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Liverpool Marine Biology Committee

L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

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

XII.

GAMMARUS

BY

MARGARET CUSSANS, B.Sc.,
Zoological Department, University of Liverpool.

(With 4 Plates)

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JULY, 1904

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XII.

GAMMARUS.

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EDITOR'S PREFACE.

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

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have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated.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

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

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

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

Memoirs from I. to XII. have now been published. It is hoped that Cycloporus, Myxine, Antedon, and the Oyster will follow soon.

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Oyster, W. A. Herdman and J. T. Jenkins.
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Botrylloides, W. A. Herdman.
Cuttle-Fish (Eledone), W. E. Hoyle.
Actinia, J. A. Clubb.
Hydroid, E. T. Browne.
Calcareous Sponge, R. Hanitsch.

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

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

W. A. Herdman.

University of Liverpool,

June, 1904.

L.M.B.C. MEMOIRS.

No. XII. GAMMARUS.

BY

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Zoological Department, University of Liverpool.

Introduction.

The Amphipoda and Isopoda form the two sub-orders of the Edriophthalma, or Sessile-eyed Crustacea, which are characterised by the possession of seven, or rarely fewer, free thoracic segments, each bearing a pair of legs.

The Amphipoda are distinguished from the Isopoda, which are depressed dorso-ventrally and bear lamelliform appendages functioning as gills on the frequently reduced abdomen, by their laterally compressed body with an elongated abdomen, and gills borne on the thoracic legs. Usually quite small, being only in rare cases as much as three inches long, the Amphipoda abound in both salt and fresh water, through which they move by springing and swimming. They form an important factor in the food-supply of the sea.

They may be divided into three groups:—

(1) The Læmodipoda, including *Cyamus ceti*, which is parasitic on the skin of whales, and the thin, curiously elongated Caprellidæ, mostly found living among Polyzoa and Hydroids.

(2) The Hyperina, with large head and eyes, which swim rapidly, and are frequently found as commensals in jellyfish.

(3) The Gammarina, with comparatively small head and eyes, including the Corophiidæ which move chiefly by walking, the Orchestiidæ of which many species live on the land and move by springing, and the Gammaridæ which move more by swimming than jumping.

The Amphipod chiefly described below is *Gammarus pulex*, first so named by Fabricius (6) in 1775, but previously referred to by Geoffroy (7) in 1762, as "La crevette des ruisseaux," and probably the "*Cancer pulex* occurring both in fresh and salt water," mentioned by Linnæus (12) in 1767. It was described by Zenker (28) in 1832, but his conclusions are not in agreement with modern investigations. Sars (20) figured and described it in 1895. He regards it as synonymous with *Gammarus fluviatilis*, Milne-Edwards, *G. lacustris* Sars, *G. neglectus* Sars, and *G. locusta*, var. B., Holk. For the convenience of those working at the seaside, a comparison is made, where necessary, with the corresponding parts of the commonest marine species- *G. locusta*.

Gammarus pulex, as was observed by Turton (23) as early as 1802, is very common in running water in temperate climates. Zenker (28) remarks that it is "universally distributed in the rivers and streams of Europe." It is also found in lakes and ponds.

The creatures bury themselves beneath loose leaves, bits of wood, &c., and, if disturbed, dart rapidly back into shelter, evincing a strong disinclination to remain in the light. When at rest, they lie curled up on one side. The last three thoracic legs, or peræopods, are bent back and up, so that their tips project above the back. These attach the creature to the under side of a dead leaf, or other rough surface, the dactylopodite being reduced to a slightly curved spine. The pleopods move backwards and forwards briskly, keeping up a stream of water which washes the ventral surface of the body and the branchiæ which it bears. The first four thoracic feet and mouth parts maintain a regular movement forwards, scooping up water and food to the mouth. The uropods and telson, and more rarely the antennæ, are now and then drawn through the thoracic feet, doubtless to free their hairs of any particles adhering to them. Usually, the creatures move along on their side, close to some surface; by pushing against this, the long clawed peræopods thrust the body forwards. The first four thoracic feet seem to be of little use in progression, but the pleopods move briskly backwards and forwards. If the animal is crossing an open space, it swims rapidly by alternately flexing and extending the abdomen, the last three segments of which move together, so that it darts forward somewhat spasmodically. When creeping slowly, it feels its way with the long antennæ, the first pair being held out horizontally in front, whilst the second pair are bent downwards to touch the floor of the passage. The antennæ seem to be more used in the avoidance of obstacles than the eyes are.

In *G. pulex* the colour is a dull greenish yellow or brown, of variable shade. Brilliant spots of vermilion on the abdomen and basal joints of the legs mark the position of unicellular glands. The sexes are separate, the male being distinguished from the female by its greater size and stronger gnathopods, as well as by the absence of oostegites on the first four thoracic legs. The adult male is usually from 18 to 20mm. in length, the female from 10 to 12mm.

In *G. locusta* the colour is somewhat variable, being in the female a dark brownish green with a conspicuous pinkish patch at each side at the origin of the pleopoda, as in *G. pulex*. The male is usually a lighter yellowish brown. The length of the adult male is about 20mm., of the female 18mm.

Spence Bate (1) remarks that the Amphipoda in general do not throw off an injured limb, the wound becoming cicatrized with a black scar. *Gammarus pulex* appear able to withstand very low temperatures, though they die instantly in warm water. Turton (23) and Zenker (28) state that they are phosphorescent, but this has not been confirmed by the writer in some casual experiments.

External Characters.

The body is elongated and compressed laterally, with the back evenly rounded. It is covered by a calcified cuticle, which is thin enough to be partially transparent, even in a full-grown specimen, and bears numerous spines and setæ. Externally, it consists of (1) the cephalothorax, (2) the seven free segments of the thorax forming the mesosome, (3) the first three segments of the abdomen forming the metasome or pleon, and (4) the last three segments of the abdomen forming the urosome or urus, of which the last segment bears the telson. Thus there are thirteen free segments in addition to the cephalothorax and telson. Morphologically the body is composed of nineteen segments and the telson; of these five form the head, eight are included in the thorax, and six in the abdomen, of which the last bears the telson.

The head is united with the first segment of the thorax to form the cephalothorax, and is covered by a cephalothoracic shield, produced downwards at the sides into somewhat angular plates (Pl. II.), which are separated from the rest of the shield by an imperfect hinge, and enclose below a very deep sinus. Like the rest of the animal, the cephalothorax is flattened laterally. It bears the eyes, the first and second antennæ, the mandibles, the first and second maxillæ, and the maxillipeds, which belong to the fused first segment of the thorax. The mouth (Pl. II., *m.*) opens from out of the sinus between the lateral plates of the cephalothoracic shield. In front it is protected by a small labrum, divided into an upper and lower part by an imperfect hinge, and fringed with numerous setæ. It is guarded at the sides by the scoop-like projections of the mandibles (Pl. I., fig. 4), and behind by the maxillipeds, the basal joints of which are fused, so that they form a lower lip (Pl. I., fig. 7). The excretory organ opens on the elongated tip of the antennary cone (Pl. II., *ant. c.*), on the basal joint of the second antenna. The eyes (Pl. I., fig. 15) are compound, sessile and reniform, the posterior margin being convex. The corneal cuticula, as Leydig (11) noted, is smooth and without facets.

The thorax consists of eight segments, of which the first, bearing the maxillipeds, is fused with the cephalon; the remainder are free. The seven free segments (Pl. II.) bear each a pair of legs, which normally carry branchiæ on the inner side of their basal joints, though in some cases these are absent from the first pair. The first four bear legs directed forwards and carrying enlarged coxal plates (Pl. II., *c.p.*) which gradually increase in size from the first to the fourth segment, the last being notched in the upper part of its posterior edge to give play to the fifth leg. These coxal plates are of moderate size compared with those of some other species of *Gammarus*. They are somewhat larger in *G. locusta* than in *G. pulex*. They function as accessory respiratory organs, being covered on the inner surface with very thin cuticle. They bear a few scattered spines on their edges, which overlap, the anterior edge of one plate lying over the posterior edge of the one in front. On the inner side of the base of each of these legs is borne a soft, thin, flexible branchia, oval in form and covered by extremely thin cuticle; it is marked by distinct transverse bands of tissue (Pl. IV., fig. 1 *br.*, and fig. 3). In the female a pair of thin lamellæ, edged with long hairs, are also borne on each segment, internal to the branchiæ. These fold over in the middle line to form the brood pouch containing the developing ova. They are the oostegites, and are absent in the young animal. The first four thoracic segments increase in size from before backwards. The terga are produced at their lower edges into short, crescentic epimeral plates (Pl. II., *epim. p.*). They only slightly overlap one another, the posterior edge of each tergum lying above the anterior edge of the succeeding one, except in the case of the first segment, in which the anterior edge of the tergum overlaps the cephalic shield, so as to allow the head to be bent down with ease. The last three segments of the thorax bear long peræopods, directed backwards, with enlarged basal joints; these are more slender and elongated in *G. pulex* than in *G. locusta* (Pl. II., *per. 3, 4, 5*). These segments gradually decrease in size from before backwards, and their terga, which are produced into short, broad epimeral plates, overlap to a large extent, so as to allow considerable flexion of the body. As in the other free thoracic segments, their appendages bear branchiæ. In the female, the oviducts open at the base of the fifth pair of legs; in the male, the vasa deferentia open at the base of the seventh pair of legs on the summits of a pair of small tubercles.

The abdomen consists of six segments and the telson

(Pl. II., *tel.*). These segments decrease rapidly in size from before backwards, and their terga overlap to a great extent, allowing the abdomen to be bent right forward under the thorax. The terga of the first three abdominal segments or metasome are produced into large epimeral plates (Pl. I., fig. 13 and Pl. II., *epim. p.2*), which increase in size from before backwards and are pointed at the infero-posteal corners, though the last pair are less drawn out in *G. pulex* than in other species of *Gammarus* (Pl. I., fig. 13, *epim. p. 2*). In *G. locusta*, the last pair of epimeral plates of the metasome are considerably produced at the lateral corners, and bear setæ along the posterior edge. Each segment of the metasome bears a pair of pleopods or swimming feet, consisting of a single, stout, elongated protopodite, bearing two similar, many-jointed rami (endopodite and exopodite) furnished with long, plumose setæ (Pl. I., fig. 12). The last three body segments or urosome usually move as one, slipping between the last pair of epimeral plates when flexed, and forming a powerful propelling organ. They bear the uropods (Pl. II., *uro. 1, 2, 3*), the last pair being the largest (Pl. II., *uro. 3*), and have no epimeral plates. In *G. pulex*, the posterior edge of each tergum bears two small dorsal spines and a single lateral one; in *G. locusta*, each bears a small dorsal projection armed with from three to five spines, and having from three to four spinules on each side. The telson (Pl. I., fig. 11, and Pl. II., *tel.*) is very small and consists of a basal joint with two rami, each bearing two apical spines and one lateral one in *G. pulex*; in *G. locusta* each ramus bears three apical spines, and two groups of lateral ones, the proximal group consisting of three, the more distal group of two spines. The anus opens below the telson and above the last pair of uropods, not below the latter, as Sars (19) figures for *G. neglectus*.

The external apertures are:—The openings of the paired excretory organs at the base of the second antennæ, the mouth, the openings of the oviducts at the base of the fifth or of the vasa deferentia at the base of the seventh pair of legs, and the anus.

There are nineteen pairs of appendages:—The first and second antennæ, the mandibles, the first and second maxillæ, the fused maxillipeds, the two pairs of gnathopods (which with the first two pairs of peræopods are directed forwards), five pairs of peræopods, three pairs of pleopods or swimmerets, and three pairs of uropods.

The first or superior antennæ (Pl. I., fig. 1, and Pl. II., *ant. 1*) are nearly half as long as the body. Each consists of a three-jointed peduncle or protopodite, bearing a long flexible many-jointed flagellum or endopodite, and a shorter similar secondary flagellum or exopodite (Pl. I., fig. 1, *fl. sec.*). In *G. pulex* the latter is very small, consisting only of four joints; in *G. locusta* it is considerably longer, consisting of eight or nine joints. In *G. pulex* the first joint of the peduncle is shorter than the other two combined, and the long flagellum is twice the length of the peduncle; in *G. locusta*, the first joint of the peduncle is as long as the other two combined, and, as in *G. pulex*, the long flagellum is twice the length of the peduncle, or rather longer. Each joint of each flagellum bears small, finely plumose setæ, probably auditory in function (Sars 20). It was noted that specimens of *G. pulex* placed in a cell and examined under the microscope twitched the first antennæ violently when the college clock struck the hour,* though the rest of the body did not move.

The second or inferior antennæ (Pl. I., fig. 2) are shorter than the superior, and consist of a three-jointed

* The note to which the first antennæ were found to react was B_1 (240 vibrations per second); higher notes chimed by the same clock had not the same effect.

peduncle or protopodite bearing a stout many-jointed flagellum, which may correspond to the endopodite, and which is about the length of the last two joints of the peduncle combined. This flagellum bears a number of setæ, some being plumose, as well as two spines, on each segment. In addition, on the upper margin of the distal end of each segment is a calceolus (Pl. I., fig. 3, *calc.*). This is a cup-shaped, stalked projection, with a beaded rim, within the body of which may be distinguished a darker, curved mass, which Blanc (2) considers may be a sensory nerve mass. Since, contrary to the belief of earlier observers, calceoli are present on the antennæ of females as well as males in *G. pulex* (though apparently absent in female *G. locusta*), Blanc (2) thinks they are probably organs of hearing rather than of smelling or clasping. Observations of the behaviour of the antennæ during the chiming of a bell do not confirm this. The first joint of the second antenna is enlarged and fits into a notch in the cephalic ring. On its ventral surface it bears the antennary cone (Pl. I., fig. 2, *ant. c.*; Pl. II., *ant. c.*), on the pointed apex of which opens the duct of the excretory organ, which occupies the basal joint of the antenna.

The mandibles (Pl. I., fig. 4) each consist of a strong undivided protopodite bearing two jaws armed with double rows of saw-like teeth (Pl. I., fig. 4, *mn. t.*) and furnished in front and at the sides with scooplike projections, which occupy the deep sinus between the lateral corners of the cephalic shield (Pl. II.) and apparently aid in holding up the food between the saw-like jaws. Each mandible is provided with a three-jointed mandibular palp, which is probably the endopodite, and is armed with slanting rows of setæ, projecting in three planes at right angles to one another (Pl. I., fig. 4, *mn. p.*).

The first maxillæ (Pl. I., fig. 5) are tri-partite. The protopodite is divided into two segments which extend inwards as thin lamellæ; the lower is a flattish plate, edged with a row of long curved setæ, the upper is unjointed, like the former, and bears on its distal end, and also on the sides, a row of stout setæ with a serrated lower margin. The protopodite bears on its outer side a two-jointed endopodite, the second joint of which is armed near the end with transverse rows of short conical spines, like the teeth of a saw. Along its outer edge it bears two spines in *G. pulex*, three in *G. locusta*.

The second maxillæ (Pl. I., fig. 6) consist of two flat elongated plates, the inner, which may be the protopodite, being a little smaller than the outer, which may be the endopodite. Both are fringed, except on their outer margin, by rows of long, curved, slender spines.

The maxillipeds (Pl. I., fig. 7) are fused by their protopodites so as to form a lower lip, but the two seven-jointed endopodites are free. The second and third joints of the latter are produced on their inner margins into large plates which bear spines similar to those of the second maxillæ. The last four joints can be easily moved on one another, so that the last joint, which bears a strong claw, may be bent right in and down in the middle line. They are armed with strong spines and bundles of setæ.

The gnathopods (Pl. I., figs. 8 and 9) are composed of a two-jointed protopodite (coxopodite and basipodite) bearing a five-jointed endopodite (ischiopodite, meropodite, carpopodite, propodite and dactylopodite), like the rest of the thoracic legs. The propodites are large and broad, that of the second gnathopod being rather more quadrangular than that of the first in *G. pulex*. In *G. locusta* the propodite of the second gnathopod is much larger than that of the first, and in the female both are smaller than in the male. They are armed with short, stout spines on the lower or posterior edge, on which the strongly-clawed dactylopodite shuts down like the blade of a knife, so that they are sub-chelate. Both gnathopods are thickly beset with setæ, especially on the lower edge, and both bear an enlarged coxal plate (Pl. I., fig. 9, *c.p.*) and internally a branchia (Pl. I., fig. 9, *br.*) on the coxopodite. In some specimens examined, the branchia was absent from the first gnathopod.

The first and second peræopods (Pl., fig. 10) are very similar. The coxopodite bears externally a coxal plate, and internally a branchia (Pl. I., fig. 10, *c.p.* and *br.*) as in the gnathopods. The basipodite is long, and the meropodite is provided with two very strong spines, the dactylopodite being reduced to a strong, movable claw. The whole appendage bears a row of long setæ on its lower or posterior margin as well as fascicles at the joints.

The last three peræopods (Pl. II., *per. 1, 2, 3*) are similar to one another. The coxopodite which bears a branchia on its inner side is short and broad, the basipodite being elongated, broad and flat, and the ischiopodite small. The dactylopodite is reduced to a strong, movable claw, and the other three joints are all long and slender, bearing fascicles of setæ, and are usually carried bent upwards from the ischiopodite, so that their tips extend above the dorsal line of the animal. The last one is the longest. They are more slender and elongated in *G. pulex* than in *G. locusta*. In *G. locusta* the basal joint of the antepenultimate pair is produced at the infero-posteal corner to an acute point. The creature aids itself in creeping along by thrusting these long, clawed peræopods, turned up over its sides, against any rough surface.

The pleopods (Pl. I., fig. 12, Pl. II. *pl. 1, 2, 3*) consist of a large basal joint or protopodite bearing two similar many-jointed rami (exopodite and endopodite). Each joint of these bears long, plumose setæ, and the protopodite bears a single long spine. These are the swimming legs, and they keep up a constant current of water over the branchiæ, for they move rhythmically backwards and forwards even while the animal is resting.

The uropods (Pl. II., *uro. 1, 2, 3*) are composed of a basal joint or protopodite, bearing two stout rami (endopodite and exopodite) which are armed with two strong spines on the upper margin, and two at the tip. The protopodite of the first uropod is longer than that of the second, so that the extreme tip of the former extends about as far backwards as that of the latter (Pl. II.). In both first and second uropods the upper margin of the protopodite bears two strong spines. The last uropod (Pl. I., fig. 14) has a short, thick protopodite, bearing two rami, of which the endopodite is shorter than the exopodite. Both rami bear long plumose setæ in addition to the spines, and are apparently divided into many joints; this is not really the case, though they bear numerous circular ridges. The inner ramus bears only one spine, near its base. In *G. locusta* the last uropod is not so large as in *G. pulex,* and does not bear plumose setæ.

The Body-Wall and Body-Cavity.

The body-wall consist of (1) the calcified chitinous cuticle or exoskeleton, (2) the hypodermis, (3) connective tissue, which is mostly adipose. The chitinous cuticle is continuous with the chitinous lining of fore and hind-gut, and is cast at intervals, carrying with it these extensions as well as the numerous spines and variously-formed setæ which it bears. It forms a complete covering for the body, and penetrates deeply between the joints of the segments and legs. It is formed by the cellular hypodermis, which underlies it, and is a typical cylindrical epithelium, with large, deeply-staining nuclei. Masses of adipose tissue, formed of large, rounded, non-staining cells, without intercellular substance, ensheathe the alimentary canal and gonads, filling up the space between the former and the heart. This adipose connective tissue is also found attached to the ventral nerve cord, and separating the bands of muscle. It connects the various organs with one another and the body-wall, and is believed by Wrzéniowski (27) to form the serous covering of the heart. A thin plate attached to the base of the heart and the sides of the body forms the pericardium (Pl. IV., fig. 1, *p.*), and divides the body cavity into an upper half, the pericardial cavity, and a lower one, the sternal sinus (*p.c.* and *st. s.*).

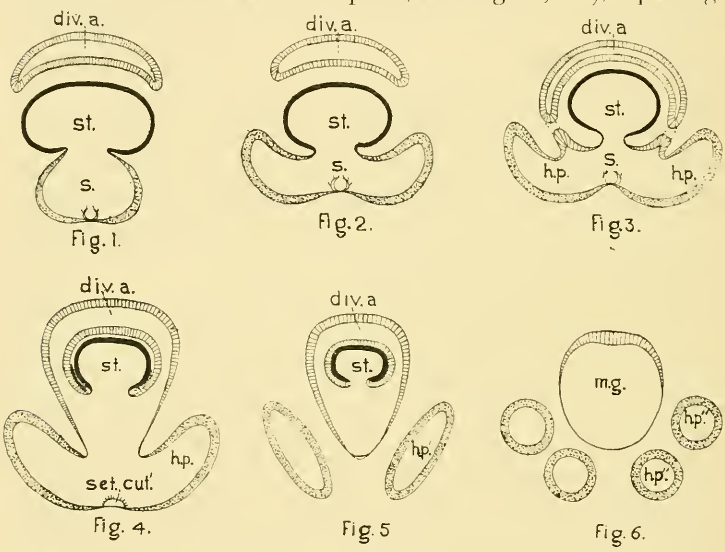
The body-cavity is a system of blood lacunæ, as in *Astacus*, the alimentary canal and its diverticula, as well as the nervous system, being washed by the colourless blood filling the sternal sinus, which has no definite walls. The end-sacs of the nephridia at the base of the second pair of antennæ (Pl. II., *e.s.*) are, probably, the only remnants of the true cœlom, as in *Palæmon serratus*, according to Weldon (26).

The Digestive System.

The slit-like mouth (Pl. II., *m.*), which opens out of the deep sinus between the two lateral extensions of the cephalothorax, leads into a short, wide œsophagus connected by bands of muscle surrounding it and united with the exoskeleton. The opening of the œsophagus into the ventral wall of the stomach is guarded by two pairs of chitinous plates armed with teeth, which are directed upwards and backwards so as to prevent the return of food which has entered the stomach.

The stomach (Pl. II., *st.*) is widest at its anterior end, which extends forward a little distance in front of the opening of the œsophagus, and gradually narrows behind. The anterior wall is furnished with two strong vertical plates, which project backwards into the lumen of the stomach, and are armed with strong spines. Thick bands of striated muscle inserted into these plates, as well as bands inserted into those guarding the opening of the œsophagus, pass down in front of the anterior wall of the stomach, their lower ends being inserted into the labrum; they enable the creature to depress or raise the chitinous plates at will. The stomach, like the œsophagus, is thin-walled and lined with thick cuticle, toothed ridges of which divide it more or less completely into three chambers, the middle one only containing the food. A pair of thin horizontal plates of cuticle, armed with long setæ, shut off a shallow upper portion, in which no food is seen; these plates extend from the anterior end of the stomach to the narrow posterior opening, which their long, backwardly-directed setæ help to close. This upper chamber probably serves as a channel to facilitate the distribution of digestive juices through the stomach, its lower wall being formed, in the middle line, only by the long, interlocking setæ of the two plates. Behind the opening of the œsophagus runs a deep, longitudinal, ventral groove, divided into two for the first part of its length by a median ridge, and shut off in front by two pairs of narrow vertical, leaf-like plates of chitin, attached to its sides, and having their free edges fringed with long setæ. This groove is cut off from the middle of the stomach by overlapping horizontal plates, which, like the sides and floor of the chamber, are thickly covered with deeply-staining unicellular glands, each furnished with a fine chitinous duct, through which the contents are, probably, ejected. These side plates are continued back to the point of origin of the hepato-pancreatic tubes, and the groove which they cut off may serve to carry forward the secretion of the latter into the anterior part of the stomach. They are shown in the diagrams of a section through the point of origin of the hepato-pancreatic tubes (Pl. IV., fig. 2, *set. cut.*). The ventral groove with its protecting plates appears to be the "gizzard-like" structure described by Spence Bate (1). The posterior end of the stomach is joined to the dorsal integument by strong, obliquely-placed muscles, which are inserted into the various chitinous plates of its lining. The plates of the dorsal wall are also joined to the cephalothorax by strong bands of muscle.

The mid-gut (Pl. II.) extends from the second segment of the thorax to the third segment of the abdomen. It is a long, straight tube, with an unpaired anterior dorsal diverticulum, two pairs of anterior ventral diverticula, and one pair of posterior dorsal diverticula. The ventral wall of the mid-gut, where it joins the stomach (*st.*), is drawn down into a sac (text fig. 1, *s.*), the lower part of which divides, further back, into two lateral halves, while the upper part (text fig. 3) becomes drawn upwards and forwards over the stomach, like a double hood, and extends forwards dorsally as the anterior dorsal diverticulum (Pl. II., *div. a.*, and Pl. IV., fig. 3, *div. a.*). This extends forwards as far as the beginning of the first thoracic segment, overlying the stomach, from which it is but slightly separated. It is a flattened, broad sac, lined with columnar epithelium, the cells of which rise to the same level, forming a flat wall to the shallow, wide lumen, which is lined by a very fine cuticle (Pl. IV., fig. 2, *cut.*″). As will be seen from the accompanying text figures, the alimentary canal at the point of origin of the anterior dorsal diverticulum (text fig. 4) is a double tube; the inner one, which is the stomach, and to the wall of which the inner wall of the anterior diverticulum is closely applied, is incomplete ventrally, so that in transverse section it is horseshoe-shaped (text fig. 4, *st.*), opening



Series of sections to illustrate the relations of the stomach and mid-gut to the five anterior diverticula. They are selected at intervals, and the order is from before backwards commencing with fig. 1.

below into the sac-like dilation of the mid-gut. The more ventral lateral halves of this sac-like dilation (text figs. 3, 4, 5, 6, *h.p.*) pass backwards, and each half again divides to form two pairs of long, straight diverticula, which extend backwards at the side of the mid-gut, as far as the third and fifth segments of the abdomen. They form the hepato-pancreatic tubes, so-called because their secretion apparently acts upon all classes of food. They do not themselves contain food, but they form a secretion which passes down their wide lumina to be poured into the mid-gut, and probably also into the stomach. Two longitudinal plates of cuticle, thickly studded with setæ (Pl. IV., fig. 2, *set. cut.'*) pass from the stomach backwards along the floor of the sac from which the hepato-pancreatic diverticula arise. These partially enclose a channel which is continuous with the ventral groove of the stomach, and probably serves to carry forwards into the latter the hepato-pancreatic secretion.

As Murlin (13) found in the Isopoda, the walls of the hepato-pancreatic tubes show four layers:—(1) a serous membrane, (2) muscle fibres collected into a more or less distinct band taking a spiral course, (3) a fine basement membrane, (4) an epithelial layer. As Weber (25) pointed out, the spiral muscle band ensures greater efficiency of the peristaltic wave in discharging the contents of the tubes. The epithelial layer consists of tall, conical cells projecting considerably into the lumen, and separated by lower, non-projecting cells (Pl. IV., fig. 1, *h.p.*). For some distance behind the point of origin of the tubes, as well as near their ends, the two forms of cells merge into one another, and are probably, contrary to the supposition of Weber, merely the same kind of cell in different stages. The tall cells are much distended by colourless globules, the contents of which are emptied into the lumen of the tube by the bursting of the cell, which then appears much shrunken in size. Cells may be observed containing globules of every intermediate size, the globules being formed on that side of the cell near the lumen of the tube, the nucleus lying nearer the basement membrane. The mid-gut itself consists of four layers:—(1) a serous membrane, (2) a very thin muscular layer, consisting chiefly of transverse fibres, as Wrzéniowski

(27) observed, (3) a thin basement lining, (4) an epithelial layer, which is somewhat columnar just behind the stomach, where it is lined by a thin cuticula. Further back, the epithelium rapidly becomes flatter, and loses its chitinous lining in the fourth segment of the thorax. In the sixth thoracic segment the dorsal epithelium again becomes columnar, and the basement lining appears distinctly cuticularised, projecting inwards between the cells of the epithelium so as to form a kind of palisade. From the first segment of the abdomen backwards the epithelium is distinctly columnar and stains deeply, the chitinous basement palisade being strongly marked. In the third segment of the abdomen the dorsal epithelium becomes thicker and is drawn out laterally; in the next segment it becomes prolonged at the sides into a pair of diverticula which run forwards, side by side, above the mid-gut, as far as the sixth thoracic segment (Pl. II., *div. p.*). That these posterior diverticula arise from the mid-gut as pointed out by Wrzéniowski (27) and Nebeski (14) and not from the hind-gut, as Sars (19) supposed, is clear from the fact that their epithelium is gradually differentiated from, and closely resembles, that of the mid-gut, whilst a distinct break occurs between their epithelium and that of the hind-gut, which joins the mid-gut immediately behind their point of origin. The epithelium of the posterior diverticula is composed of very tall columnar cells, with deeply staining nuclei at their bases, which were found by Spencer (21) to contain phosphoric acid in the case of *Talitrus locusta*. They are surrounded by thin connective tissue, which separates them from the posterior aorta, in which they apparently lie (Pl. II., *div. p.*). Their lumina are constricted dorso-ventrally though wide from side to side, and they have no intima. Between the mid- and hind-gut, depending from the dorsal wall of

the former, just in front of the diverticula, is a flap of epithelium, which, as Wrzéniowski suggests, may serve to prevent what is passing along the alimentary canal from returning, or it may prevent such material from entering the diverticula.

The hind-gut lies in the last three segments of the abdomen (Pl. II.), and is sharply differentiated from the mid-gut, though its ventral portion extends forward further than the dorsal part, which ceases immediately behind the origin of the posterior diverticula of the mid-gut. Its walls consist of (1) a membrana propria of much greater thickness than that of the mid-gut, (2) a thick layer of striated circular muscle fibres, (3) scattered bundles of longitudinal muscle, (4) columnar epithelium. The last is raised into broken longitudinal ridges, and covered by a thick layer of cuticle which penetrates into the hollows between them. These ridges become higher towards the anus, and, probably, aid in passing along excreta.

The anus is a vertical slit, opening on the last segment, just below the telson (Pl. II., *an.*); bands of muscle connect its lateral walls with those of the last body segment.

Around the alimentary canal is a diffuse fat body (Pl. II., *ad. t.*), which is thickest round the reproductive organ, but is also well developed around and behind the œsophagus, and at the sides of the rectum. It diminishes in fasting Amphipods, according to Wrzéniowski (27).

The Vascular System.

The circulation of the Amphipoda has been described by Délage (3), who also summarised the work previously done on the subject. The following account agrees with his results, except that in *Gammarus pulex* the posterior aorta divides into two branches instead of into three, as he found to be the case in *Talitrus locusta*, and that the excretory organ breaks the continuity of the pericerebral vascular ring. The facts given below have been drawn from observation of the course of the corpuscles in the living animal, checked, however, by the examination of serial sections.

The heart is a long wide tube (Pl. II., Pl. III., fig. 1, *ht.*) extending from the middle of the first segment to the middle of the sixth, beyond which it is continued backwards as the median dorsal posterior aorta. In front, it is continuous with the median dorsal anterior aorta. In its anterior part, the ventral wall of the heart touches the dorsal wall of the anterior diverticulum of the alimentary canal, but further back it is separated from the gut by connective tissue. The dorsal wall of the heart is attached to the integument in the middle of each segment by a bundle of connective tissue fibres (Pl. III., fig. 1., *al. c.*); these are the alæ cordis, between which the heart hangs freely, forming five arcades through which the blood of the pericardial cavity can pass over the heart from side to side. In the middle of each segment, the lower part of the heart is widened by lateral fibres attached to its walls and the pericardium, which draws out the former laterally. In section, the wall of the heart appears to be formed of thin connective tissue, supporting somewhat scattered muscle fibres, which are most closely packed round the ostia. The latter (Pl. III., fig. 1, *os.*) are three pairs of obliquely-placed slit-like openings, without valves, situated a little behind the middle of the second, third and fourth segments. They open during diastole, and their edges are drawn together by the muscle fibres surrounding them during systole, and through them the blood from the pericardial cavity enters the heart. Its pulsations may be observed with the naked eye, and range from 120 to 130 beats per minute.

The pericardial cavity (Pl. III., fig. 1, *p.c.*) extends throughout the whole length of the body, from the first segment of the thorax to the last segment of the abdomen, which it occupies almost entirely. In section (Pl. IV., fig. 1) it is crescent-shaped, its dorsal wall lying close below the integument, which it follows closely down to the junction of the terga and the epipodal plates. The arched ventral wall (Pl. IV., fig. 1, *p.*) is separated from the alimentary canal and its diverticula by connective tissue, and is closely applied to the ventral wall of the heart. It is perfectly closed, except where the efferent vessels (Pl. III., fig. 1, *eff. v.*) from the appendages open into it, above the level of the heart. In addition to the heart, it encloses the posterior aorta, and the beginning of the anterior aorta.

Four arteries arise from the heart. These are the median dorsal posterior aorta, the median dorsal anterior aorta, and the paired facial arteries, the last three arising together at the beginning of the first thoracic segment (Pl. II.; Pl. III., fig. 1).

The posterior aorta (Pl. III., fig. 1, *a. post.*) arises, in the middle of the sixth segment, from the ventral wall of the heart. It is separated from the heart by a two-lipped valve, lying in a horizontal plane. From the beginning of the last thoracic segment to the end of the fourth abdominal one, it encloses the two posterior diverticula of the gut. The latter do not, however, lie in its lumen, but are surrounded by a double wall, the outer one corresponding to the wall of the aorta, which has apparently been pushed in by the development of the diverticula, so as to closely invest them. The greater part of the blood flowing back through the aorta passes below the posterior diverticula, since the latter lie nearer to the dorsal wall of the aorta than to the ventral one, which is only slightly separated from the mid-gut. The aorta is continued backwards above the rectum to the middle of the last abdominal segment, where it splits into two branches which turn downwards, one on each side of the rectum, piercing the pericardium, and empty their contents into the sternal sinus (Pl. III., fig. 1, *st. s.*).

The anterior aorta (Pl. III., fig. 1, *a. ant.*) is formed by the sharp lateral constriction, and more gradual lessening in diameter, of the anterior portion of the heart, at the beginning of the first thoracic segment. A careful examination failed to bring to light any valve. The aorta passes gradually downwards, following closely the dorsal wall of the stomach, till it reaches the level of the first antennæ. It then divides into two branches, the upper one passing straight forward, above the eyes, to the first antennæ, etc., the lower one passing downwards close to the wall of the stomach. After giving off a small vessel which runs forwards and supplies the brain, the lower branch receives a pair of small vessels from the excretory organs (Pl. III., fig. 1, *exc. or.*), and splits into two large vessels, which separate to enclose the œsophagus and again unite, forming the periœsophageal ring. After giving off a pair of branches to the maxillæ and another pair to the maxillipeds, this single median vessel opens into the sternal sinus. The upper branch of the anterior aorta passes forward to the base of the first antennæ, to which it sends off a pair of branches, one running down the lower edge of each antenna. The main artery then turns downwards, gives off a pair of branches to the second antennæ, and, a little lower, divides into two vessels, one running to the excretory organ on one side, one to that on the other. The blood which has filtered through the spongy tissue surrounding the nephridia is collected by the paired vessels which open into the lower branch of the aorta before it forms the periœsophageal ring. There is thus formed a median vertical pericerebral ring in the course of which lie the excretory organs (Pl. III., fig. 1).

The paired facial arteries (Pl. III., fig. 1, *fac. art.*) arise from the heart at the same level as the anterior aorta, and pass down on either side, ramifying immediately below the integument of the head, in the lower part of which they finally lose themselves. The head contains many lacunæ filled with blood, which is probably obtained from these arteries, and ultimately finds its way into the ventral blood sinus.

The sternal or ventral sinus (Pl. III., fig. 1, *st. s.*) fills the lower part of the body, below the alimentary canal, and bathes the ventral nerve cord and the two pairs of long hepato-pancreatic diverticula (Pl. III., fig. 1, *h.p.*) lying below the alimentary canal. Its cavity is somewhat cylindrical, extending from the concave ventral surface of the pericardium to the sternal body-wall; it has apparently no definite walls. It is filled with mixed blood, derived from (1) the two short branches into which the posterior aorta divides, (2) the median anterior aorta, which opens into the sinus after having formed the periœsophageal ring, (3) the blood lacunæ of the head. In each segment of the thorax and abdomen, it sends off a pair of afferent vessels (Pl. III., fig. 1, *aff. v.*) to the appendages of that segment. In each of the first four thoracic and first three abdominal segments, a separate afferent vessel is given off to each of the large coxal plates (Pl. III., fig. 1, *aff. c. v.*), which function as accessory respiratory organs, being covered internally with very thin cuticle.

The circulation of the appendages is as follows:—

(1) In the first antenna, the afferent vessel (Pl. III., fig. 1, *aff. v.*[1]), which is a branch of the anterior aorta, passes along the lower edge. On reaching the end of the second segment most of the blood turns back along the upper edge, but a little passes down a median vessel of the flagellum, returning by the same channel, which is thus alternately afferent and efferent. The efferent vessel of the appendage passes backwards just below the integument and opens into the anterior end of the pericardial cavity.

(2) In the second antenna, the afferent vessel, which is also a branch of the anterior aorta, passes along the upper edge. The blood returns along the lower edge, the efferent vessel passing backwards, more superficially than the aorta, and emptying itself into the sternal sinus.

(3) The mouth appendages are fed by two pairs of branches given off by the anterior aorta, just behind the œsophagus. Their efferent vessels apparently open into the sternal sinus.

(4) In the first four thoracic appendages the afferent vessel from the sternal sinus passes down the posterior edge to the tip, where it is continuous with the efferent vessel, which passes up the anterior edge of the appendage, and round the side of the body, opening into the dorsal part of the pericardial cavity. As the afferent vessel enters the proximal joint of the leg, it gives off a branch (Pl. IV., fig. 1, *aff. br. v.*) to the branchia. This is a highly vascular, thin, oval plate attached to the under side of the leg and covered by very thin cuticle (Pl. IV., fig. 3). It has a striated appearance, due to the fine horizontal bars of tissue, broken at intervals, which separate the

transverse vessels (Pl. IV., fig. 3, *tr. br. v.*). A large vessel (Pl. IV., fig. 3, *aff. br. v.*) runs round the edge of the branchia, the two sides of the loop being connected by fine transverse vessels, occasionally anastomosing, in which the blood is brought into the closest contact with the water. The blood passes down the posterior edge, some of it flowing through the transverse vessels, some flowing right round the branchia, not leaving the large encircling vessel, which returns up the anterior edge and empties itself (Pl. IV., fig. 3, *eff. br. v.*) into the efferent vessel of the leg (cp. Pl. III., fig. 1). A separate afferent vessel from the sternal sinus enters the middle of the coxal plate (Pl. IV., fig. 1, *c.p.*, and Pl. III., fig. 1), which is very large, especially in the fourth thoracic segment. Passing down to the lower edge of the plate, it bifurcates, each branch following more or less closely the edge of the plate. These efferent branches (Pl. III., fig. 1, *eff. c. v.*) reunite at the top of the plate and empty themselves into the efferent vessel of the appendage. In the female, another branch from the afferent vessel of the leg supplies the oostegite, the efferent vessel from which empties itself into the efferent vessel of the appendage.

(5) The last three thoracic legs have no enlarged coxal plates or oostegites, but they bear branchiæ. The afferent vessel passes down the anterior edge of the leg, giving off a branch to the branchia as in the first four thoracic legs; the efferent vessel follows the posterior edge and receives the efferent branchial vessel as it leaves the leg (Pl. IV., fig. 1).

(6) In the abdominal appendages, which do not bear branchiæ, the blood passes down the anterior margin and up the posterior one, as in the last three thoracic legs. The first three abdominal appendages—the meropods—are protected by large epimeral plates (Pl. III., fig. 1, *epim.*

p. 2), in which the circulation is similar to that in the coxal plates of the thorax.

On the course of the efferent vessels of the thoracic and abdominal appendages, in the basal joint of each leg, lie a group of unicellular glands (Pl. III., fig. 1, *gl.*) which are excretory in function.

The blood is a clear, colourless liquid, in which are numerous large corpuscles about 0·03mm. in diameter, for the most part in rapid motion, as well as a number of orange or vermilion-coloured oil globules of varying sizes. The corpuscles are granular with a clear nucleus and dark nucleolus (Pl. III., fig. 2); they show amœboid movement, and are somewhat pear-shaped when travelling rapidly, but become round when at rest. When the creature has been fed upon carmine for some days, the corpuscles contain carmine granules. A number of these globules are frequently to be seen more or less at rest, about the excretory organ at the base of the second antenna.

The circulation of the blood is partly vascular, partly lacunar, and the blood itself is mixed, the difference in purity between that in one part of the body and that in another being very slight. The purest blood passes through the anterior aorta to the brain and antennæ, from the heart, but even this cannot be regarded as pure, since the efferent vessels which supply the pericardial cavity return blood from the appendages as well as from the respiratory organs.

The Muscular System.

The muscles moving the segments of the body and the appendages can be seen, with their points of insertion, through the transparent exoskeleton. In addition to those of the alimentary canal (see above in the digestive system), the muscles may be divided into (1) those moving the segments of the body, and (2) those moving the appendages.

(1) The muscles of the segments may be divided into flexors and extensors. Of the former there are in each segment two sets, oblique muscles and muscles running parallel to the ventral wall of the body. In the thorax and first three segments of the abdomen, the oblique muscles, of which there are a pair in each segment, pass from the ventral surface of one segment to half-way up the body-wall of the next one behind. In the last three segments of the abdomen, the oblique muscles are inserted in the opposite way, running from half-way up one segment to the ventral surface of the one behind. This difference is, probably, due to the fact that when the abdomen is flexed, the last three segments are bent so completely under the body as to describe a curve opposite in direction to that formed by the rest of the body. The oblique muscles of the segments produce a telescoping movement. In the lower part of the body, pairs of muscles (Pl. IV., fig. 1, *long. m.*[1]) run parallel to the ventral surface, on either side of the middle line, joining the middle of one segment to that of the next. The points of insertion of each pair approximate very closely to those of the next, so that they appear to form a continuous double chain of muscle along the ventral surface of the body. In the last three abdominal segments, which are flexed simultaneously, these muscles are not segmented and attached to the middle of each segment, but form a continuous double band from the third abdominal segment to the sixth.

The extensors are much stronger than the flexors, forming broad bands of longitudinal muscle (Pl. III., fig. 1, *long. m.*), joining the front edge of the dorsal part of one segment to the front edge of that of the next. In the abdomen they occupy the greater part of the body, and in the last three segments they are united to form continuous bands, these segments being extended as one, so that the creature is forced through the water with great rapidity.

(2) Each appendage possesses large flexor and extensor muscles. The former are inserted into the side of the body-wall a little behind the point of origin of the leg, the latter a little in front of it, so that they pass down into the leg somewhat obliquely. The joints of the thoracic legs are connected with one another by an elaborate system of flexors and extensors, so that the joints may be moved separately. The muscles of the antennæ are attached to the sides and roof of the cephalothorax, so that these appendages can be moved in any direction. The mouth parts are produced internally into short calcified rods, which are attached laterally to the floor of the cephalothorax by broad, strong bands of muscle; this ensures powerful leverage for the masticatory apparatus.

It will appear from the above that the muscles are segmentally arranged, being broken up into successive segments by the connective tissue which forms their insertion into the body-wall. The muscle segments do not correspond with the external segmentation of the body, their divisions falling in the middle of each segment of the exoskeleton. As in all the Arthropoda, the muscle fibres are all striated, the striation often showing with extreme clearness. Koehler (10) states that in Isopods and Amphipods the usual relative positions of contractile element and protoplasm are reversed, the contractile substance being situated in the central region of the muscular cell of the primitive fibre, and surrounded by a layer of protoplasm, which separates it from the sarcolemma or sheath.

Nervous System and Sense Organs.

The nervous system consists of a paired chain of ganglia, each pair of ganglia being united to the next by two distinct cords. The first, or supra-œsophageal ganglion, which forms the brain (Pl. II., *br.*), lies immediately below the eyes, and is connected with the ventral nerve chain (Pl. II., *n.c.*) by a periœsophageal nerve ring (Pl. II., *peri. n. r.*). In the brain, as in the other ganglia, there are, as Packard (15) observed in *Asellus*, three kinds of elements.—(1) Ganglion cells, with large, deeply-stained nuclei, which are grouped round the ganglion in pyramidal masses, the bases of which are applied to the ganglion; (2) nerve fibres which arise from the ganglion cells and connect the ganglia; (3) myeloid tissue or substance (the "punktsubstanz" of Leydig), in which the nerve fibres are embedded, and which forms the mass of the ganglion.

The brain (Pl. II., *br.*), which has been very fully described and figured by Koehler (9), is a syncerebrum, consisting of (1) two large superior lobes, to the external extremities of which are attached the optic lobes connected with the retina by parallel nerve fibres, (2) two smaller median lobes, (3) two large inferior lobes, named by Koehler the "olfactory lobes," each with a lateral olfactory bulb, which appears to be an aggregation of spherical masses of myeloid tissue. Some fibres from both median and inferior lobes pass to the superior lobes, those from the inferior lobes intercrossing to form a chiasma. Into the inferior lobes run the nerves from the first antennæ, and, a little further back, those from the second (Pl. II., *ant.* 2). These lobes are continued backwards as large nerves, which pass one on each side of the œsophagus, forming the periœsophageal nerve ring (Pl. II., *peri. n. r.*).

The mouth parts are not innervated from a single pair of post-œsophageal ganglia. Immediately behind the œsophagus, the main nerves give off ventrally a pair of branches passing to the mandibles, after which they unite, forming the first pair of post-œsophageal ganglia, from which a pair of branches innervate the first maxillæ (Pl. II). Separating slightly, the main nerves become drawn out from above downwards, and, giving off laterally a pair of very small nerves which pass to the body-wall, they re-unite to form a large pair of ganglia, from which a pair of branches run down to the second maxillæ. Between this and the third pair of post-œsophageal ganglia the nerve cords again separate, giving off dorsally a pair of fine nerves, which run upwards and backwards to the point of origin of the hepato-pancreatic tubes (Pl. II., *h. p.*). The third post-œsophageal ganglion (Pl. II., *p.g.* 3) is four-lobed, the lower two lobes being continued into a large pair of nerves which pass first backwards and then downwards and forwards to the maxillipeds. The upper pair separate and pass back to form the double ventral nerve chain of seven thoracic and four abdominal ganglia.

Between each pair of ganglia in the ventral chain and the next the nerve cords separate and give off a pair of branches which innervate the longitudinal muscles of the body-wall connecting one segment with the next (Pl. II., *n.c.*). From each pair of ganglia, except the fourth abdominal one, two pairs of branches arise, the anterior pair small and non-ganglionated, the posterior large and ganglionated. The latter pass to the appendages, the nerve on each side being joined, in the first segment of the appendage by the corresponding non-ganglionated nerve of the more anterior pair. A few fibres are given off at their junction to the longitudinal muscles connecting the leg to the body-wall. The abdominal ganglia are smaller than those of the last three thoracic legs or peræopods (Pl. II., *per.* 1, 2, 3).

The fourth pair of abdominal ganglia (Pl. II., *abd. g. 4*) innervate the last three segments of the body (which almost always move together), giving off two pairs of branches to the first pair of uropods, a pair running directly backwards, and a pair of fine nerves which run upwards to the alimentary canal in the neighbourhood of the point of origin of the posterior diverticula.

The chief sense-organs connected with the nervous system are the eyes. Many of the setæ scattered over the body are probably tactile in function, and those of the antennæ, which have a rich nerve supply, may be auditory or olfactory. The calceoli of the second pair of antennæ are probably olfactory, and appear to contain a nerve-mass (see above). With regard to the eyes, the external features of which have been already described, the ommatidia or component simple eyes, appear from above to be four-sided masses of black pigment, embedded in a surrounding pigment which appears white by reflected light, though by transmitted light it is pale violet. Each ommatidium consists of a transparent axis, formed distally of a two-celled crystalline cone, proximally of a slender rhabdome, sheathed by five retinular cells. The proximal end of each of the retinular cells contains a nucleus and is drawn out to form a retinal fibre which passes to the optic ganglion. The space between the ommatidia is filled by the light-reflecting pigment, contained in cells of which the walls are very indistinct. The five retinular cells contain black pigment, which Parker (16) observed to migrate from the more proximal parts to the more distal ones in the presence of light, and to return to the proximal ends in comparative darkness. He suggests that by this means the more oblique rays are turned back on the rhabdome in dim light, since the removal of the black pigment surrounding the rhabdome exposes the whitish reflecting pigment of the surrounding cells. Parker believes that the pigment surrounding the cone is merely concerned with the absorption of the lateral rays, oblique light being prevented from reaching the underlying rhabdome by the shape of the cone, which is therefore catoptric in action, and is regarded by him as being in many respects primitive in type. The number of ommatidia increases with the age of the animal, the new ones being formed at the posterior or convex margin of the eye (Pl. I., fig. 15).

The Excretory System.

In *Gammarus* which had been fed upon carmine for a week no granules were visible in the diverticula of the gut, though the mid-gut contained a quantity of the substance. Staining was observed (1) at the base of the second antenna, *i.e.*, in the antennary gland, (2) in the protopodite of the second maxilla, (3) in patches just below the cuticle at the base of each of the thoracic legs and of the first three abdominal ones, and also on the posterior margin of the last three abdominal segments.

The antennary gland is similar to that of *Gammarus marinus*, described by Grobben (8). It lies in the enlarged basal joint of the second antenna, and consists of an end-sac (Pl. II., *e.s.*), and a convoluted tube leading from it to the exterior (Pl. II., *con. t.*), the whole being surrounded by spongy tissue full of blood, and innervated by branches from the antennary nerve. The end-sac occupies the lower part of the proximal end of the basal joint; it is somewhat reniform, and the anterior end is slightly narrower than the posterior one. It has very thin walls, a delicate membrane supporting the epithelium, each cell of which contains coarsely granular protoplasm, and projects into the lumen or sac, its outer wall being very convex. From the posterior end of the sac arises the convoluted tube, which passes backwards and downwards, then forwards and upwards, and then again backwards and downwards into the antennary cone (Pl. II., *ant. c.*), at the apex of which it opens to the exterior. The tube is lined with cells containing fibrous protoplasm and oval nuclei. It has a cuticula which becomes distinctly chitinous in the terminal section, and passes directly into the cuticle covering the outside of the body. Just before entering the antennary cone, the tube widens considerably, forming a small bladder.

A mass of spongy tissue occupies part of the protopodite of the second maxilla, a convoluted tube running through it to the exterior. It may be homologous with the shell-gland of the Entomostraca according to Waite (24), though Leydig considers that this gland is entirely wanting in all adult Malacostraca.

The groups of unicellular glands (Pl. II., *gl.*), lying just below the cuticle at the base of the thoracic and first three abdominal appendages, and on the posterior margin of the last three abdominal segments, are placed above the point of exit of the efferent vessel of each appendage (Pl. III., fig. 1., *gl.*), and are evidently excretory in function. In animals living under normal conditions they contain brightly-coloured globules, usually orange or vermilion;

these are most evident in the groups of glands lying on the posterior margin of the last three abdominal segments. Each gland consists of a single large cell, with a deeply stained nucleus of considerable size, surrounded by granular protoplasm, and is provided with a chitinous duct, which apparently opens on to the exterior. In animals which had been fed on carmine, granules of that substance were present in the protoplasm of the gland cells. They appear to be similar to those described by Nebeski (14) in the Corophiidæ, but, unlike the latter, they have no ducts running down to the dactylopodite. Similar unicellular glands are present in the setigerous plates of cuticle found on the floor of the stomach. Globules of the coloured oil are present in the blood of the creature, and increase in number when it has been kept in captivity for some time, the patches of unicellular glands becoming at the same time less noticeable, owing to their comparative freedom from oil.

Reproductive Organs and Life History.

As already stated, the sexes are separate. In both, the reproductive organs are paired straight cylindrical tubes, surrounded by adipose tissue, lying dorsally upon the gut, below the heart (Pl. II., *gon.*).

In the male, they extend from the second to the seventh segment of the thorax. The vasa deferentia (Pl. II., *g.d.*) are straight tubes arising from their ends, in the seventh segment, and passing down the sides of the body, close to the body-wall, to the inner side of the basal joint of the last pair of thoracic legs or peræopods, where they open on a pair of small tubercles. Each tubercle is supplied with a strong musculature, and forms an external penis. The testis proper extends from the end of the second segment to the end of the fifth. It consists of a cylindrical epithelium, without a perceptible muscle layer, surrounded by a thin tunica propria. The anterior end and upper part only produce spermatozoa, the epithelium of these regions being thickened, and containing spindle-shaped nucleoli and granular protoplasm. The cells of this epithelium become rounded, develop a long tail, and are set free as immature spermatozoa. The newly-liberated spermatozoon (Pl. IV., fig. 4, *a.*) consists of a rounded mass of granular protoplasm with a spindle-shaped nucleolus surrounded by a clear nucleus, the whole being attached to a long whip-like tail which is inserted into a tiny bead-like projection of the nucleolus. When treated with methyl green, only the nucleolus is stained. At a later stage (Pl. IV., fig. 4, *b.*) the head becomes smaller, owing to the absorption of the granular protoplasm by the nucleolus, which increases in size and becomes curved. Later (Pl. IV., fig. 4, *c.*), the protoplasm becomes all absorbed, and the spermatozoon consists of a long tail and a somewhat reniform small head, the whole of which is stained by methyl green, and which is clear in structure. The head gradually lengthens, and in the mature spermatozoon (Pl. IV., fig. 4, *f.*) is a long, narrow flexible tongue, which appears clear when stained. Della Valle (4) has figured corresponding stages in the development of the spermatozoa of *Gammarus pungens.* The lower part of the male reproductive organ consists of a lumen, the walls of which are formed of large cells, which apparently secrete the fluid, in which the spermatozoa pass through a constricted part of the reproductive tube into the wider vesicula seminalis, which extends from the end of the sixth segment to half-way through the seventh. The wall of the vesicula seminalis resembles that of the generating portion of the gland except that the tunica propria is separated from the cylindrical epithelium by a very thin layer of muscle.

The ovaries extend from the end of the second segment of the thorax to the end of the seventh, and sometimes even into the first segment of the abdomen. The oviducts are a pair of straight wide tubes in the fifth segment, opening on to the inner side of the basal joints of the fifth pair of legs, as noted by Sars (19), and not, as St. George (22) supposed, in the fourth segment. At their lower ends they widen into sac-like dilations. The ovary contains a single row of eggs, which are large and surrounded by a very thick covering of granular yolk, so that they impart a slightly-lobulated appearance to the otherwise cylindrical tube. The wall consists of cylindrical epithelium, with a basement layer of finely granular appearance, surrounded by a thin tunica propria. According to St. George, an ovum is formed by a single epithelial cell increasing in size, its nucleus becoming the germinal vesicle and filling itself with germinal spots. The eggs when fully developed are slightly ovoid in form, about 0·05mm. in diameter, and contain violet and also yellow-brown yolk. Della Valle (5) states that the female undergoes ecdysis before laying eggs. The latter pass into the brood-pouch formed on the ventral side of the thorax by the four pairs of lamelliform oöstegites attached to the first four thoracic legs, and there develop. Della Valle has shown that the eggs are passed on into the brood-chamber without an external envelope, and only secrete the vitelline membrane after fertilisation. In confirmation of Leydig, he has proved that in both *G. locusta* and *G. pulex*, the cleavage is at first total, sixteen cleavage spheres of equal size being formed, but later appears superficial, the originally distinct cells becoming secondarily fused together in the interior of the egg, so as to apparently fill the cleavage cavity. The superficial cells finally contain only formative yolk, and become separated from the nutritive yolk by a distinct line. When the formation of the blastoderm is completed, a ventral thickening, the germ-disc, appears, the ingrowing cells forming the mesoderm. According to Rossijskaya (18), the elements of the endoderm arise from an immigration of separate blastomeres into the deeper layers; these, after dispersing in the food-yolk, soon become arranged as two lateral endoderm bands, lying superficially on the food-yolk.

The germ-disc, at first round, spreads out into a germ-band covering the whole ventral surface of the egg. The anterior end becomes enlarged to form the cephalic lobes from which the rudiments of the eyes and brain arise, while the germ-band itself becomes divided up by furrows into the separate body-segments. As the germ-band lengthens, a ventral curvature of the abdomen is brought about, and is seen throughout embryonic life. During the differentiation of the germ-band, a dorsal disc-shaped thickening of the blastoderm is formed. When the larval integument develops, this dorsal organ adheres closely to it, the central part becoming invaginated to form a small cavity, which communicates with the exterior by a small perforation, the micropyle. It has been regarded by St. George (22) as a respiratory apparatus. Later, when the heart develops, it degenerates. As the germ-band broadens, its lateral portions grow up over the food yolk, forming the lateral parts of the embryo, and ultimately coalesce in the mid-dorsal line.

The whole of the central nervous system arises as a paired ectodermal thickening. Two longitudinal ectoderm swellings may be regarded as the first rudiments of the ventral chain of ganglia; they show segmental swellings, and are separated by the primitive groove. The brain arises in the form of three pairs of ganglia, corresponding to the eyes and the first and second antennæ, and belonging to three separate body-segments, of which the first is, probably, the only original pre-oral segment, the remaining two being apparently trunk-segments, originally post-oral in position, which have been drawn into the head. The eye arises as a part of the ectoderm, which becomes multilaminar and produces from its superficial layers the cells of the cornea and crystalline cones, while the lower layers give rise to the retinulæ and the pigment cells.

The alimentary canal is formed by the union of three separate rudiments, the fore-gut and hind-gut arising as ectodermal invaginations (stomodæum and proctodæum), while the mid-gut is formed from the endoderm. The fore-gut arises before the hind-gut. The mid-gut is formed by the union of the two lateral bands of endoderm lying on the food-yolk, which grow round it and enclose it. A pair of very large hepatic sacs are formed by constriction at its sides; they give rise later to two pairs of tubes, by longitudinal constriction. From the posterior section of the mid-gut arise the pair of posterior dorsal diverticula. The alimentary canal is largely composed of the fore and hind guts, so that only a small portion of it is endodermal in origin.

The heart arises in the middle of the body by the fusing of two grooves which arise from a single row of mesoderm cells on each side; the ventral precedes the dorsal fusion. The ostia develop at the boundaries of the mesoderm segments. Rossijskaya (18) observed that the genital cells were mesodermic in origin.

The embryos when hatched already have the full number of segments and limbs of the adult, metamorphosis being reduced to small alterations of shape, increase in number of the joints, &c., of the antennæ, and additions of setæ and teeth.

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Explanation of Plates.

Reference Letters.

a. ant. = anterior aorta.
abd.g. 4 = fourth pair of abdominal ganglia.
ad.t. = fat body.
a.post. = posterior aorta.
aff.br.v. = afferent branchial vessel.
aff.c.v. = afferent vessel of coxal plate.
aff.epim.v. = afferent vessel of epimeral plate.
aff.v. = afferent vessel of leg.
aff.v'. afferent vessel of antenna.
al.c. = alæ cordis.
al.can. = alimentary canal.
am.c. = amœboid corpuscle of blood.
an. =anus.
ant. 1 = first antenna.
ant. 2 = second antenna.
ant.c. = antennary cone.
art. 10 = tenth joint of second antenna.
br. = brain.
calc. = calceolus.
c.ep. = columnar epithelium of anterior diverticulum.
con.t. = convoluted tube of excretory organ.
c.p. = enlarged coxal plate.
cut'. = basement cuticle of stomach.
cut''. = cuticle lining anterior diverticulum.
div.a. = anterior diverticulum of mid-gut.
div.p. = posterior diverticulum of mid-gut.
eff.br.v. = efferent branchial vessel.
eff.c.v. = efferent vessel of coxal plate.
eff.v. = efferent vessel of leg.
eff.v'. = efferent vessel of antenna.
eff.epim.v. = efferent vessel of epimeral plate.
epim.p.1 = epimeral plate of thorax.
epim.p.2 = epimeral plate of abdomen.
e.s. = end-sac of excretory organ.
exc.or. = excretory organ.
fac.art. = facial artery.
fl.sec. = secondary flagellum of first antenna.
g.d. = reproductive duct.
gl. = unicellular glands.
gnath.1 = first gnathopod.
gnath.2 = second gnathopod.
gon. = reproductive organ.
h.p. = hepato-pancreatic tubes.
ht. = heart.
long.m. = exterior muscle of body.
long.m'. = flexor muscle of body.

m. = mouth.
mnp. = mandibular palp.
mn.t. = mandibular teeth.
m.p. = membrana propria.
mxp. = maxilliped.
n. = nucleus.
n' = nucleolus.
n.c. = ventral nerve cord.
os. = ostium.
p. = pericardium.
p.c. = pericardial cavity.
per. 1 = first peræopod.
per. 2 = second peræopod.
per. 3 = third peræopod.
per. 4 = fourth peræopod.
per. 5 = fifth peræopod.
peri.n.r. = periœsophageal nerve ring.
p.g. 3 = third pair of post-œsophageal nerve ganglia.
pl. 1 = first pleopod.
pl. 2 = second pleopod.
pl. 3 = third pleopod.
s. = sac-like dilation of mid-gut.
set.cut. = setigerous plates of cuticle of stomach.
set.cut'. = setigerous plates of cuticle at origin of hepato-pancreatic tubes.
st. = stomach.
st.s. = sternal sinus.
t. = tergum.
tel. = telson.
tr.br.v. = transverse branchial vessel.
uro. 1 = first uropod.
uro. 2 = second uropod.
uro. 3 = third uropod.
v. = valve separating heart from posterior aorta.

Plate I.

Fig. 1. First antenna, with four-jointed secondary flagellum (*fl. sec.*) or exopodite.

Fig. 2. Second antenna, with enlarged basal joint bearing the antennary cone (*ant. c.*) and stout flagellum bearing plumose setæ and calceoli (*calc.*).

Fig. 3. Ninth and tenth joints of second antenna (enlarged) showing calceoli.

Fig. 4. Left mandible, showing three-jointed mandibular palp (*mn. p.*), and saw-like jaws bearing double rows of teeth.

Fig. 5. Left first maxilla, also enlarged single spine.

Fig. 6. Right second maxilla, showing long curved spines.

Fig. 7. Maxillipeds, viewed from under side, showing that they are joined to form a lower lip.

Fig. 8. First gnathopod from left side, showing coxal plate (*c.p.*) attached to coxopodite.

Fig. 9. Second gnathopod (left), showing coxal plate and branchia (*c.p.* and *br.*).

Fig. 10. First peræopod, showing hooked dactylopodite, coxal plate and branchia.

Fig. 11. Telson, showing two apical spines, and one lateral one on each of the two rami.

Fig. 12. First pleopod (left) showing long plumose setæ on many-jointed similar endopodite and exopodite, and single spine on protopodite.

Fig. 13. Last epimeral plate (left) of metasome, showing somewhat pointed infero-posterior corner.

Fig. 14. Last uropod (left), showing plumose setæ and exopodite, and single spine on protopodite.

Fig. 15. The eye, showing the somewhat quadrangular pigmented ommatidia. These are variable in number.

Plate II.

Diagram of male *Gammarus pulex*, seen extended in optical section from the left side, and enlarged twenty times. The diagram is built up from a number (560) of transverse serial sections, stained with Mann's methyl blue eosin. The heart and the aortæ, which are cut short, are coloured pink. The pericardium and the other vessels are omitted. The nervous system is dense black and the alimentary canal and its diverticula are dark grey. The reproductive organ of the left side, with its duct, is shown to the side of the mid-gut, sheathed in adipose tissue. The appendages are shown *in situ*, but the first and second antennæ have been cut short.

Plate III.

Fig. 1. Diagram showing the circulatory system. The pericardial cavity, heart, arteries and efferent vessels of the appendages are coloured pink. The sternal sinus, with its afferent vessels to the appendages, is coloured blue. The vessels of the branchiæ are shown cut short in the first four thoracic segments, in the last three they are omitted. The heart and the anterior and posterior aortæ are shaded to distinguish them from the rest of the pericardial cavity, in which they lie. The colouring is purely arbitrary, and introduced for the sake of clearness, since the blood is mixed throughout, though the purest blood on the whole is that in the pericardial cavity. The colouring, however, serves to show at a glance the sternal sinus and pericardial cavity and the vessels respectively related to these spaces.

Fig. 2. An amœboid corpuscle of the blood.

Plate IV.

Fig. I. Diagram of a transverse section through the body in the neighbourhood of the fourth segment of the thorax, showing the pericardial cavity and the sternal sinus, and their connection with the vessels of the coxal plates, legs and branchiæ. Afferent and efferent vessels are shown on different sides of the section, diagrammatically, though the afferent vessels of the appendages are really in a plane posterior to that of the efferent vessels (Pl. III., fig. 1). The colouring is as in Plate III.

Fig. 2. Diagram of a transverse section through the alimentary canal in the neighbourhood of the point of origin of the hepato-pancreatic tubes (*h.p.*). It is drawn from Section 112 (Pl. II., scale), and shows the mid-gut apparently enclosing the stomach (*st.*). The mid-gut is here drawn forward over the stomach, forming the anterior dorsal diverticulum (*div. a.*), which is lined with a thin cuticle (*cut.''*). The ventral or inner wall of this diverticulum is very closely applied to the wall of the stomach, the mucous coat of which rests on a well-developed basement cuticle, showing a slight palisade structure; this cuticle is produced at the lower end of the stomach with setigerous plates covered with unicellular glands (*set. cut.*). On the floor of the mid-gut, in transverse section, are seen the ends of the longitudinal plates of cuticle (*set. cut.'*), which are prolonged forwards to guard the ventral groove of the stomach.

Fig. 3. Diagrammatic view of a branchia from the side. The afferent vessels are coloured blue, the efferent red. The half of the transverse vessels first entered by the blood is coloured blue, the second part pink.

Fig. 4. Spermatozoa in various stages of development:—

a. Spermatozoon just set free, with long tail and readily-stained nucleolus.

b. Spermatozoon in which the nucleolus has increased in size at the expense of the granular protoplasm.

c. Spermatozoon in which the whole of the head is occupied by a clear, small, easily-stained body, probably the altered nucleolus.

d., *e.*, *f.* Successive stages in the evolution of the long, ribbon-like tail of the mature spermatozoon, as shown in *f.*

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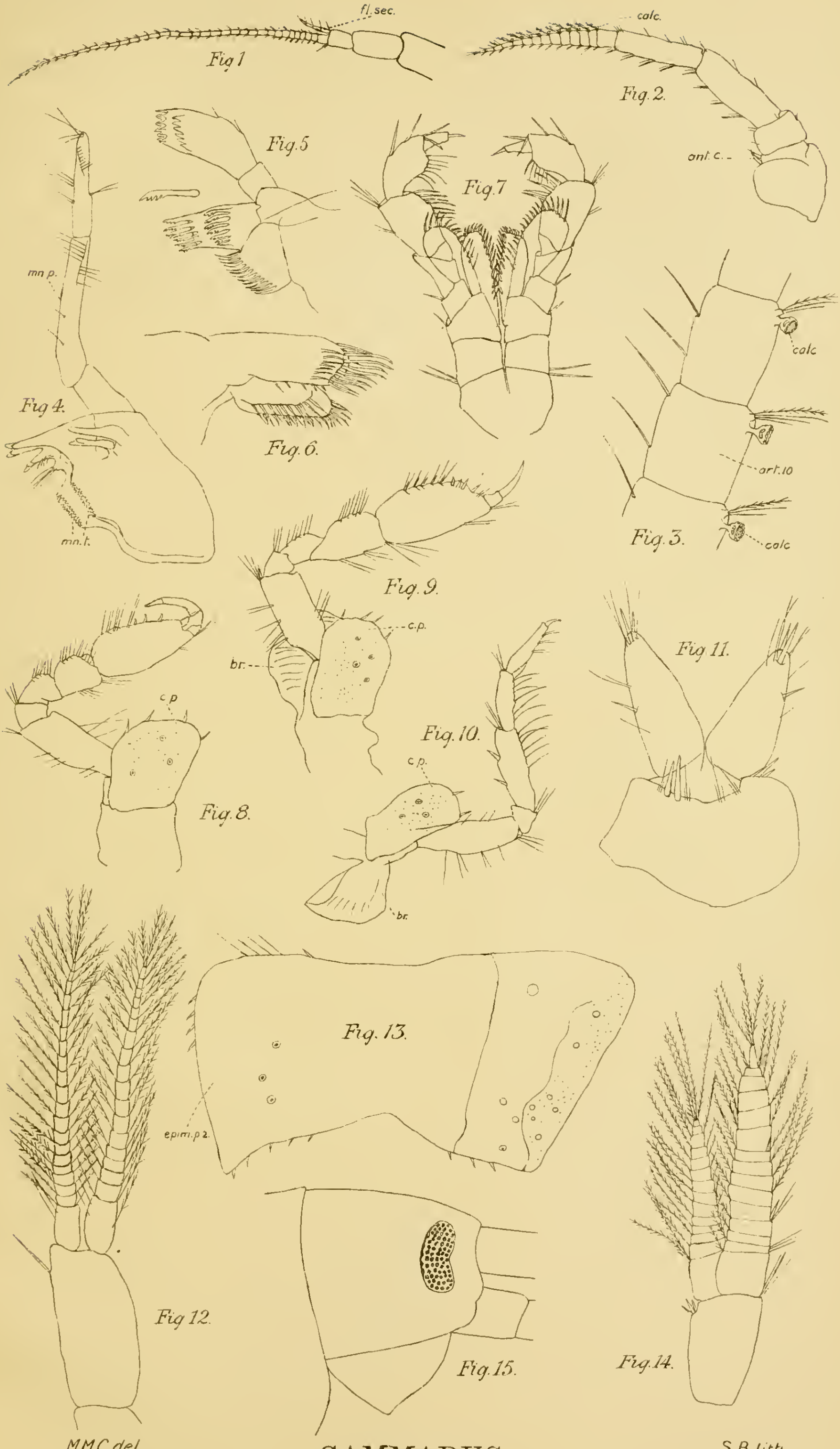
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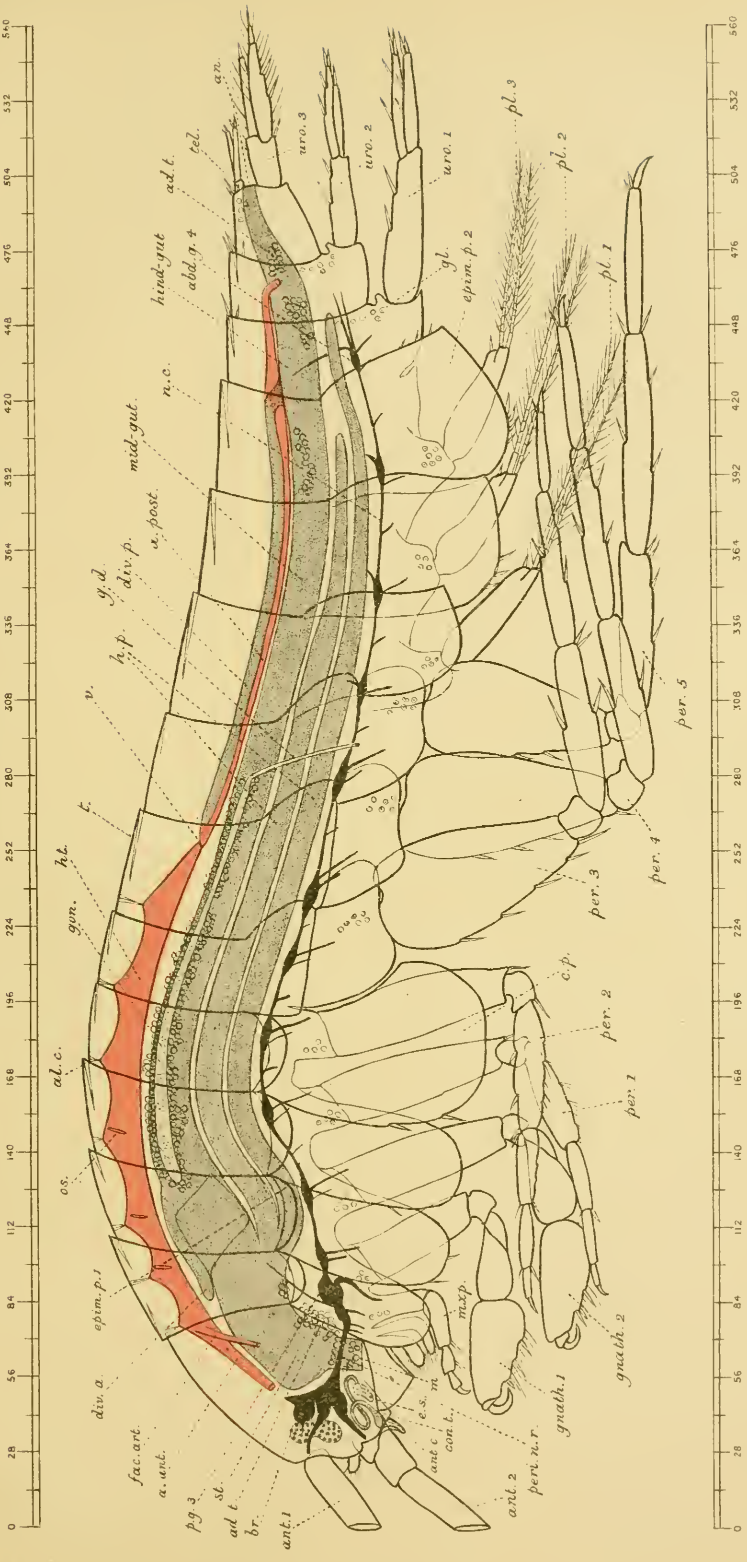

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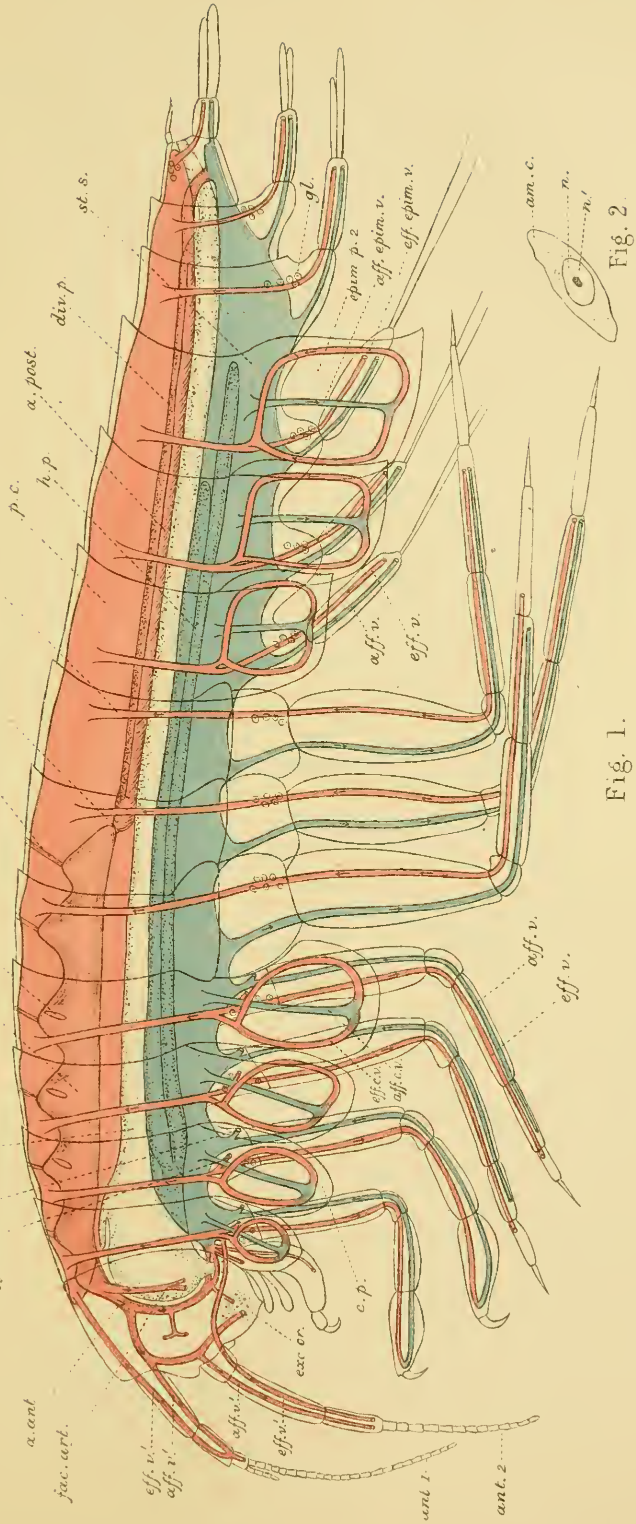

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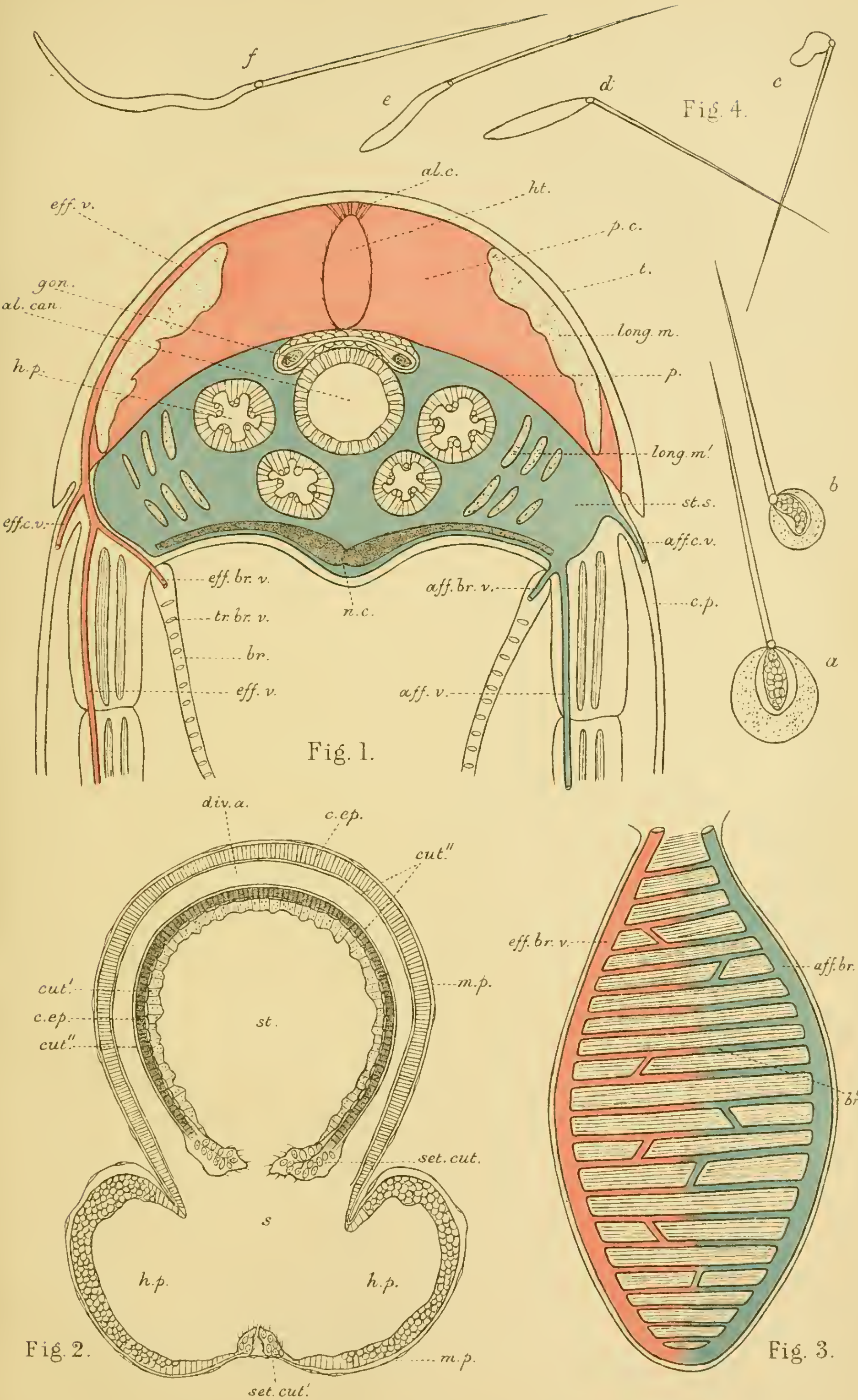

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