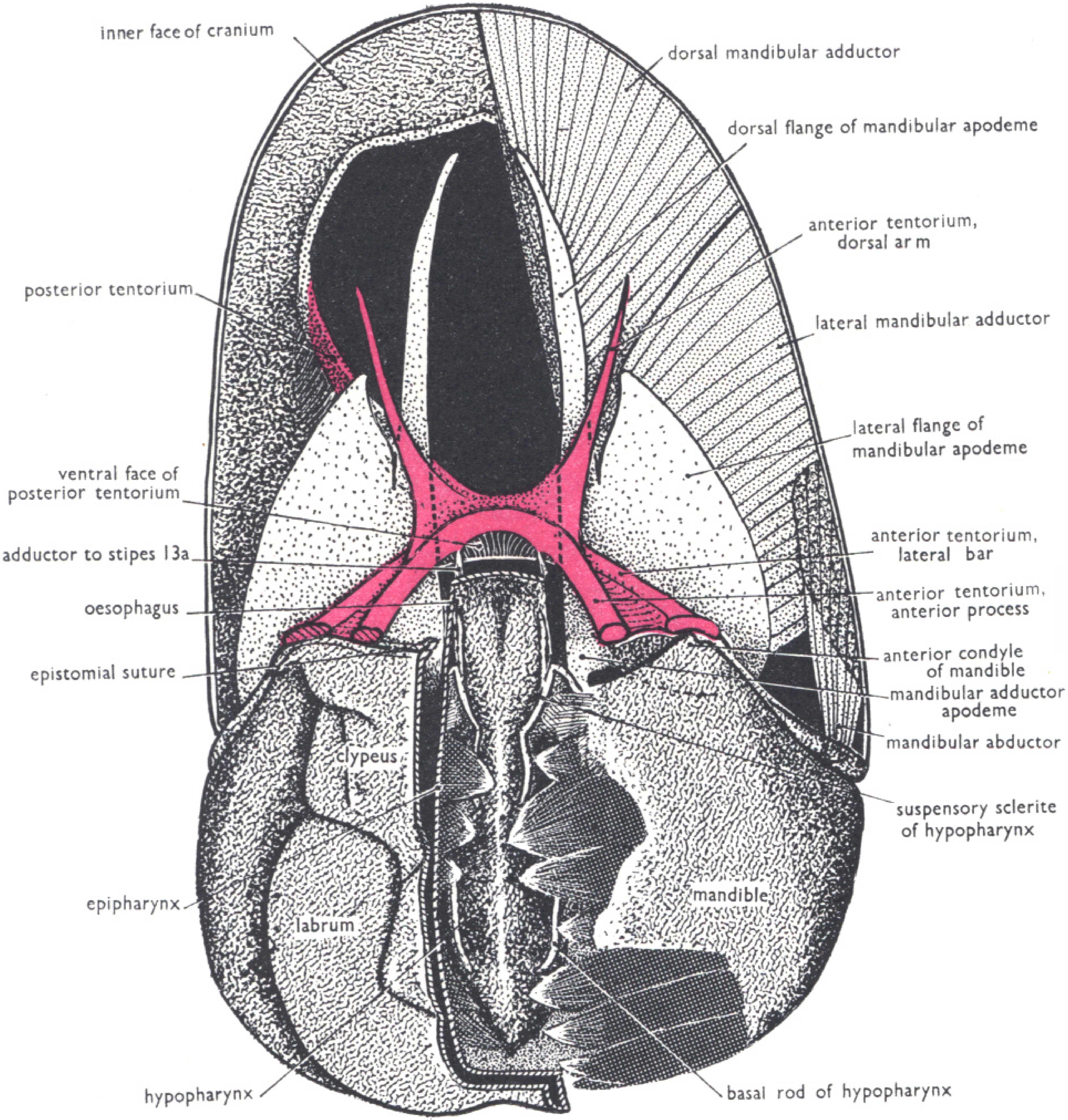


FIGURE 28. Oblique anterior view of the head of *Locusta migratoria* L., the mandibular hinge on the animal's left side being visible. Part of the clypeo-labrum is removed together with the whole front wall of the head. The cerebral ganglia, alimentary canal and antennal muscles have been removed to display the tentorium and mandibular muscles.

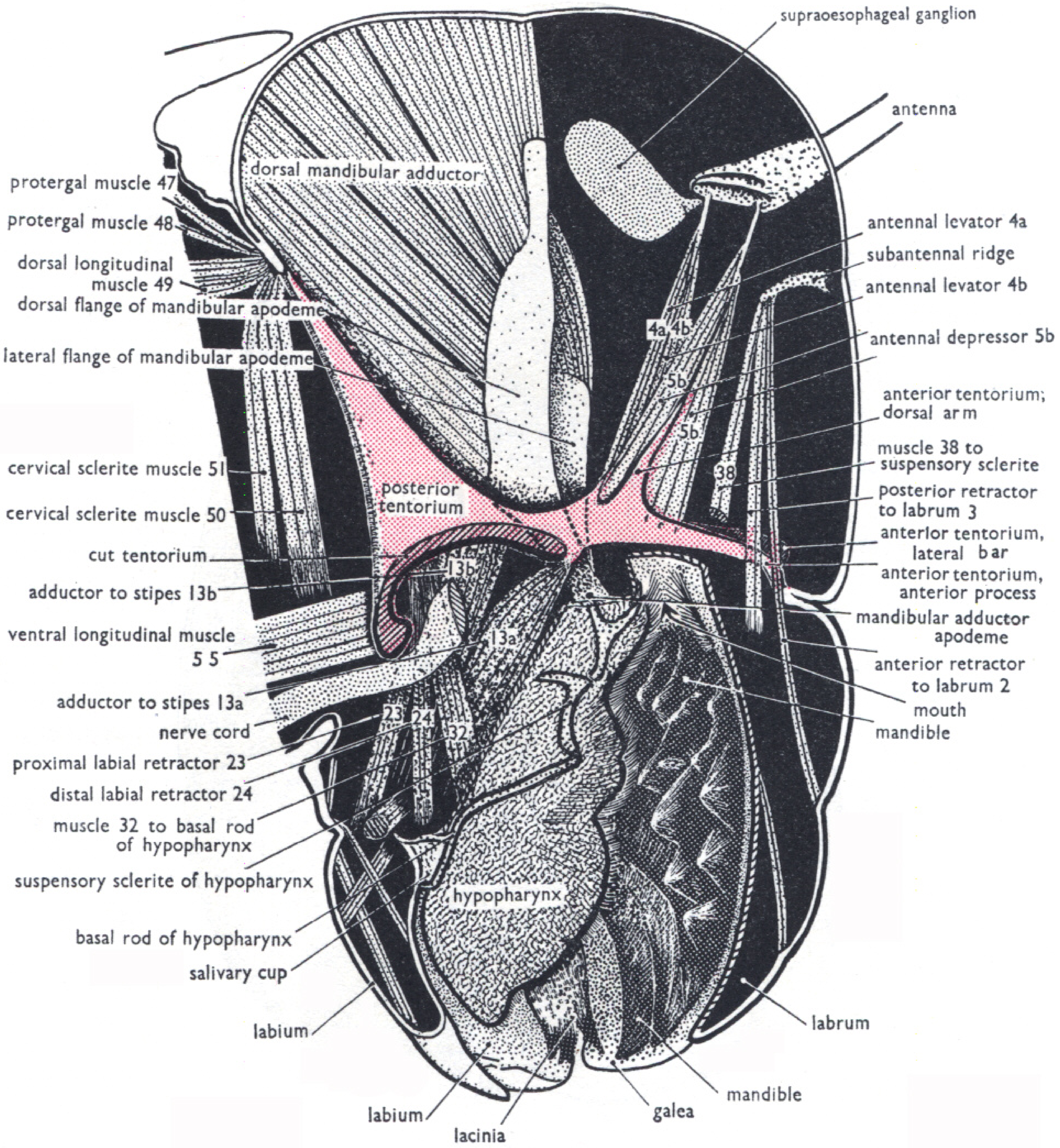


FIGURE 29. Sagittal half of the head of *Locusta migratoria* L. the hypopharynx being left intact. The circumoesophageal commissures have been removed in order to display the antennal and mandibular muscles and the tentorium. The upper sector of the suspensory sclerite of the hypopharynx sends one branch to the oesophagus and the other unites with the mandible close to the origin of the mandibular apodeme. The mandibular muscles are removed on the left to show the posterior part of the cranium and tentorium. The muscle numbers are those of Albrecht (1953).

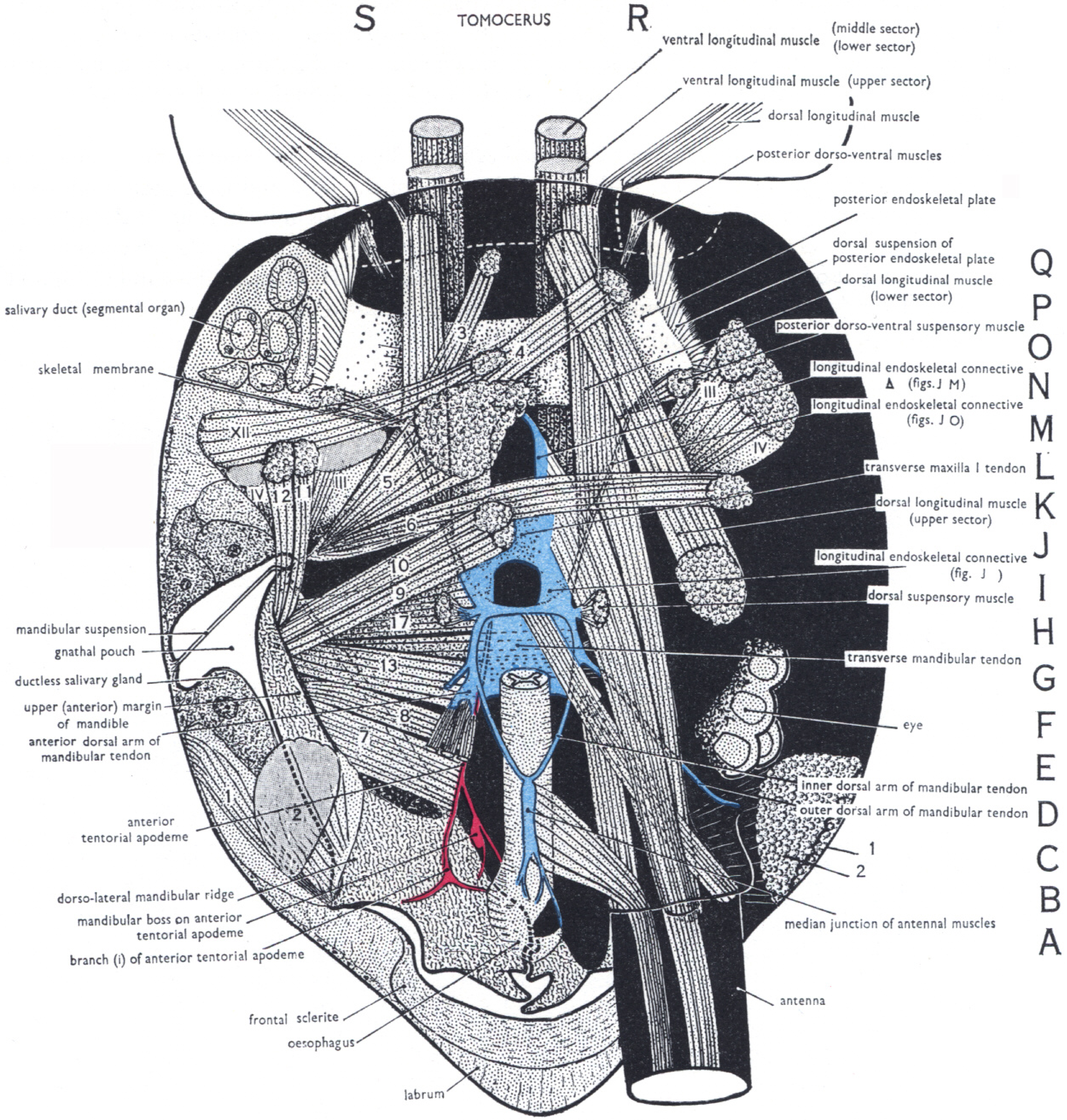


FIGURE 32 (see also legend on p. 149). Level R is superficial, the muscles and their antero-dorsal insertions being shown as if the head wall was transparent. The ocelli and the base of the antenna are shown, and the tip of the animal's left mandible is drawn as if the front of the head was transparent (see sagittal view in figure 35). Muscles from the animal's left mandible are omitted except for the dorso-lateral insertions of muscles 1 and 2.

Level S shows the entire right mandible and its most superficial muscles, muscles 4 to 6 crossing over to the other side. Muscles 7 to 12 arise from the anterior margin of the mandible, muscles 3 to 6 from the homologue of the posterior mandibular apodeme, here a short chitinous process at the postero-ventral corner of the mandible (see origin of muscle 6 in figure 37I), and muscles 13–17 arise from the mandibular concavity. Muscle 2 is cut short, it arises with muscle 1 from the dorso-lateral mandibular ridge (figures 33, 42 and 36D). The antenna and some of its muscles are omitted, others are cut short. Branch (i) of the anterior tentorial apodeme lies in the head above the gnathal pouch and has been drawn superimposed upon the mandible; its natural position is seen in level T and figure 36D. Maxilla 1 muscles III and IV are cut short their dorsal insertions appear in level R.

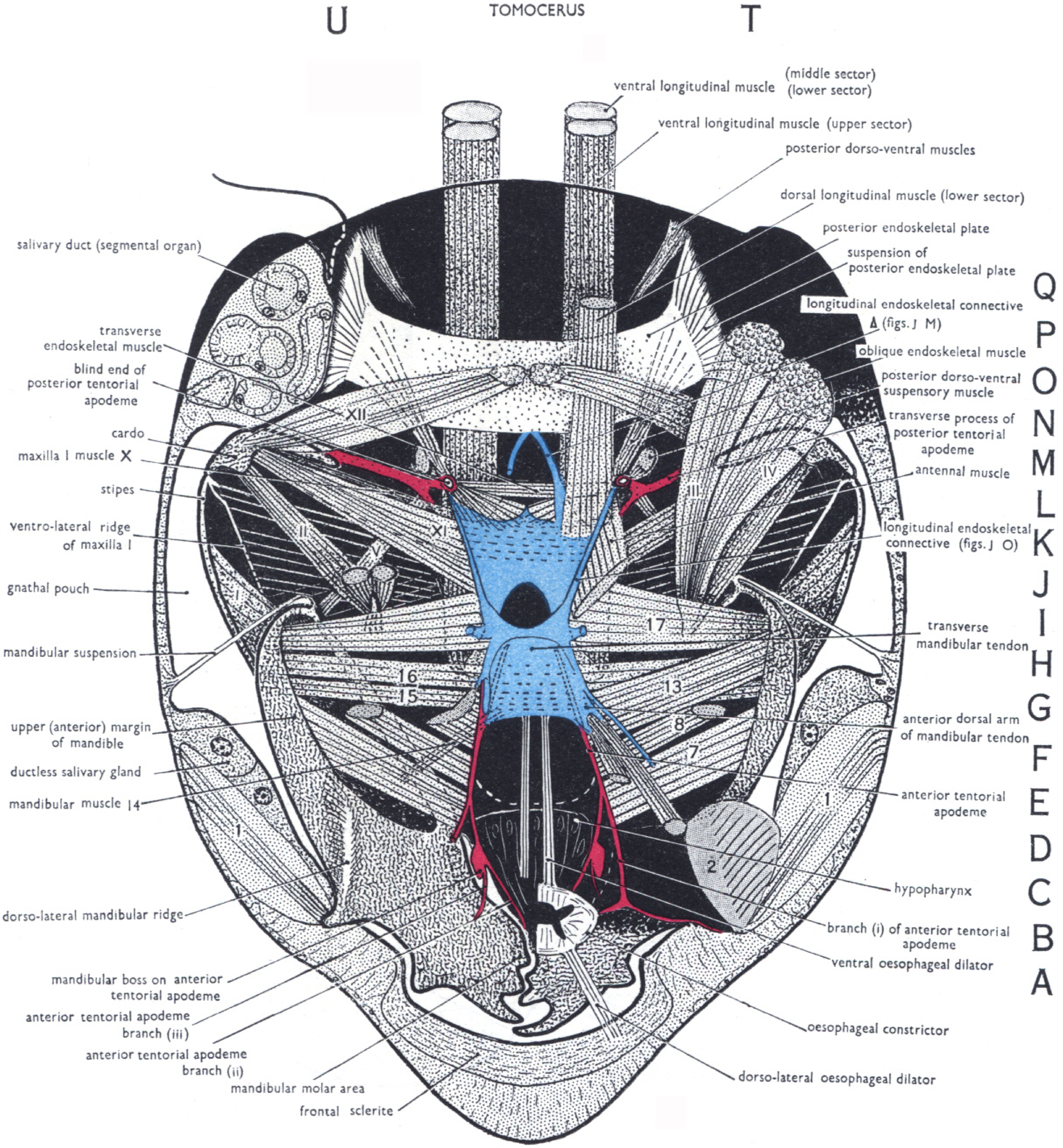


FIGURE 33 (continuation of figure 32). Conventions as on figure 32. Level T shows a deeper view of the mandibular muscles, which are further cut away in level U to show the transverse mandibular muscles 15 and 16 which unite with their fellows below the transverse mandibular tendon. The counter-rotator (promotor) muscles from the anterior margin of the mandible are removed. In level U muscle 2 and part of muscle 1 are cut away from their origins on the dorso-lateral mandibular ridge; the antennal muscles, the dorsal suspensory muscle, and the posterior dorso-ventral suspensory muscle are all removed; the latter is entire in level T. The proximal parts of maxillae 1 are shown, muscles III and IV being entire in level T and cut short in level U. The lower sector of the dorsal longitudinal muscle is omitted in level U and the longitudinal tendinous connective, marked by a triangle here and on the transverse sections, is cut away from the maxilla 1 tendon in U. The anterior tentorial apodeme is almost entirely shown in level T, branch ii to the superlingua and branch iii to the preoral cuticle above (anterior to) the mandible being marked on level U. The edge of the suboesophageal ganglion is indicated by a dotted white line.

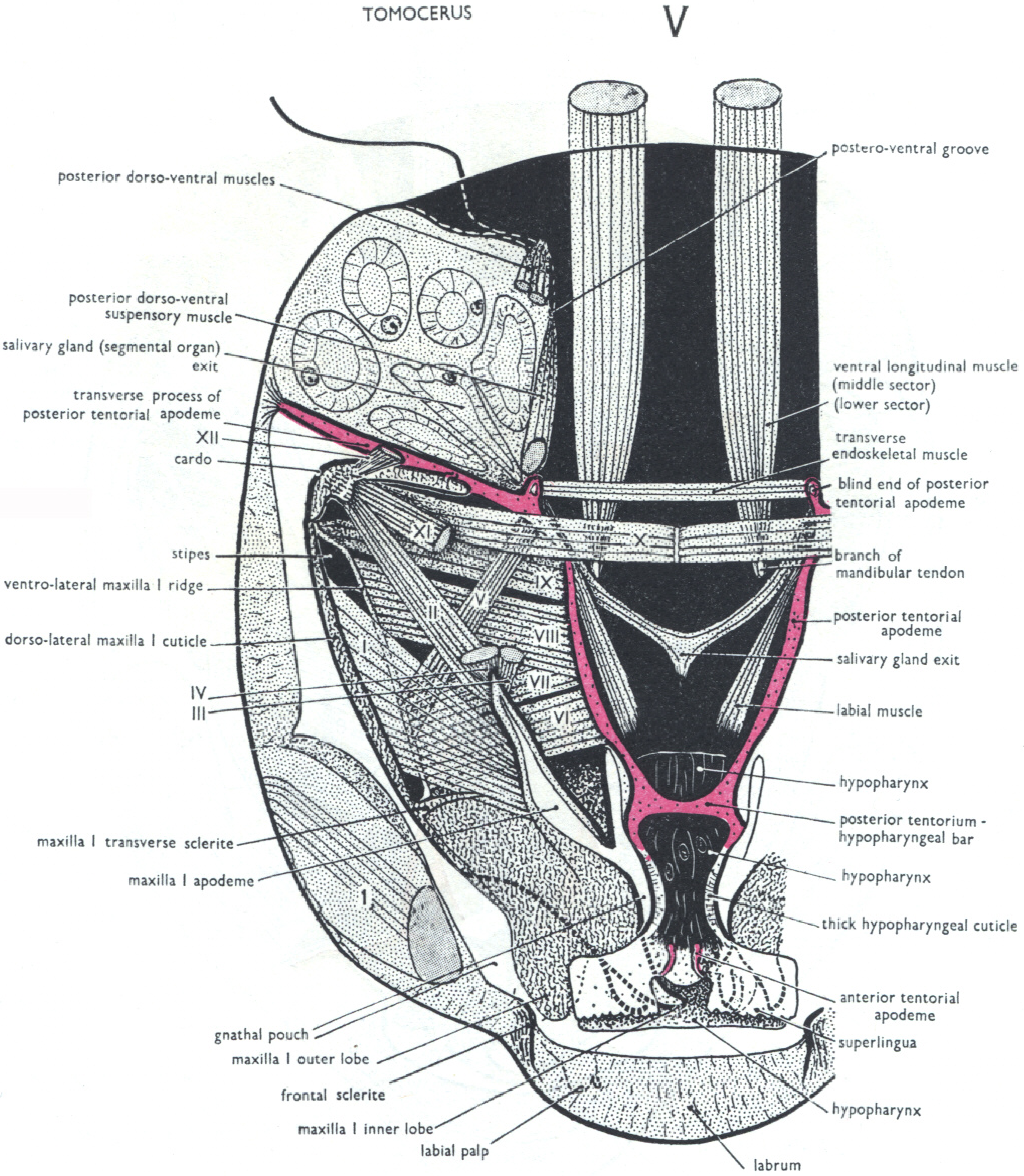


Figure 34 (continuation of figures 32 and 33). Conventions as on figure 32. A deeper level than figure 33U displaying the whole of the posterior tentorial apodeme and maxilla 1 with maxilla 1 muscles other than III, IV, XI and XII which are cut short or omitted, they are shown in levels T and U. The blind end of the posterior tentorial apodeme rises in the head and is foreshortened in this view. The mandible with its muscles, the transverse segmental tendons of the mandible and maxilla 1 and the posterior endoskeletal plate have been removed. The point of exit of salivary juice from the paired ducts is shown diagrammatically. The whole oesophagus has been removed, leaving the hypopharynx and superlinguae between which the inner maxillary lobe projects. A cut portion of the anterior surface extension of the anterior tentorial apodeme lies on the hypopharynx, but the spines which this apodeme supports are omitted (see figure 36B). The complexities in form of the biting end of the inner maxillary lobe are not shown; they are indicated roughly in figure 42 (for details see Hoffmann (1908)).

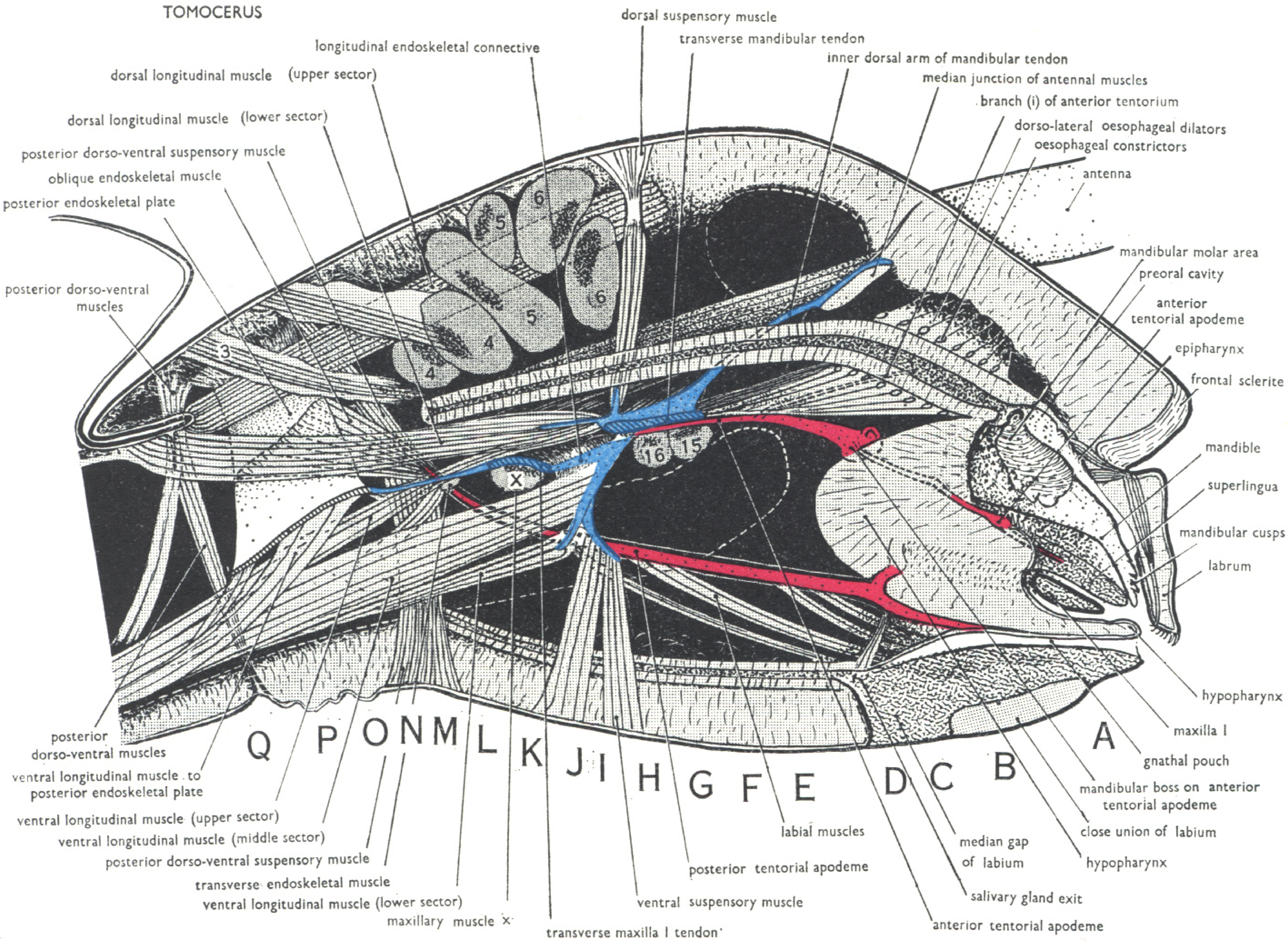


FIGURE 35. Reconstruction of a sagittal half of the head of *Tomocerus longicornis* viewed from the middle line. Conventions as on figure 32. The transverse maxilla 1 and mandibular tendons and the posterior endoskeletal plate are cut, as are the mandibular muscles 4 to 6 which cross to the other side of the head, and mandibular muscles 15 and 16 and maxillary muscle X which are transverse in position. These muscles cut transversely show the small central area of cut fibrils (dark) surrounded by bulky nucleated cytoplasm (stippled). Almost the whole of the anterior tentorial apodeme is shown, branch i being indicated by dotted lines. The internal part of the posterior tentorial apodeme is shown with its superficial arm alongside the maxilla 1, but the details of its fade out into the elaborate cuticular thickenings of the hypopharynx are not shown. The more important branches of the tendinous endoskeleton visible in this aspect are shown.

The dorsal longitudinal muscle runs in two sectors, the upper inserting dorso-laterally on the head wall and the lower on to the outer fork of longitudinal endoskeletal connective, marked by a cross on the transverse sections in figures 38K, 39L to O and 40P, Q. The ventral longitudinal muscle forms an upper sector inserting on the longitudinal endoskeletal connective (see figures 39, 40L to Q); a middle sector inserting on the upper part of the ventral suspensory arm of the transverse mandibular tendon (figures 38J, 37H, I); and a small lower sector inserts on a branch of the ventral suspensory arm (figures 39M, 38K). A branch of the ventral longitudinal muscle inserts on the hollow part of the posterior tentorial apodeme (unlabelled) (see also figures 39M, N).

The median opening of the paired (salivary) ducts of the labial segmental organs is more complex than shown, the ducts open into a median diverticulum of the gnathal pouch (see figures 37E and 36D). The gnathal pouch is freely open to the exterior between the paired parts at the marked median gap (see figure 36D), but distal to this there is a close, possibly fused, union between the two halves of the labium over the finely stippled area, see (figure 36B).

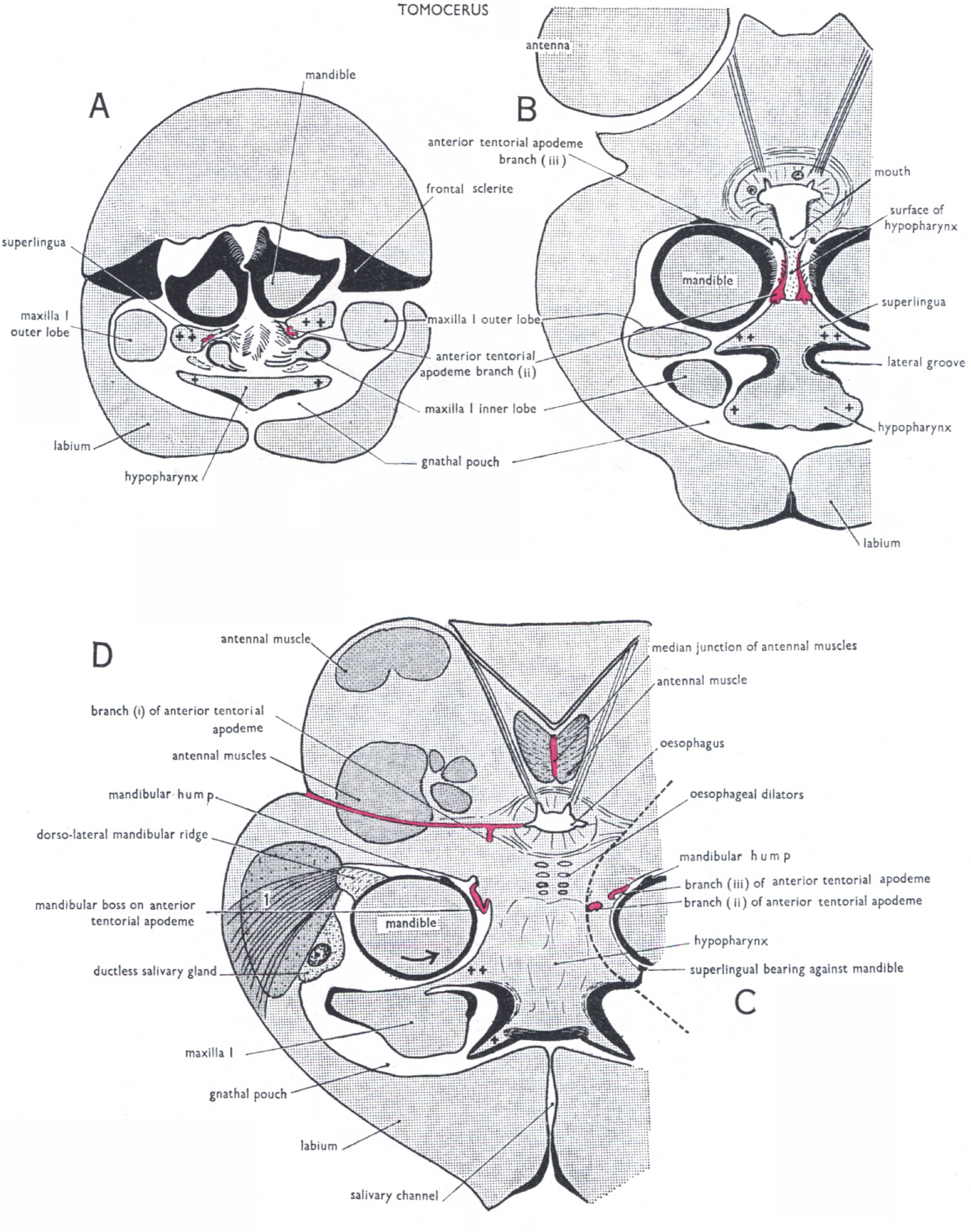


FIGURE 36. For legend see p. 158.

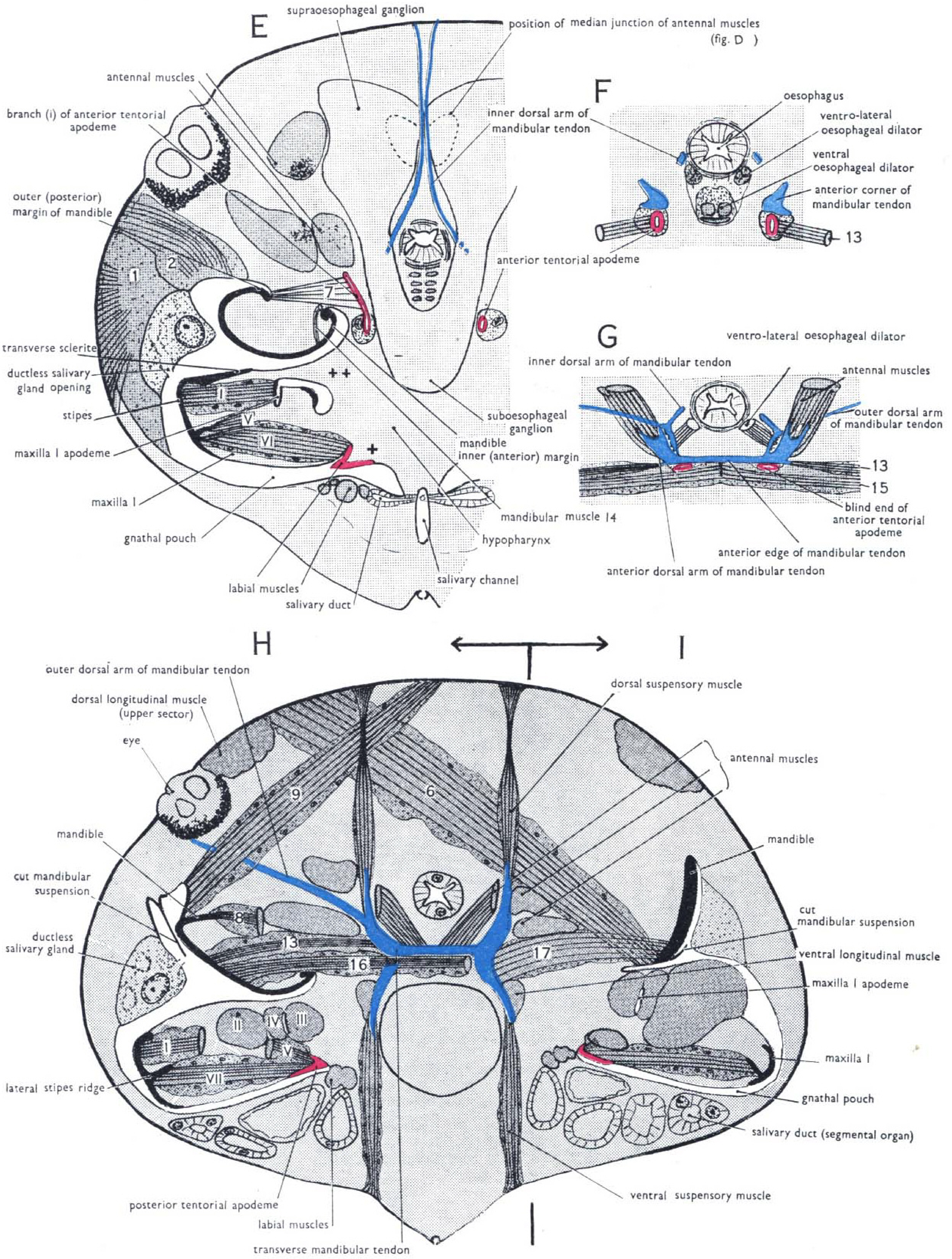


FIGURE 37 (continuation of figure 36). Level E. Through the anterior part of the eye, circum-oesophageal commissures, and the point of discharge of the salivary ducts (labial segmental organs). Giant ductless gland cells on the inner walls of the gnathal pouch discharge by irregular intracellular spaces. The upper face of the mandible is open to the body cavity and maxilla 1 is united on its mesial side to hypopharyngeal tissue, the superlingual tissue passing to the upper maxillary face (two crosses) and the hypopharyngeal tissue passing to the lower face (one cross). The maxilla 1 apodeme is here internal (cf. figure 36D). Laterally maxilla 1 cuticle is sclerotized and stiff; at this level a transversely directed sclerite passes on to the anterior upper face (see figure 34); a longitudinal ridge projects inwards 'lateral stipes ridge' marked in figure 37H and 'ventro-lateral maxilla 1 ridge' on figure 34, and the thick cuticle which formed the lateral angle to the hypopharynx now continues as the posterior tentorial apodeme. The anterior tentorial apodeme has sunk into the head as a hollow tube carrying with it a thick investment of ectodermal epithelium. The base of branch i of the anterior tentorial apodeme is shown on the left; its continuation is seen in figure 36D. The ventral oesophageal dilators are cut below the oesophagus (see figure 35).

Level F. Through the antero-lateral corners of the transverse mandibular tendon (blue) below which lies the anterior tentorial apodeme (red).

Level G. Close behind F, through the anterior edge of the transverse mandibular tendon where it gives rise to the antero-dorsal arms supporting the antennal muscles. Just in front arise the inner and outer dorsal arms of the transverse mandibular tendon (figures 32, 35), the forward course of the inner arm is seen in levels F and E. Below the transverse mandibular tendon the anterior ends of the anterior tentorial apodemes are attached to its ventral surface.

Level H. Through the posterior part of the eye and transverse mandibular tendon showing the outer dorsal arm and behind it the dorsal and ventral suspensory arms supporting the similarly named (and marked) muscles (see figure 41). A stiff cuticular flange gives origin to mandibular muscle 9. Maxilla 1 apodeme is clothed by muscles III and IV and the posterior tentorial apodeme is superficial.

Level I. Behind H, and through the proximal limit of the mandible where its posterior margin gives a strong cuticular process (homologous with the posterior mandibular apodeme of Thysanura, etc.) which bears rotator muscles (figure 32S), muscle 6 being shown. The origin of the suspensory sheet of cuticle from the base of the mandible (figures 32, 33) is seen in this section and its union with the upper lateral wall of the gnathal pouch in level H. The lateral stiff maxilla 1 cuticle is very limited in extent, leaving extensive arthrodial membranes on the upper (anterior) and lower (posterior) faces (cf. figures 33U, 34).

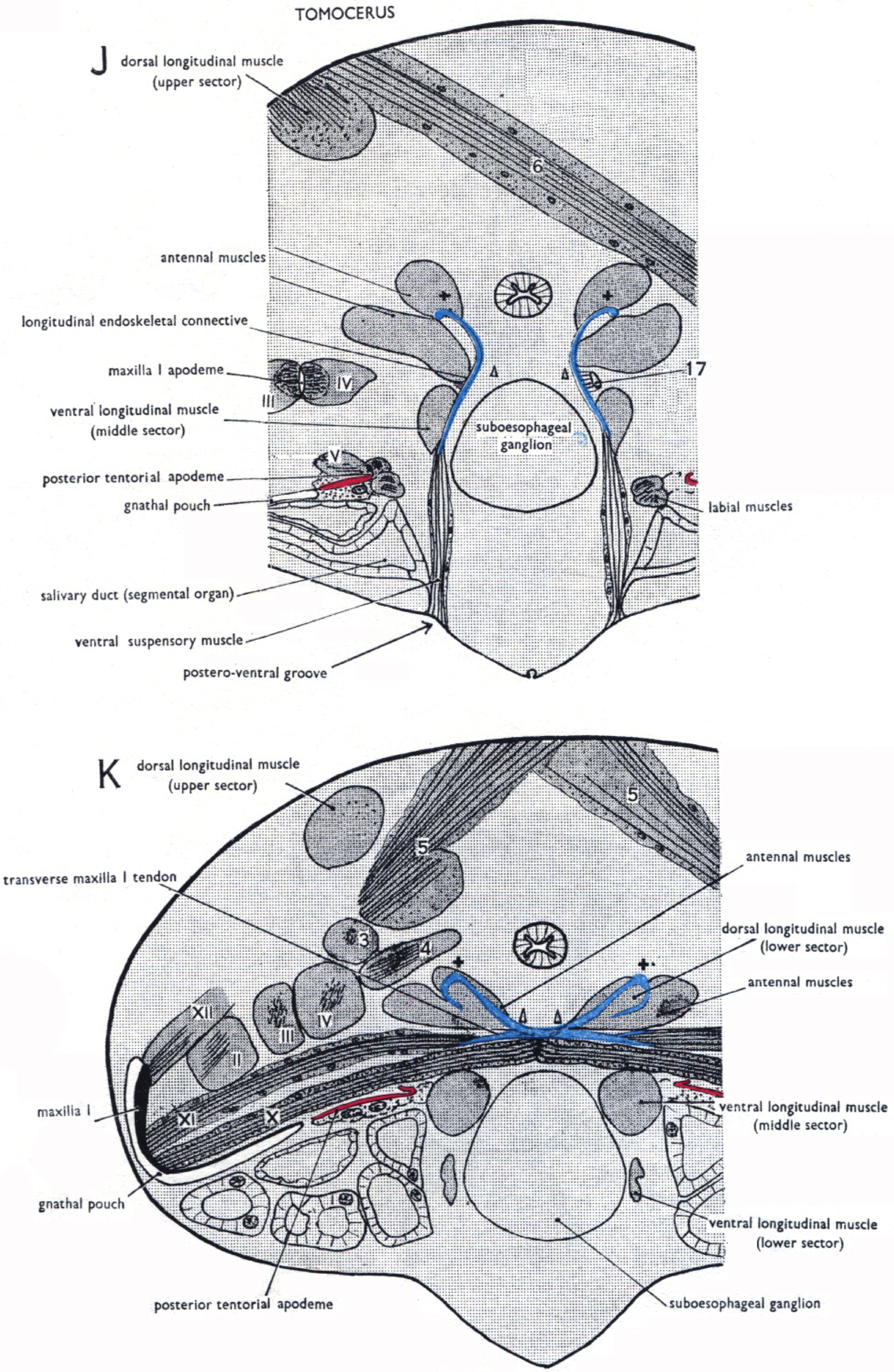
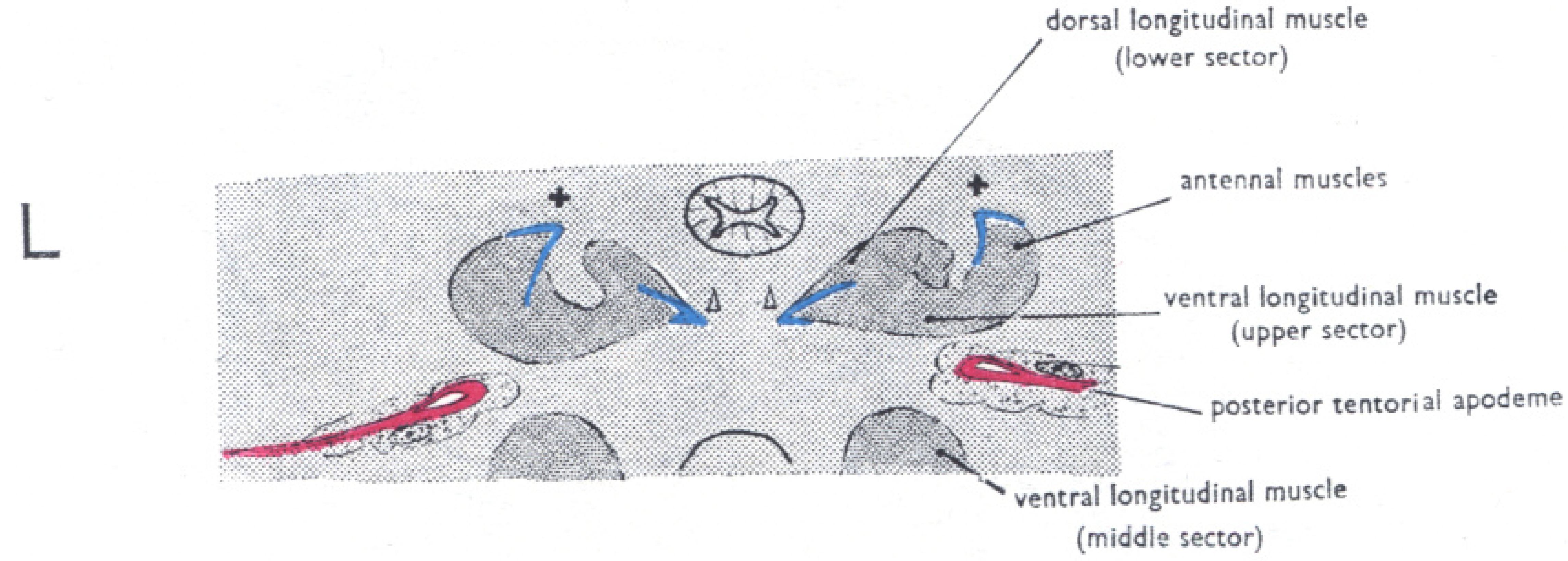
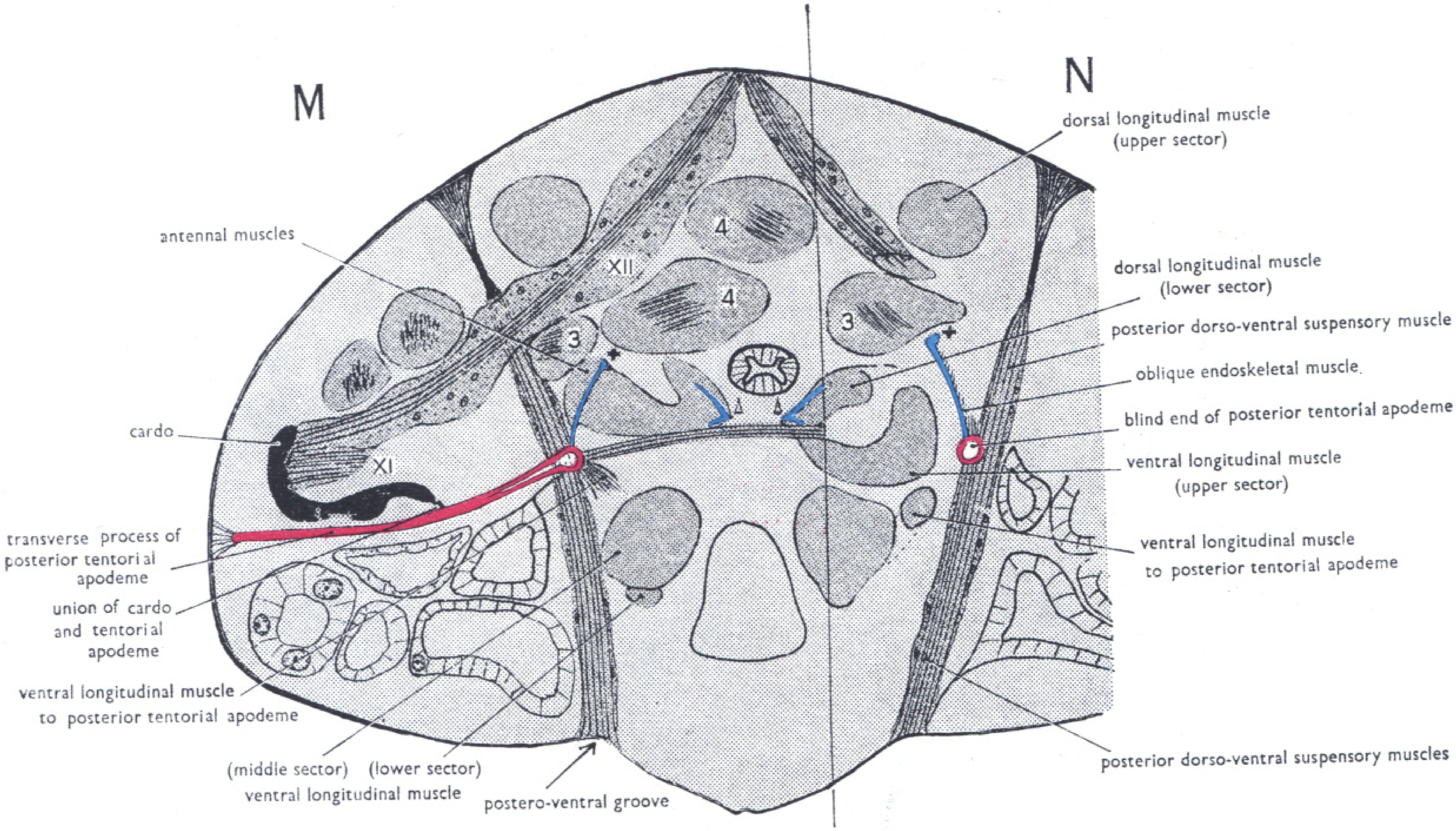
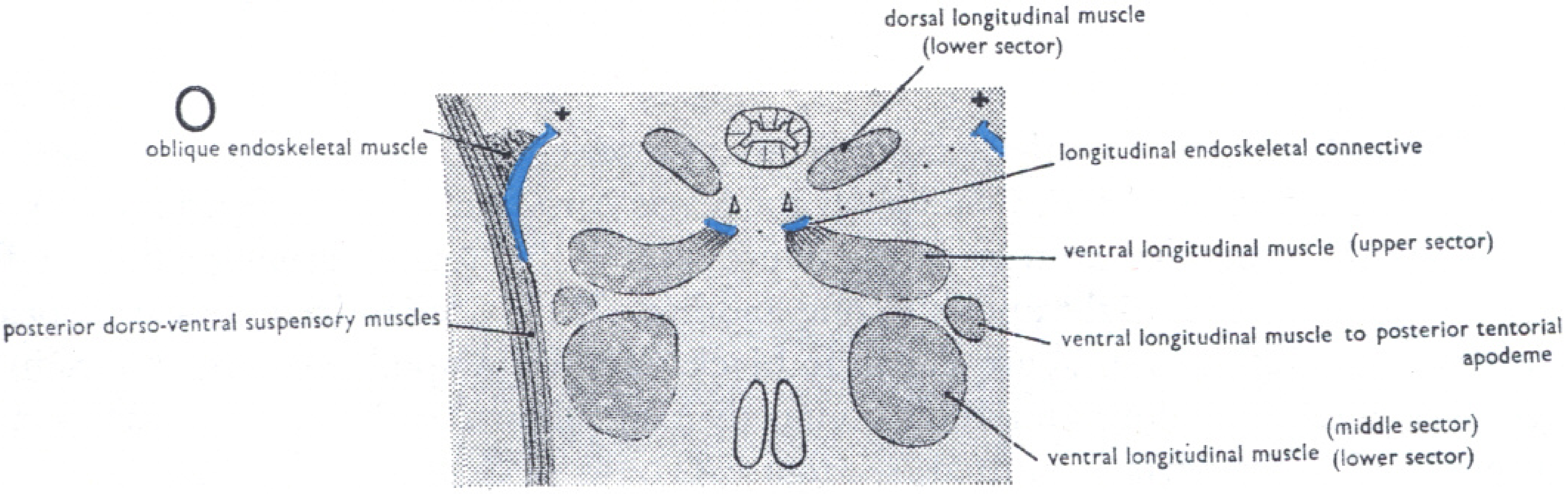


FIGURE 38. For legend see p. 159.

TOMOCERUS


L
dorsal longitudinal muscle (lower sector)
antennal muscles
ventral longitudinal muscle (upper sector)
posterior tentorial apodeme
ventral longitudinal muscle (middle sector)


M
N
4
4
XII
3
3
XI
dorsal longitudinal muscle (upper sector)
antennal muscles
dorsal longitudinal muscle (lower sector)
posterior dorso-ventral suspensory muscle
oblique endoskeletal muscle.
cardo
blind end of posterior tentorial apodeme
ventral longitudinal muscle (upper sector)
transverse process of posterior tentorial apodeme
ventral longitudinal muscle to posterior tentorial apodeme
union of cardo and tentorial apodeme
ventral longitudinal muscle to posterior tentorial apodeme
(middle sector) (lower sector) ventral longitudinal muscle
postero-ventral groove
posterior dorso-ventral suspensory muscles


O
dorsal longitudinal muscle (lower sector)
oblique endoskeletal muscle
longitudinal endoskeletal connective
ventral longitudinal muscle (upper sector)
posterior dorso-ventral suspensory muscles
ventral longitudinal muscle to posterior tentorial apodeme
ventral longitudinal muscle (middle sector) (lower sector)

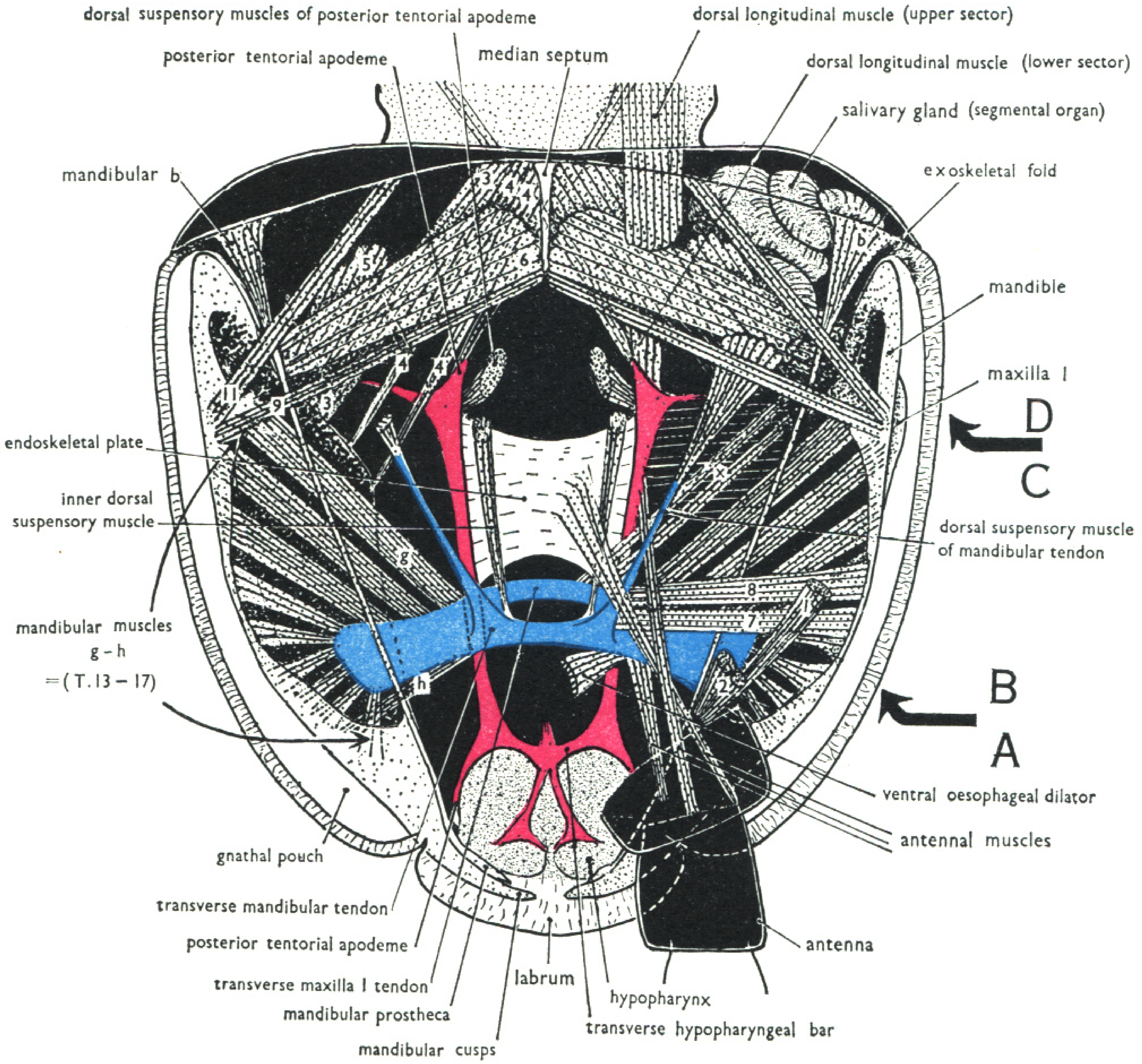


FIGURE 44. *Campodea staphylinus* West. Antero-dorsal reconstruction of the head, drawn as a transparent object. The antennal base, the antennal and superficial mandibular muscles, the unobscured muscles of maxilla 1, and some coils of the labial gland (segmental organ) are shown on the right, these structures being omitted on the left in order to display the mandible. Superficial mandibular muscles 7 and 8 are omitted on the left. Transverse segmental tendons are blue and the paired posterior tentorial apodeme and its processes are shown in red. The arrows indicate the levels and direction of view of the sectioned heads shown in figure 46. Mandibular muscles bear Arabic numerals and maxilla 1 muscles bear Roman numerals. The numbering suggests the homologies believed to exist between the muscles of *Tomocerus* and *Campodea*, figures 32 to 43, where similar numbering is employed. Mandibular muscles 1 and 2 are present in the Collembola and Diplura alone; muscles 3 to 11 here can be recognized also in *Petrobius* (see table of homologies between muscles of *Petrobius* and of *Tomocerus* in figure 21, which holds also for *Campodea* (muscles 3 to 11)). The muscles between the arrows on the left (between muscle fibres *g* and *h*) represent muscles 13 to 17 of *Tomocerus* but do not correspond in detail; they correspond more closely with *Petrobius* muscles 8 to 10, figure 21. Muscle fibres *g* and *h* are so marked by Tuxen (1959); the further relationship of his lettering with the numerals employed here is given on p. 65.

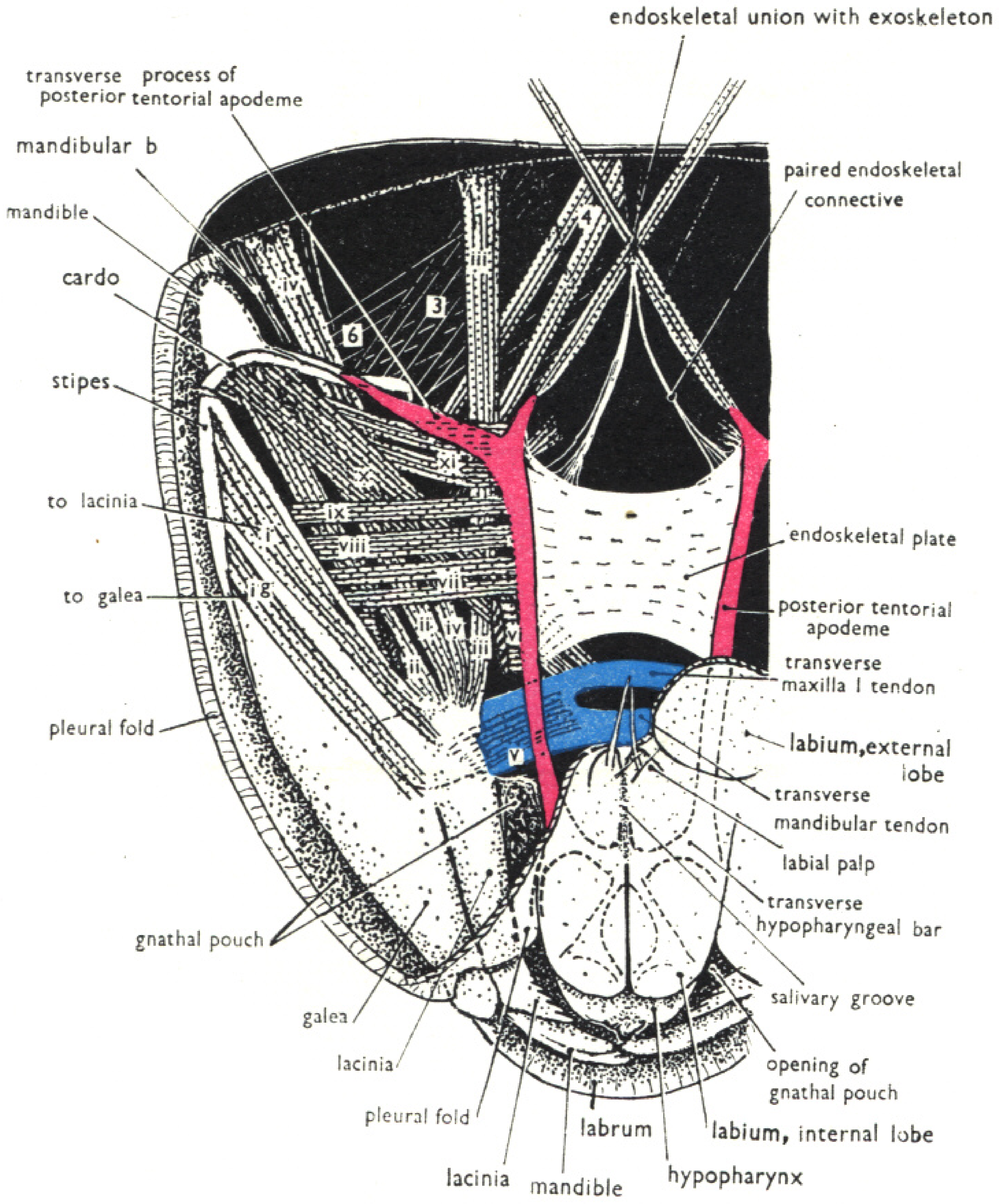


FIGURE 45. Reconstruction of the head of *Campodea staphylinus* in ventral view, drawn as if the surface cuticle and ectoderm on the right were cut away proximal to the external lobe of the labium and on the left uncovering the whole gnathal pouch, leaving only the distal part of the pleural fold (marked) forming the lip of the gnathal pouch. Cut edges are hatched. The stiff cuticle of maxilla 1 forms the postero-ventral face of the limb, here exposed in surface view (see figures 46 A to C). Head endoskeleton is indicated as in figure 44 and muscle numbering is similar. The whole posterior tentorial apodeme is shown together with the short link of arthrodial membrane from the cardo to the apodeme. The posterior end of the mandible is visible above the maxilla. The correspondence between the maxilla 1 muscles, marked by Roman numerals, and the lettering of the muscles referred to by Tuxen (1959) is given in the footnote to p. 68.

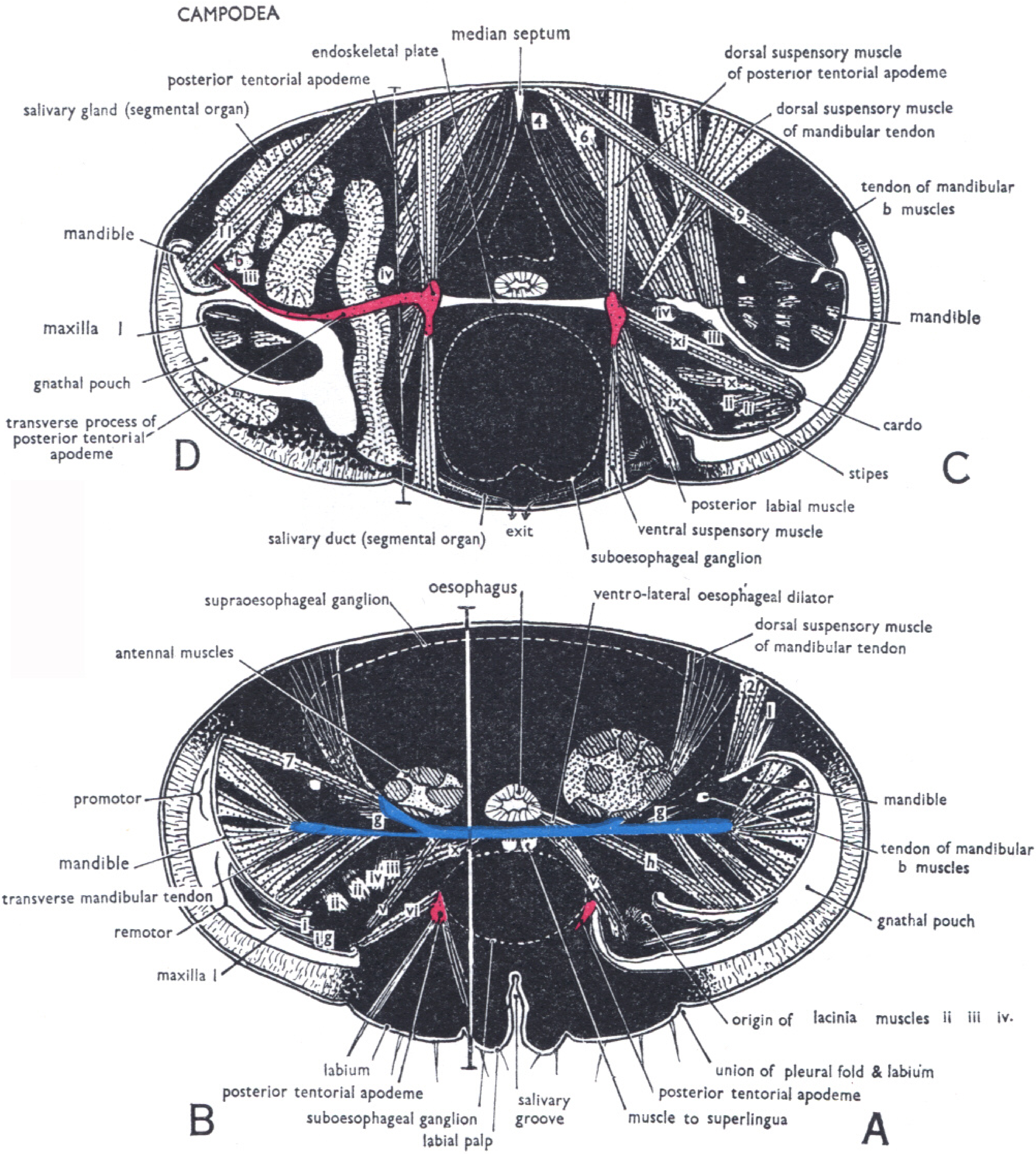


FIGURE 46. For legend see facing page.

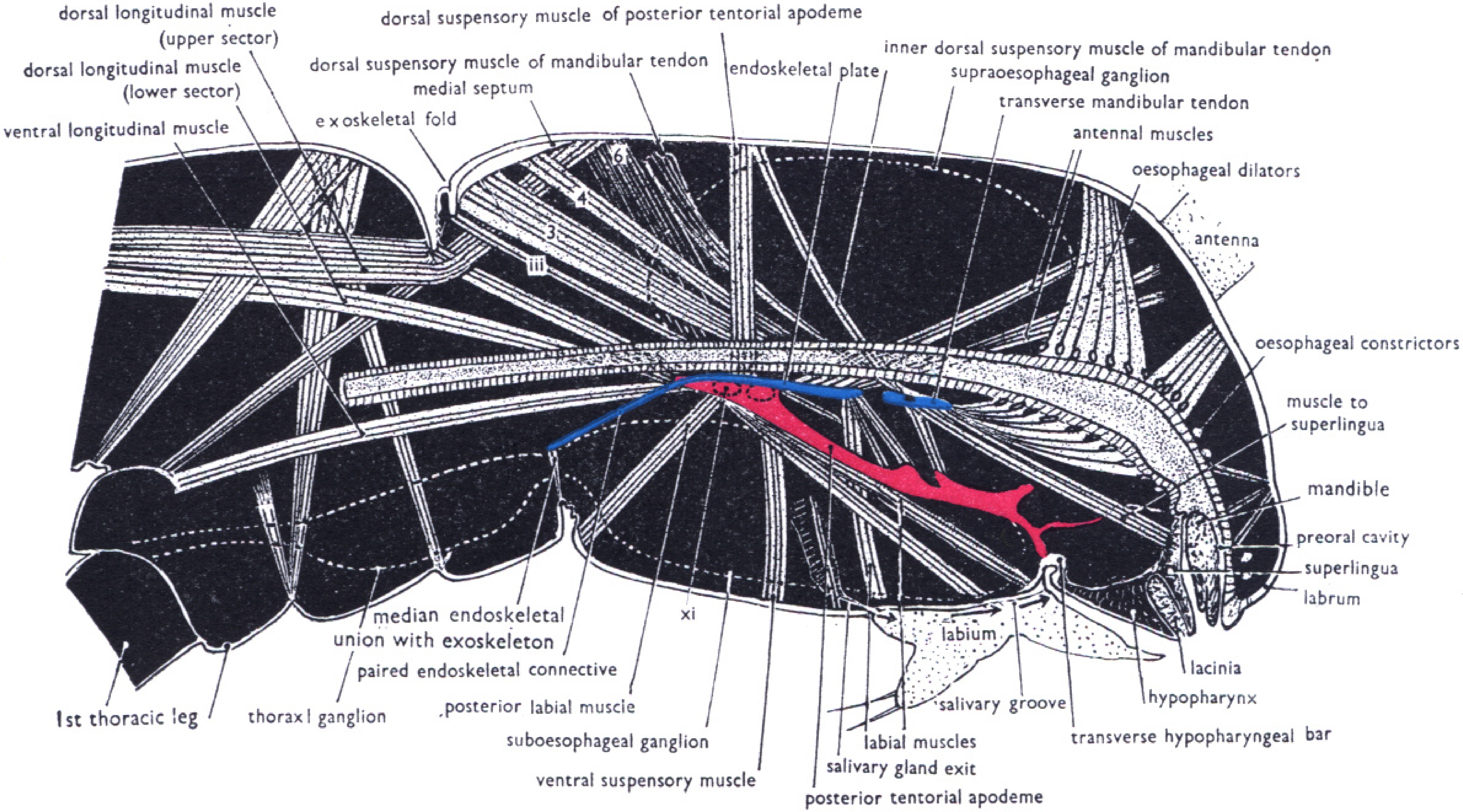


FIGURE 47. Reconstruction of a sagittal half of the head of *Campodea staphylinus* to show the relationship of the transverse tendons with the posterior tentorial apodeme of the left side and with the muscles. The opening of the salivary duct into the posterior end of the median labial groove (salivary groove in figure 46A) is indicated and the direction of flow towards the mouth is shown by arrows. On the left the section is sub-median, passing through the coxa of the first thoracic leg. The positions of the ganglia of the nervous system are indicated by dotted lines.

IULIFORM DIPLOPOD

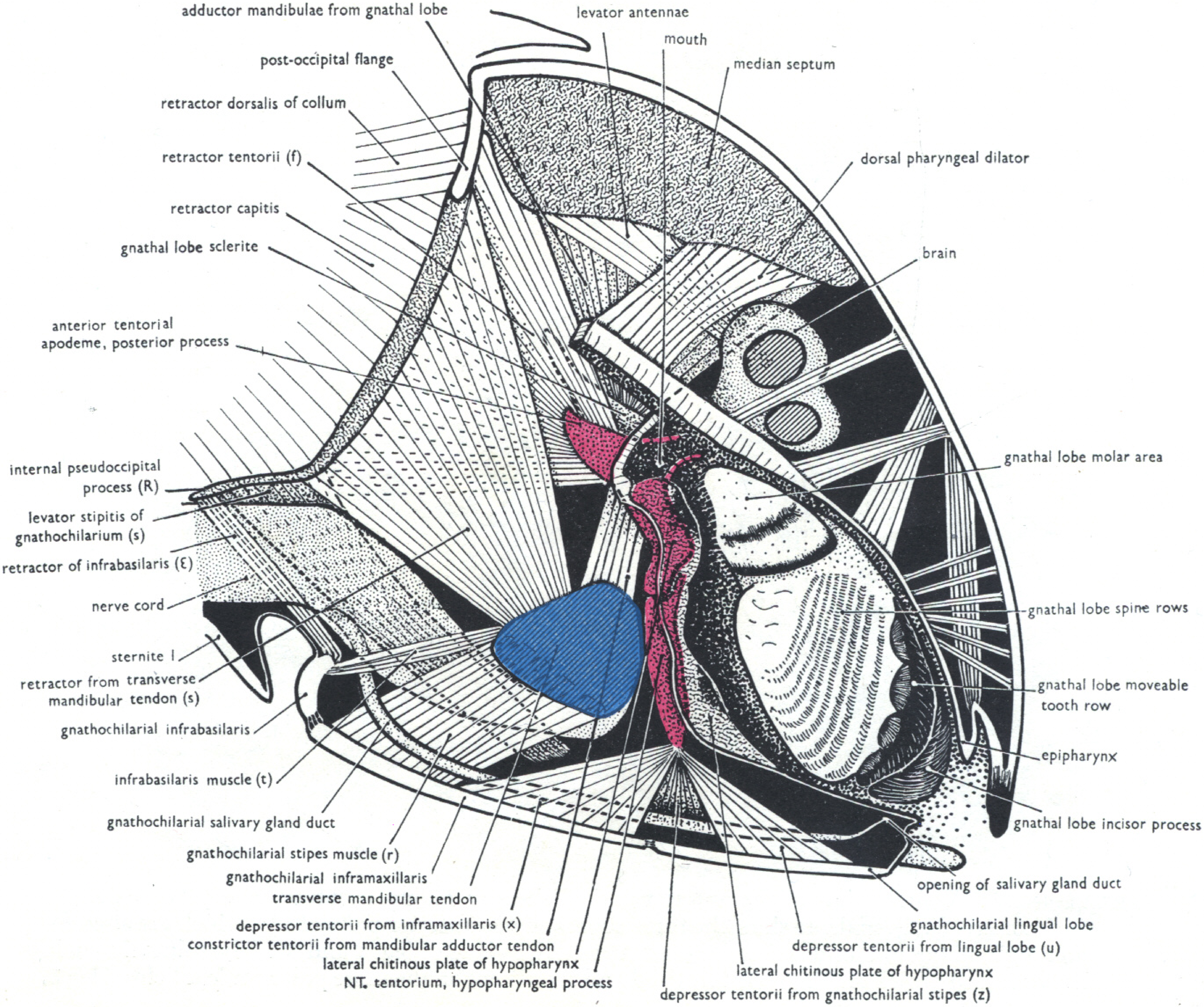


FIGURE 50. For legend see facing page.

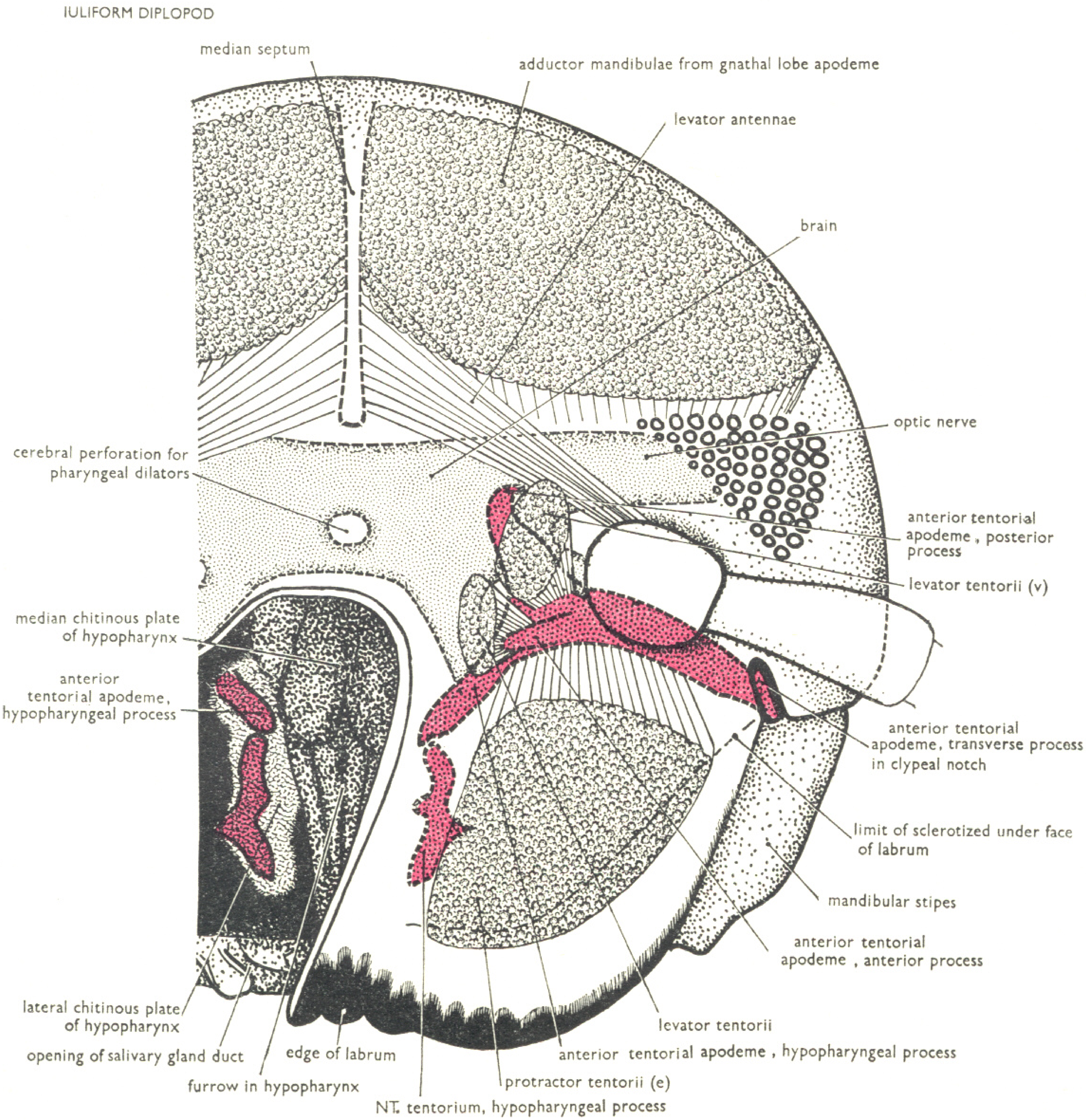


FIGURE 51. Anterior view of the head of the diplopod *Poratophilus punctatus* drawn as if the cuticle was transparent, with part of the labrum cut away to expose the hypopharynx, the gnathal lobe of the mandible being omitted. The position of the anterior tentorial apodeme and its processes is shown in red with black stipple and the heavy marginal sclerotization of the labrum is shown in black. The supraoesophageal ganglion is shown by fine stipple and a convention indicates muscle insertions on the cuticle.

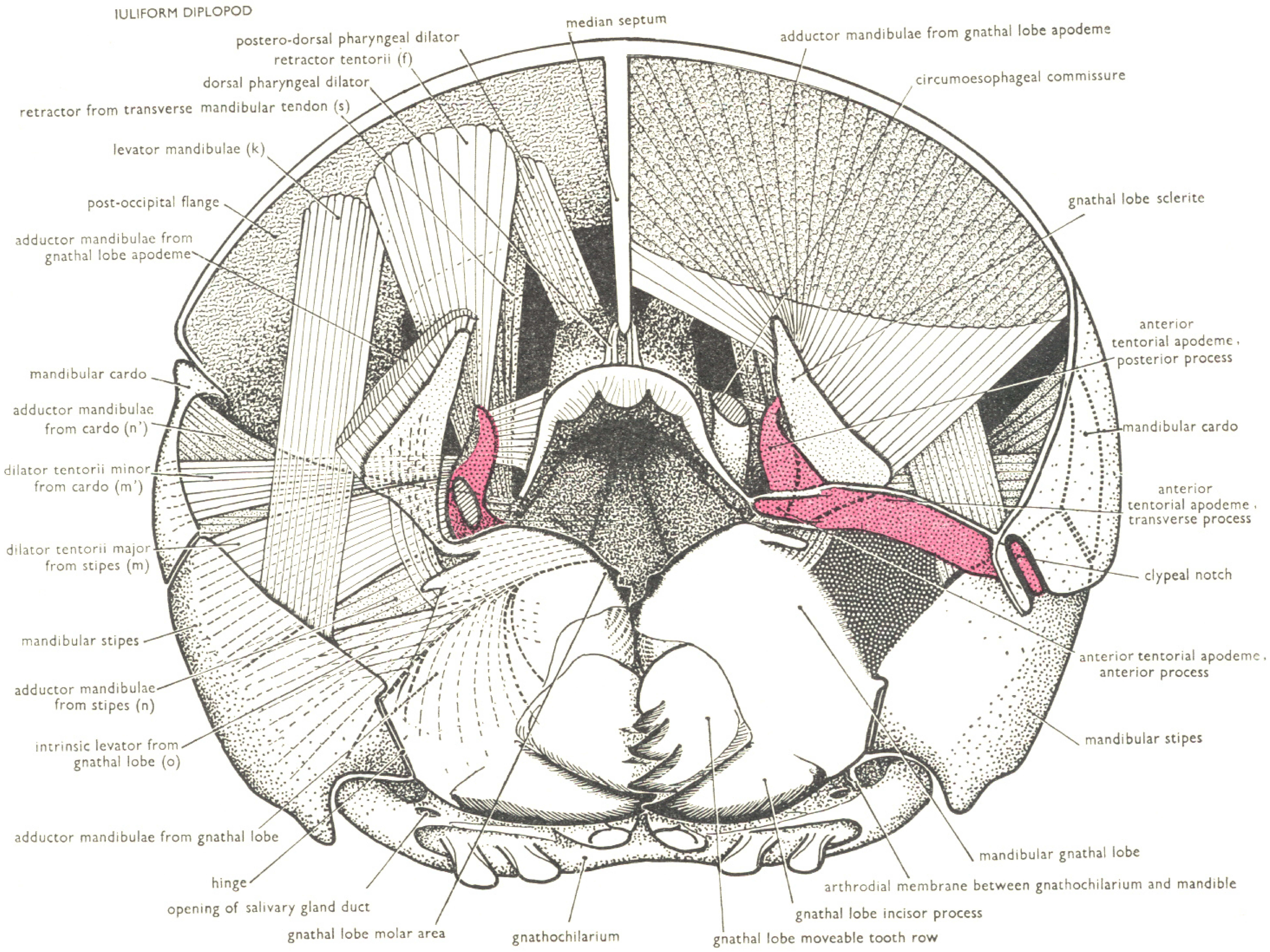


FIGURE 52. Anterior view of the head of the diplopod *Poratophilus punctatus* with the labrum cut away. The mandibular gnathal lobes are fully adducted. On the right: the preoral cavity is intact showing the transverse process of the anterior tentorial apodeme (red) lying in the arthrodial membrane (white stipple); the cranial roof has been cut away, leaving the clypeal notch; and the supraoesophageal ganglion has been removed. On the left: the transverse process of the anterior tentorial apodeme has been removed, its cut stump being hatched; the cranial wall is cut away entirely so as to expose the whole of the mandible; the gnathal lobe adductor muscle has been removed in order to show the deeper muscles and the post-occipital flange; and the circumoesophageal commissure is removed. See footnote p. 75.

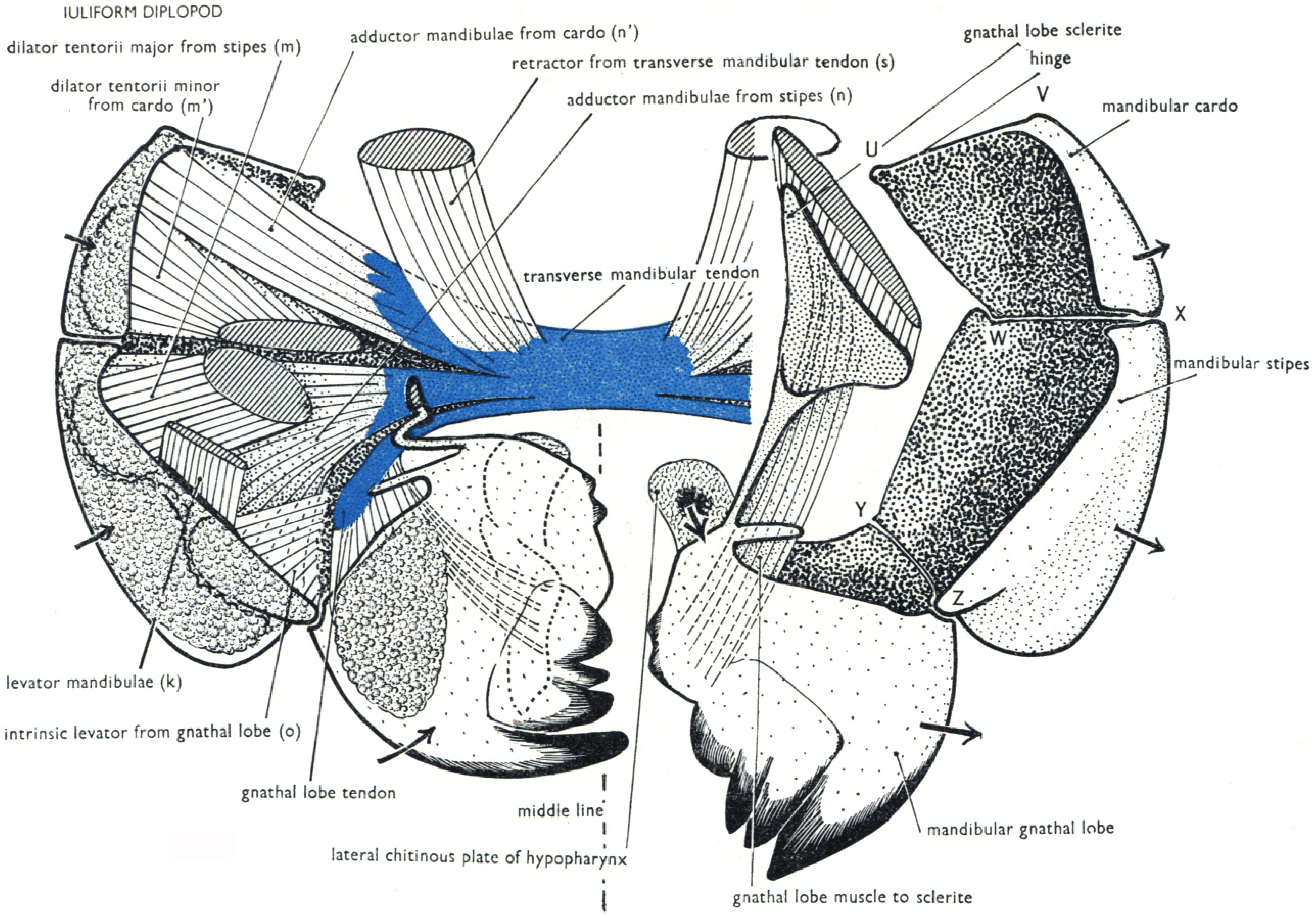


Figure 53. Anterior view of the isolated mandibles of the diplopod *Poratophilus punctatus*. On the left side the musculature is entire and the gnathal lobe and whole mandible is in a position of maximum adduction. On the right the muscles have been removed from the mandibular cuticle, with the exception of one intrinsic muscle, and the mandible and gnathal lobe are in a position of extreme abduction. The contrasting positions of the lateral hypopharyngeal scutes is also shown; the heavy arrow on the right indicates the direction of thrust of the anterior tentorial apodeme against the gnathal lobe.

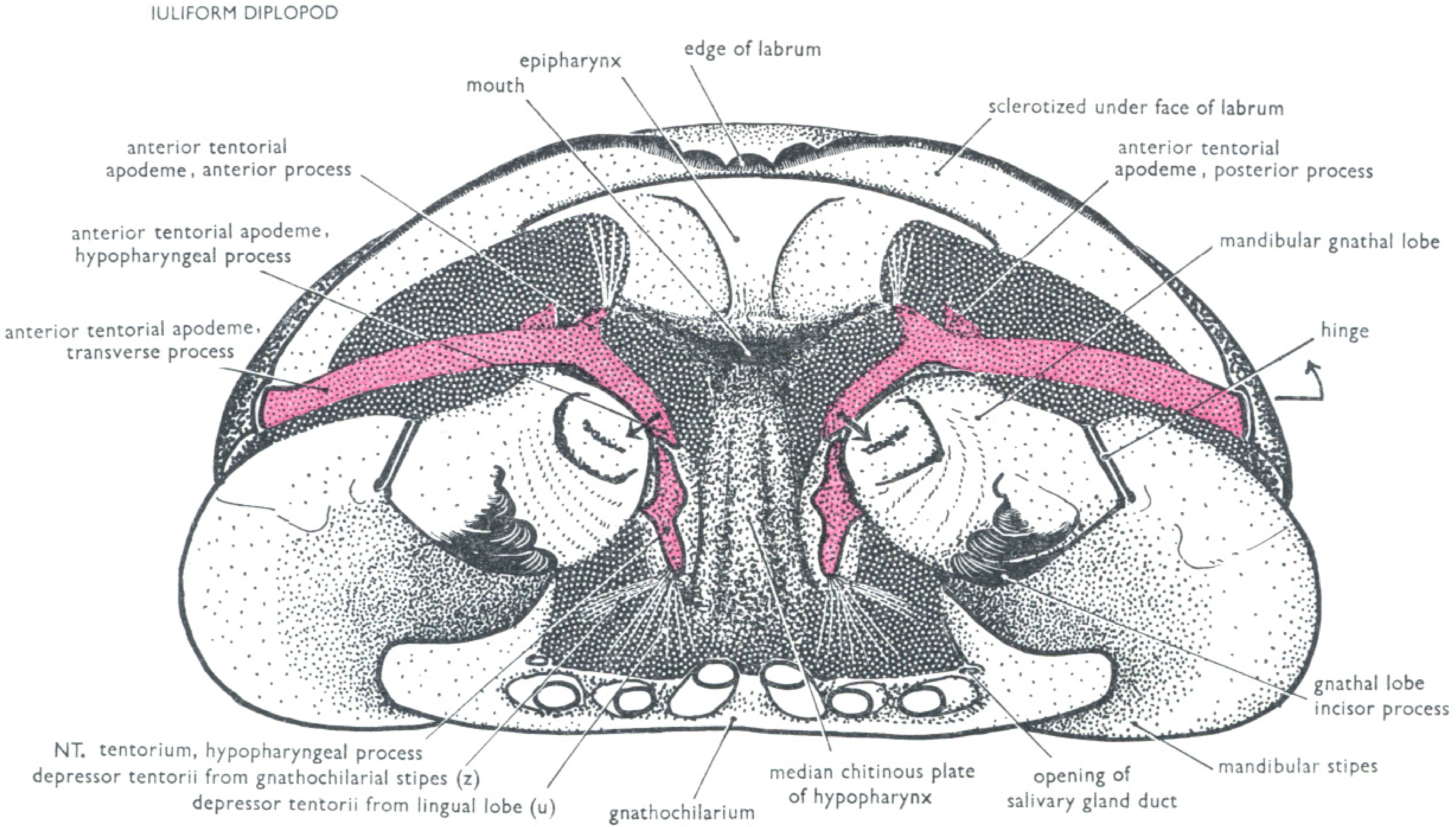


FIGURE 54. For legend see facing page.

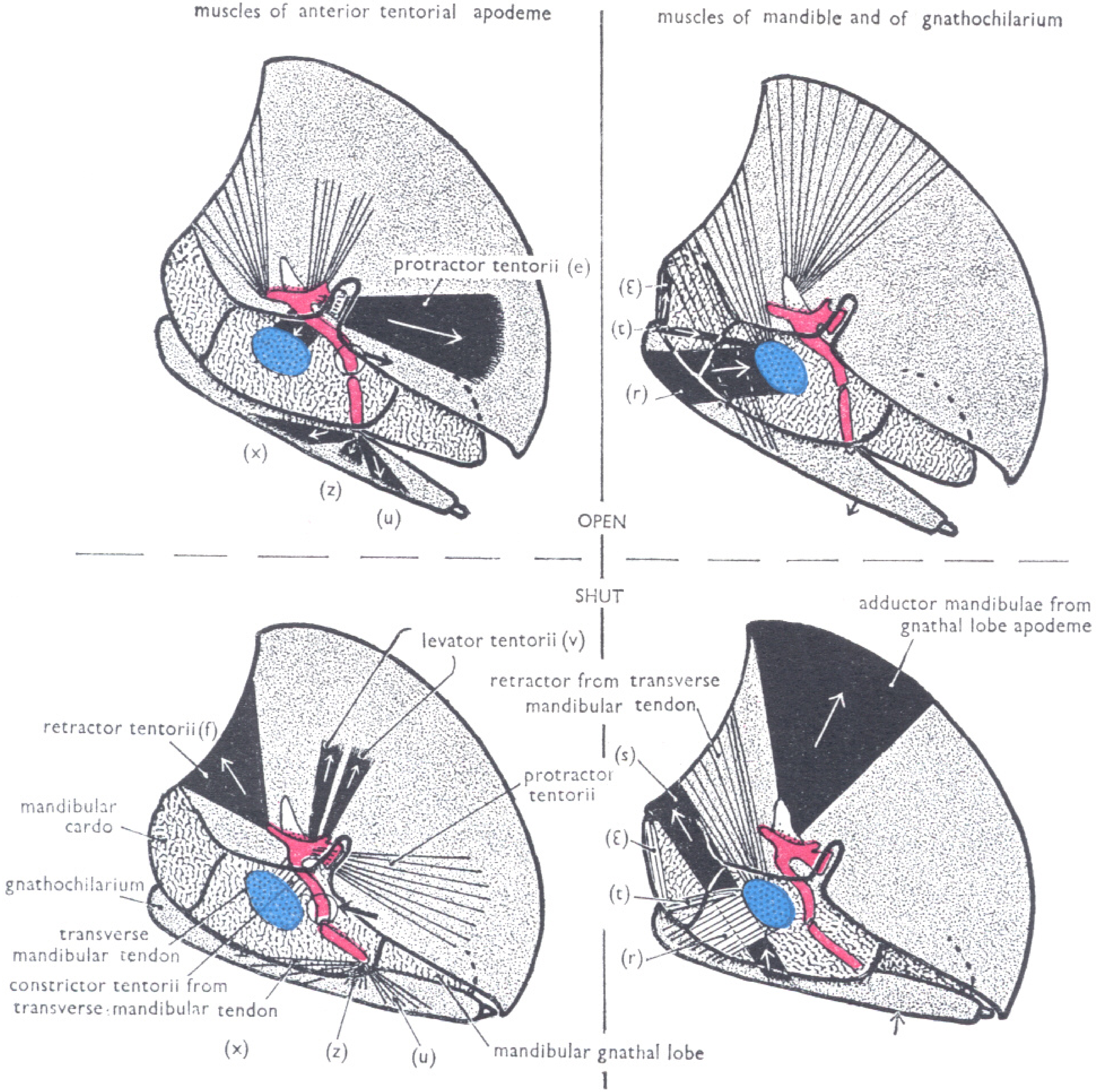


Figure 55. For legend see facing page.

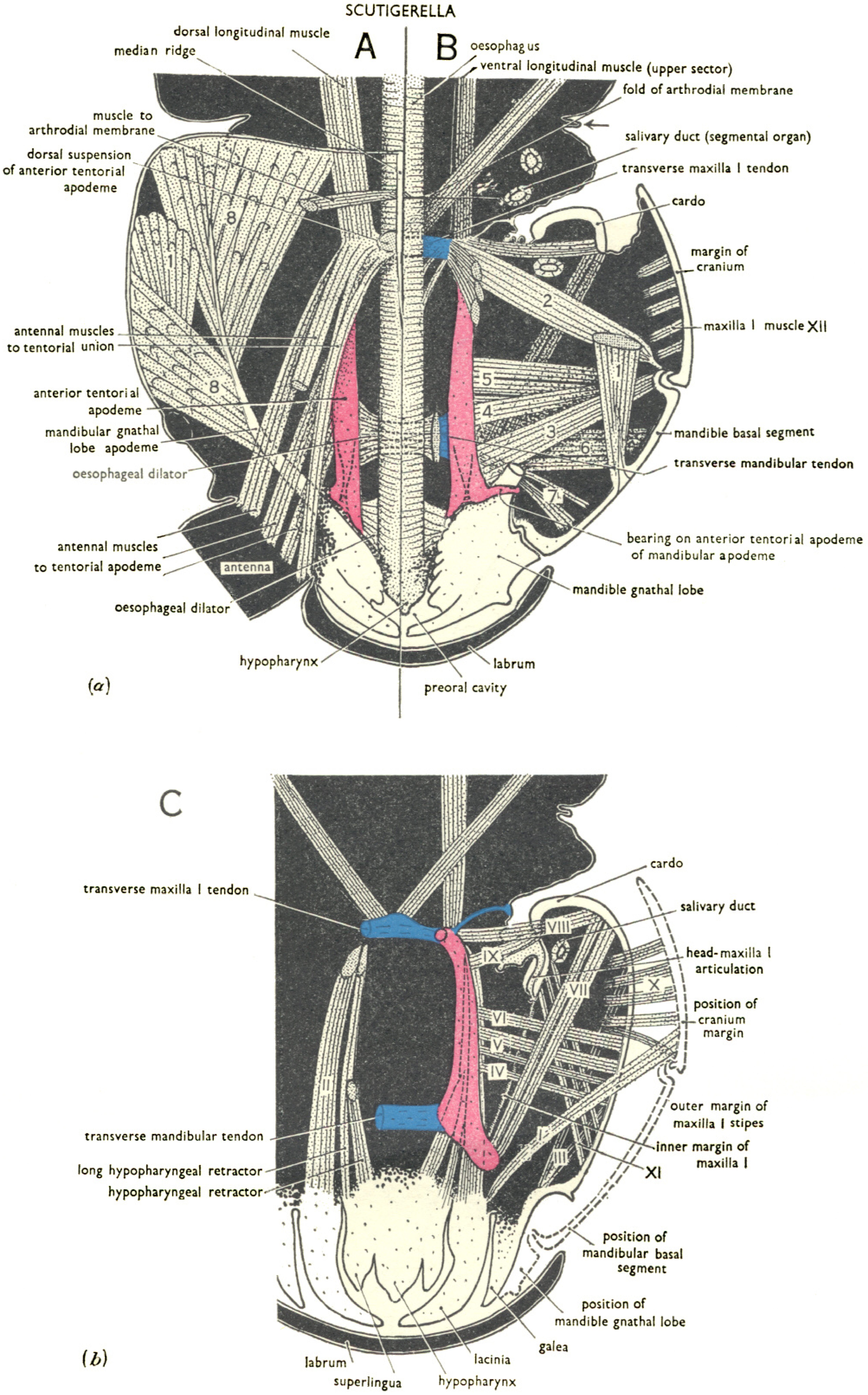


FIGURE 57. Dorsal reconstructions of the head of *Scutigerella immaculata* Newport to show the musculature, the mandibles, the maxillae and the endoskeleton. The transverse segmental tendons are blue and the tentorial apodeme is red.

Level A. Upper level showing the most superficial of the antennal muscles, the adductor muscle 8 to the gnathal lobe, the insertion of muscle 1 and the supra-oesophageal bridge with the tentorial suspension, see also figure 59K.

Level B. A lower level, the postero-dorsal overhanging part of the cranium is sliced off leaving the lateral lobe above the maxilla 1 (see figure 56). The junction of head and trunk is shown by the arrow. The antenna together with the gnathal lobe apodeme and muscle 8 is sliced away so

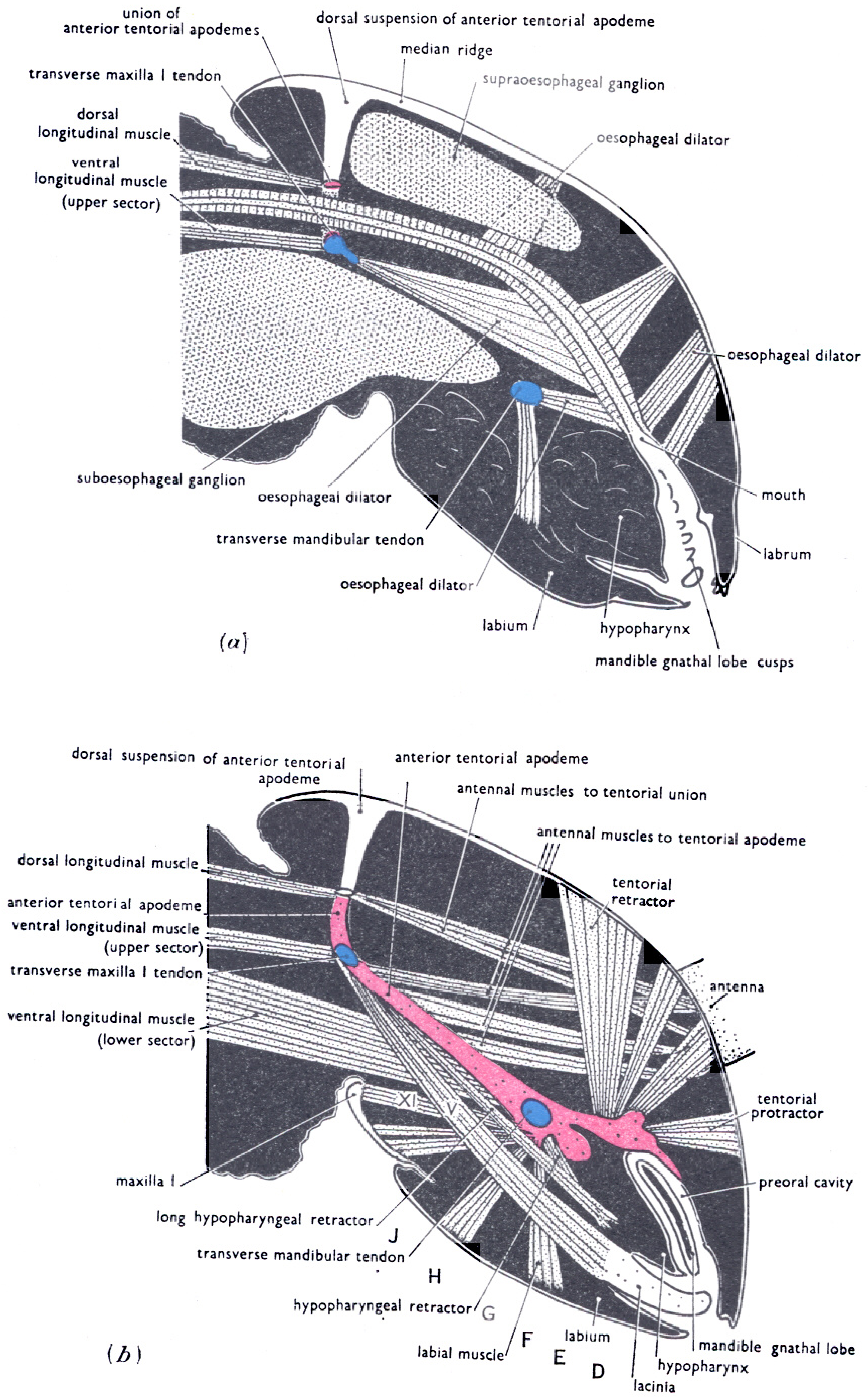


FIGURE 58. Sagittal half of the head of *Scutigerella immaculata*. Cuticle but not ectoderm is drawn. (*a*) Shows the most median structures and (*b*) shows parasagittal structures after removal of the alimentary canal and nerve ganglia. The whole of the anterior tentorial apodeme is exposed together with the muscles to which it gives attachments.

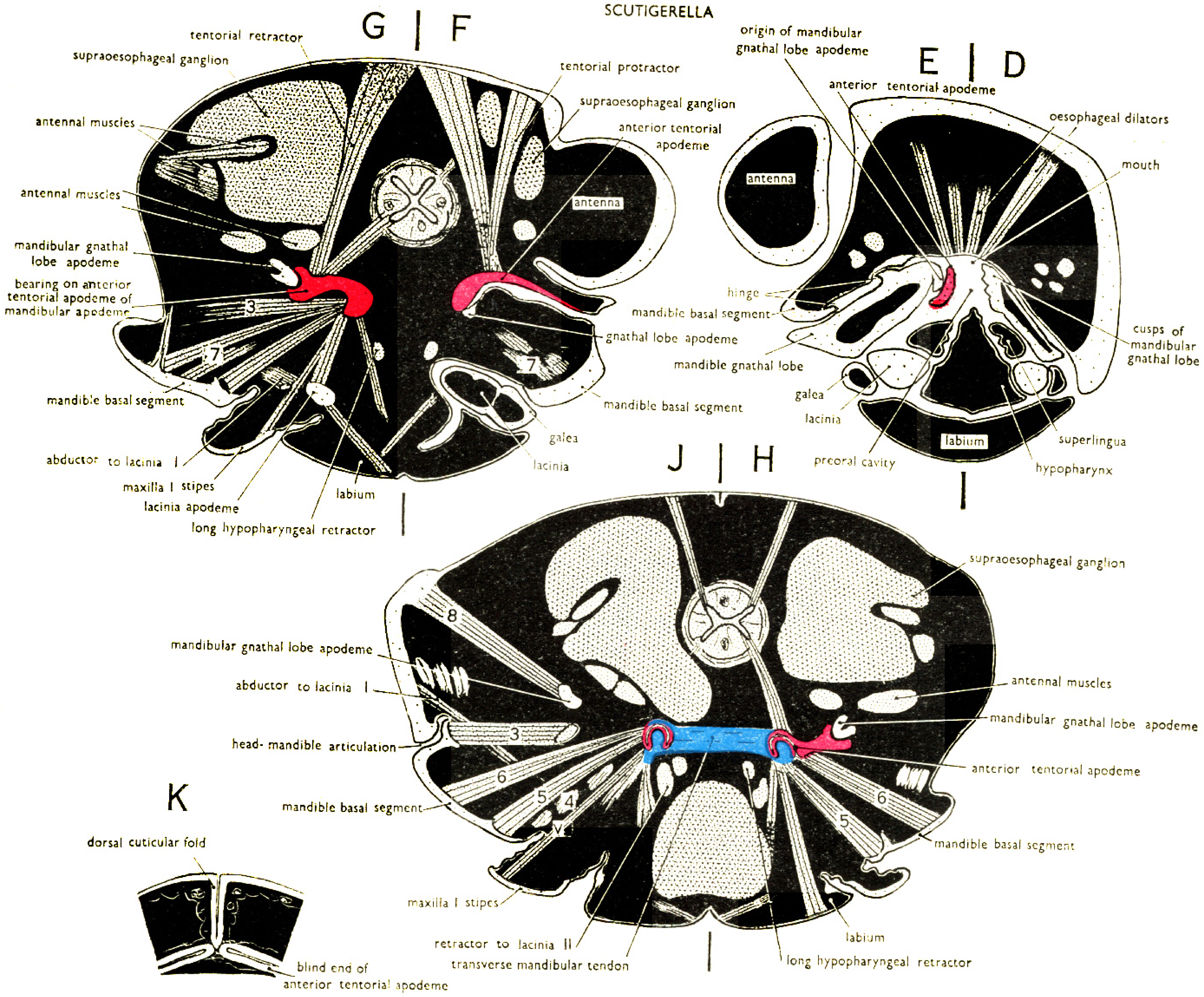


FIGURE 59. Diagrams of the head of *Scutigerella immaculata* cut transversely at the levels indicated by the letters D to K in figure 56, and viewed from in front. The diagrams include structures lying behind the plane of section. Cuticle but not ectoderm is drawn.

Level D. Through the distal part of the preoral cavity.

Level E. Through the hinge between the gnathal lobe and the basal mandibular segment, cutting the origin of the gnathal lobe apodeme and ensheathing flange from the anterior tentorial apodeme.

Level F. Through the transverse process of the anterior tentorial apodeme and origin of the galea and lacinia of maxilla 1.

Level G. Through the bearing of the anterior tentorial apodeme which grips the gnathal lobe apodeme.

Level H. The anterior tentorial apodeme, hollow and concave ventrally, is sunk into the transverse mandibular tendon. The concave face of the apodeme is largely filled by its own epithelium, not drawn.

Level J. Through the articulation between the basal segment of the mandible and the cranium.

Level K. Through the cuticular dorsal suspension of the anterior tentorial apodemes.

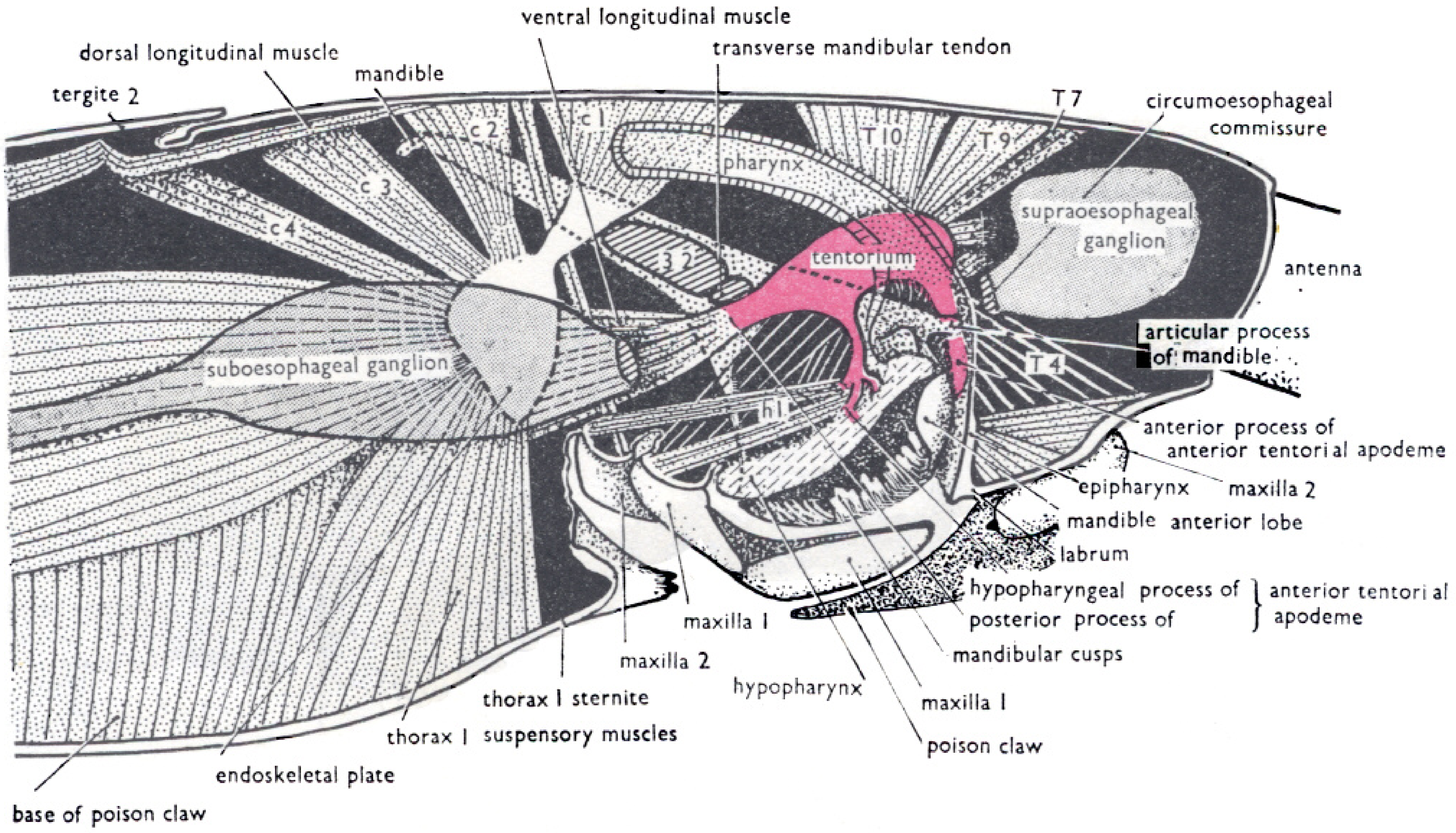
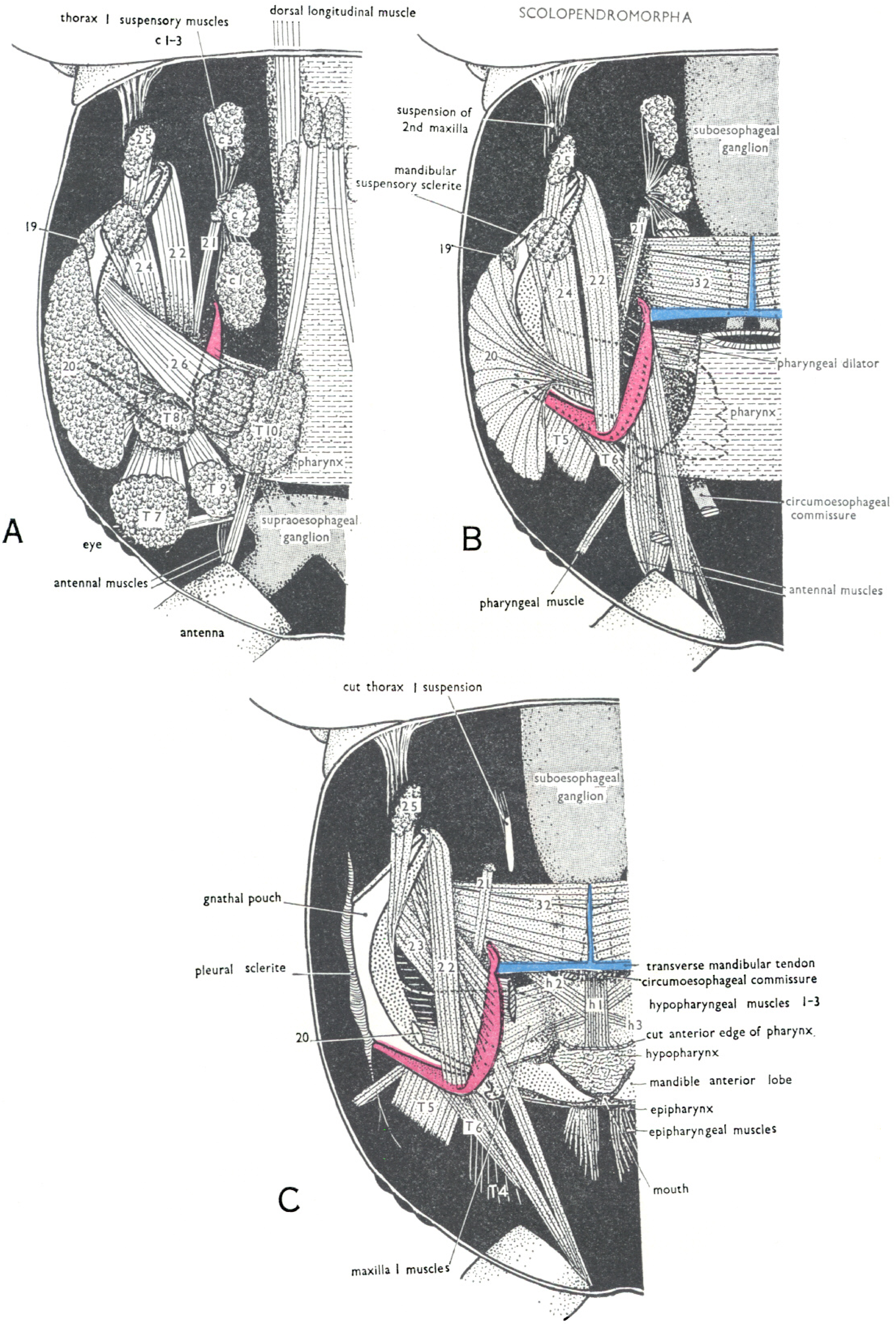


Figure 61. Sagittal half of the head of *Cormocephalus nitidosus* Por. The circumoesophageal commissure is cut away and the pharynx cut short; cuticle, but no glandular tissue or ectoderm is drawn. The preoral cavity passes into the pharynx at a level near the articulation of the mandible with the anterior process of the anterior tentorial apodeme (red). A vertical tendinous endoskeletal plate (white) bears dorsal (c. 1. to c. 4) and ventral suspensory muscles from the cranium and poison claw, and the ventral longitudinal muscles to the posterior process of the anterior tentorial apodeme; among other functions this complex raises the poison claws and retracts the tentorial apodeme (Manton 1964). The cut hypopharynx is marked by interrupted hatching, and the lateral lobe (probably homologous with a superlingua) is uncut and unlabelled, and projects into the angle of the preoral cavity near the articular process of the mandible; the whole forms a mobile tongue. The gnathal margin of the mandible is foreshortened, the soft anterior lobe of the mandible projects upwards to meet the edge of the hypopharynx, the cusp row forms the middle and the spine row the posterior parts of the free edge, which can be kept close against the hypopharynx, so retaining the food. The articular process of the mandible hooks round the anterior process of the anterior tentorial apodeme. The rest of the mandible is indicated by dotted lines and the transverse muscle 32 and transverse mandibular tendon are cut. The thick sclerotized epipharyngeal cuticle bears a muscle complex to the frons (protractor labri, d. 1 of Meinert). The muscles attached to the anterior tentorial apodeme which are here visible are: T. 4 from the anterior process to the frons; above it lies the long protractor to the pharynx (d. 12 and d. 13 of Meinert, figure 62B, unlabelled); above this lies the insertion of the antennal muscle on the tentorial apodeme, unlabelled; and dorsally muscles T. 7, T. 9 and T. 10 are labelled. Two muscles lying deep in the body are shown by white lines on black below the posterior process of the posterior tentorial apodeme, the longer and more posterior are muscles from maxilla 1 to the tentorial apodeme and the shorter and more anterior are part of muscle 27 to the mandible (figures 62C, 63D, E). The two sub-median paired hypopharyngeal muscles, h. 1, insert upon the sternites of maxilla 1 and maxilla 2 (retractor linguae duplex, d. 19 of Meinert who shows also two hypopharyngeal levators).



Figures 62, 63. Dorsal view of the head of *Cormocephalus nitidosus* showing structures at progressively deeper levels. Ectoderm and glandular tissue are omitted and no detail is shown of maxilla 1 and maxilla 2 muscles or of the musculature from the trunk. The diagrams show the mandible, its associated muscles, the gnathal pouch, tentorial apodemes and organs surrounding the preoral cavity. The apodemes are marked in red and the transverse mandibular tendon in blue.

The numerals mark mandibular muscles and correspond with the numbering of Meinert but prefixed by him with 'c', Meinert's descriptive terms for each muscle are not repeated here. Muscles c. 1 to c. 3 of Meinert, and so marked here, pass to the vertical tendinous plate of the first trunk segment. Muscles T. 2 to T. 10 of Meinert, and so marked here, arise from the anterior

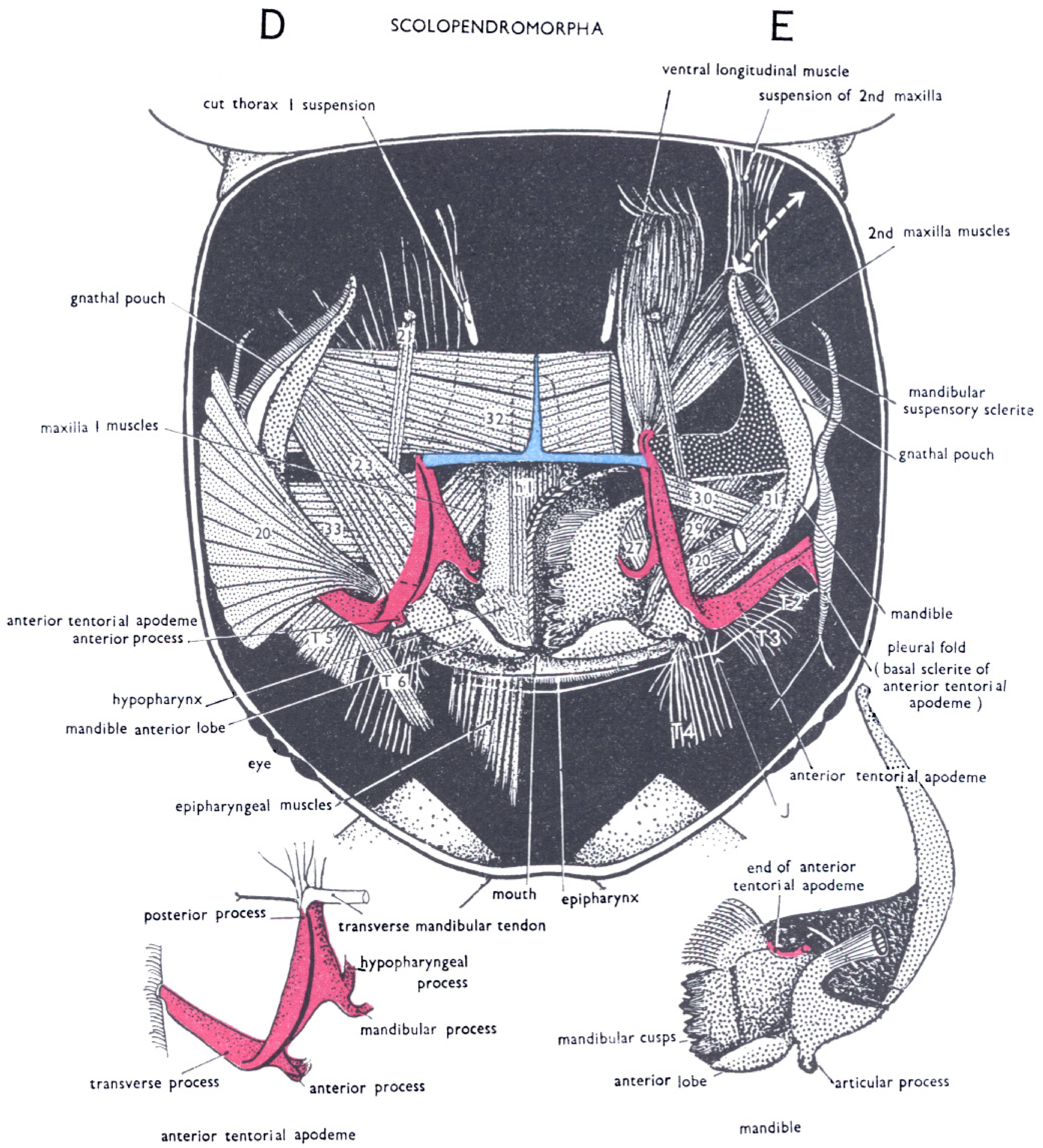


Figure 63 (continuation of figure 62). Deeper levels seen in dorsal view. The hypopharynx (exposed surface mottled) is entire in D and cut away in E so as to show the underlying gnathal edge of the mandible and the more distal mandibular muscles. Hypopharyngeal muscles h. 2 and h. 3 are cut away, the superimposed paired muscles h. 1 (see figure 61) are in place in D and cut back in E, the dotted line below muscle 32 showing the extent of muscles h. 1 which insert on the sternites of maxillae 1 and 2.

Level D. Mandibular muscle 22 is removed but muscle 20 is in part left in position.

Level E. Mandibular muscles 20, 23, 33 are removed and muscle 32 is cut short so exposing muscles 27 and 30, the origin of muscle 21 (muscle labelled on level D) and intrinsic muscles 29 and 31.