L.M.B.C. MEMOIRS.

XVI.

CANCER.

NOTICE.

The Committee desire to intimate that no copies of these Memoirs will be presented or exchanged, as the prices have been fixed on such a scale that most of the copies will have to be sold to meet the cost of production.

The Memoirs may be obtained at the nett prices stated, from Messrs. Williams and Norgate, 14, Henrietta Street, Covent Garden, London.

Memoir I. Ascidia—published in October, 1899, 60 pp. and five plates, price 2s.
,, II. Cardium—published in December, 1899, 92 pp., six plates and a map, price 2s. 6d.
,, III. Echinus—published in February, 1900, 36 pp. and five plates, price 2s.
,, IV. Codium—published in April, 1900, 26 pp. and three plates, price 1s. 6d.
" V. Alcyonium—published in January, 1901, 30 pp. and three plates, price 1s. 6d.
,, VI. Lepeophtheirus and Lernæa—published in March, 1901, 62 pp. and five plates, price 2s.
,, VII. Lineus—published in April, 1901, 40 pp. and four plates, price 2s.
,, VIII. Pleuronectes—published in December, 1901, 260 pp. and eleven plates, price 7s.
,, IX. Chondrus—published in July, 1902, 50 pp. and seven plates, price 2s. 6d.
,, X. Patella—published in May, 1903, 84 pp. and four plates, price 2s. 6d.
,, XI. Arenicola—published in March, 1904, 126 pp. and eight plates, price 4s. 6d.
,, XII. Gammarus—published in July, 1904, 55 pp. and four plates, price 2s.
,, XIII. Anurida—published in October, 1906, 105 pp. and seven plates, price 4s.
,, XIV. Ligia—published in January, 1907, 45 pp. and four plates, price 2s.
,, XV. Antedon—published in June, 1907, 55 pp. and seven plates, price 2s. 6d.
,, XVI. Cancer—published in June, 1908, 218 pp. and thirteen plates, price 6s. 6d.

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.

XVI.

CANCER

BY

JOSEPH PEARSON, M.Sc.,
Demonstrator in Zoology, University of Liverpool.

(With 13 Plates)

PRICE SIX SHILLINGS AND SIXPENCE

LONDON
WILLIAMS & NORGATE
JUNE, 1908

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have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated. Twenty-one 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 since been erected, and was opened for work in July, 1902.

In these twenty-one years' experience of a Biological Station (five years at Puffin Island and sixteen 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 XVI. have now been published.

Pecten, by Mr. W. J. Dakin: Eledone, by Dr. W. E. Hoyle; and Doris, by Sir C. Eliot, are now far advanced and ought to be out during 1908. It is hoped that Cucumaria, Buccinum, and the Oyster will follow soon.

Memoir I. Ascidia, W. A. Herdman, 60 pp., 5 Pls., 2s.
,, II. Cardium, J. Johnstone, 92 pp., 7 Pls., 2s. 6d.
,, III. Echinus, H. C. Chadwick, 36 pp., 5 Pls., 2s.
,, IV. Codium, R. J. H. Gibson and Helen Auld, 26 pp., 3 Pls., 1s. 6d.
,, V. Alcyonium, S. J. Hickson, 30 pp., 3 Pls., 1s. 6d.
,, VI. Lepeophtheirus and Lernæa, Andrew Scott, 62 pp., 5 Pls., 2s.
,, VII. Lineus, R. C. Punnett, 40 pp., 4 Pls., 2s.
,, VIII. Plaice, F. J. Cole and J. Johnstone, 260 pp., 11 Pls., 7s.
,, IX. Chondrus, O. V. Darbishire, 50 pp., 7 Pls., 2s. 6d.
,, X. Patella, J. R. A. Davis and H. J. Fleure, 84 pp., 4 Pls., 2s. 6d.
,, XI. Arenicola, J. H. Ashworth, 126 pp., 8 Pls., 4s. 6d.
,, XII. Gammarus, M. Cussans, 55 pp., 4 Pls., 2s.
,, XIII. Anurida, A. D. Imms, 107 pp., 8 Pls., 4s.
,, XIV. Ligia, C. G. Hewitt, 45 pp., 4 Pls., 2s.
,, XV. Antedon, H. C. Chadwick.
,, XVI. Cancer, J. Pearson.
Doris, Sir Charles Eliot.
Pecten, W. J. Dakin.
Eledone, W. E. Hoyle.
Cucumaria, E. Hindle.
Oyster, W. A. Herdman and J. T. Jenkins.
Ostracod (Cythere), Andrew Scott.
Buccinum, W. B. Randles.

Bugula, Laura R. Thornely.
Zostera, R. J. Harvey Gibson.
Himanthalia, F. J. Lewis.
Diatoms, F. E. Weiss.
Fucus, J. B. Farmer.
Botrylloides, W. A. Herdman.
Actinia, J. A. Clubb.
Hydroid, E. T. Browne.
Halichondria and Sycon, A. Dendy.

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

As announced in the preface to Ascidia, a donation from the late 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 Mrs. Holt, Sir John Brunner, and 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, 1908.

L.M.B.C. MEMOIRS

No. XVI. CANCER.

BY

JOSEPH PEARSON, M.Sc.,
Demonstrator in Zoology, University of Liverpool.

CONTENTS.

INTRODUCTION.

CANCER is a genus which has a world-wide distribution. Only one species, however, is found in Europe, viz., *Cancer pagurus*, the subject of the present memoir.* This species is found on almost every part of the coasts of Europe from Norway to Greece, and it is particularly abundant on the shores of North-West Europe (France, Germany and the British Isles).

Cancer pagurus, the edible crab, has been chosen as the subject of the present memoir partly on account of its economic importance, and also because, as a type for dissection, it is easily procurable and is of a convenient size. The account given below, however, may be applied with very few alterations to any of the brachyurous Decapod Crustaceans, such as the common shore crab (Carcinus) or the swimming crab (Portunus).

The edible crab is found in great abundance on the coasts of the British Isles, especially on those parts which are rocky, and gives rise to an important fishing industry. The large crabs live in fairly deep water, but the young representatives of this species may be readily obtained between tide-marks. Cancer is mainly carnivorous in its habits and feeding. It is particularly fond of dead fish, and it probably also feeds on other Crustaceans in a small degree. There is, however, no evidence to show that it has cannibalistic instincts. (For further particulars with regard to habits, distribution, crab fishery, &c., see section on Economics.)

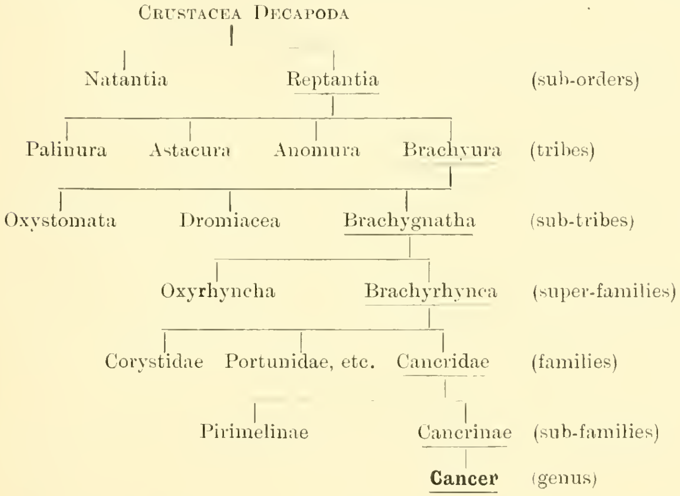
Cancer pagurus was first named by Linneus, who established both the genus and the species. In his

---

*The investigation has been assisted by a grant of £25 from the Board of Agriculture and Fisheries, and the expense of producing the lithographed plates has been met in part by a grant of £30 from the "Treasury Grant for Research" of the University of Liverpool.

"Histoire naturelle des Crustacés," Milne-Edwards named it *Platycarcinus pagurus.* This latter name appears to have been retained in many continental works up to quite recent years.

I have followed the classification of Borradaile,[*] and I give below a table compiled from the results of his work.



The main characters of the various divisions of the Decapod Crustacea are given below.[†]

NATANTIA.—Rostrum well developed and compressed. Body compressed. First abdominal somite equal to rest. Stylocerite present. Second antennal scale large. In the legs basis and ischium never fused, and one fixed point in the carpopropodal articulation. Male genital opening arthrodial. Abdominal limbs 1-5 well developed and used for swimming.

---

[*] Borradaile, L. A. "On the Classification of the Decapod Crustaceans." *Ann. and Mag. Nat. Hist.* (7), Vol. XIX, June, 1907.

[†] These characters are abstracted from Borradaile's paper.

Reptantia. Rostrum reduced or absent, depressed if present. Body depressed. First abdominal somite smaller than rest. Stylocerite absent. Second antennal scale reduced or absent. In the legs generally a basi-ischium, and two fixed points in the carpo-propodal articulation. Male genital opening coxal and sternal. Abdominal limbs 1-5 reduced or absent, and not used for swimming.

The four tribes belonging to the Reptantia are divided into two groups.

I. Third legs like the first. Abdomen macrurous. Gnathobases of second maxillae narrow. Exopodites of maxillipedes with lash directed forward. Gills numerous.

(1) Palinura.—Carapace fused to epistoma. Rostrum small or absent. Inner lobes of second maxillae and first maxillipedes reduced. Body depressed.

(2) Astacura.—Carapace free from the epistoma. Rostrum large. Inner lobes of second maxillae and first maxillipedes not reduced. Body subcylindrical.

II. Third legs unlike the first, never chelate. Abdomen rarely macrurous. Gnathobases of second maxillae broad. Exopodites of maxillipedes with lash directed inward. Gills few.

(3) Anomura.—Carapace not fused with epistoma. Last thoracic sternum free, its legs differing from the others. Abdomen anomurous. Movable antennal scale. Third maxillipedes narrow.

(4) Brachyura.—Carapace fused with epistoma. Last thoracic sternum fused with rest, its legs like the others. Abdomen brachyurous. No movable antennal scale. Third maxillipedes broad.

The following are the sub-tribes of the Brachyura:—

OXYSTOMATA.—Mouth-field prolonged forward as a gutter. No female first abdominal limbs. Gills few. Female openings sternal.

DROMIACEA.—Mouth-field square. First abdominal limbs present in female. Gills many. Female openings coxal.

BRACHYGNATHA.—Mouth-field square. Female openings sternal. No first abdominal limbs in female. Gills few.

The Brachygnatha are divided into two super-families.

OXYRHYNCHA.—Front part of body narrow. Distinct rostrum. Body more or less triangular. Orbits incomplete.

BRACHYRHYNCHA.—Front part of body broad. Rostrum reduced or wanting. Body oval. Orbits complete.

The Brachyrhyncha are sub-divided into fourteen families. I give here the chief characters of the one family—the Cancridae.

CANCRIDAE.—Marine crabs with the branchial region not greatly swollen. Carapace broadly oval or hexagonal. Rostrum often wanting. Orbits complete. Male openings coxal. Second antennal flagella short. First antennae folded lengthwise. Inner lobe on the endopodite in the first maxillipedes wanting. Legs generally not adapted for swimming.

The two sub-families of the Cancridae are as follows:—

PIRIMELINAE.—Carapace hexagonal. Epistoma sunken.

CANCRINAE.—Carapace broadly oval. Epistoma not sunken.

EXTERNAL CHARACTERS

(Pl. I, figs. 1, 2, 3).

The whole of the exterior of the animal is covered by a thick continuous chitinous exoskeleton or shell, which is highly calcified except between the movable somites of the abdomen and between the movable podomeres in the appendages.

The body may be conveniently divided into an anterior region—the Cephalon, a middle region—the Thorax, and a posterior region—the Abdomen. As in all the Decapoda the Cephalon and Thorax are fused to form the Cephalothorax.

The Cephalothorax is by far the largest portion of the body, and is the only part seen from the dorsal surface. The Abdomen is much reduced and is a flap-like structure closely applied to the ventral region of the cephalothorax between the bases of the walking legs.

There is every reason to believe that the crabs and their relatives have arisen from primitive Crustaceans having a body divided up into a number of movable segments or somites. Extreme specialisation has taken place, especially in the cephalothoracic region, and it is in the Abdomen that one sees the nearest approach to this primitive external segmentation. A careful examination, however, reveals the fact that there are *five* somites in the cephalic region, *eight* in the thorax and *six* in the abdomen—*nineteen* in all.

Before entering on a description of the more complex parts it will be useful to examine the structure of a typical abdominal somite.

The *third abdominal somite* of the female may be taken as a type (see text fig. 1).

This somite is flattened dorso-ventrally. On the dorsal side there is thick and highly calcified exoskeleton, but the ventral wall is membranous.

The dorsal wall consists of a median portion—the **tergum** (text fig. 1, *t.*)—which is continued into two broad lateral portions—the **pleura.** The median ventral wall is known as the **sternum,** and from each of the outer portions of the sternum arises an appendage. Between the point of attachment of each appendage and the pleuron the ventral wall is known as the **epimeron.**

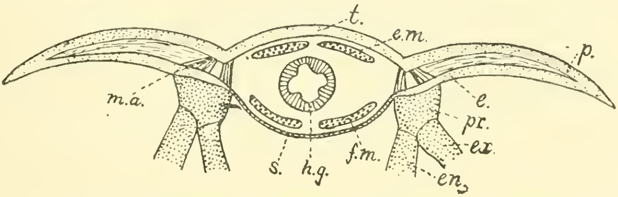


FIG. 1.—Diagrammatic section through female abdomen.

t. = tergum.
p. = pleuron.
s. = sternum.
e. = epimeron.
e.m. = extensor muscles of abdomen.
f.m. = flexor muscles of abdomen.
m.a. = muscles of abdominal appendage.
h.g. = hind gut.
pr. = protopodite.
ex. = exopodite.
en. = endopodite.

The segment is connected with the two neighbouring segments by a thin uncalcified part of the exoskeleton—the **arthrodial membrane.** This allows of free movement between the segments. Each segment articulates with the one in front by means of a pair of hinges placed at the outer and anterior part of the pleuron at each side.

The appendages will be described in detail later.

CEPHALOTHORAX.

1. Carapace.

The terga and pleura of the cephalothorax are fused to form the large Carapace. This is a broad shield the width of which is about 1½ times as great as the length.

Instead of taking an even sweep downwards the carapace passes outwards almost horizontally and then suddenly bends inwards and passes down to the bases of the walking legs. An examination of a rough section of the animal will show that at the base of the legs the carapace turns suddenly upwards and is continuous with the membranous wall of the spacious **Branchial Chamber** (Pl. IV, fig. 56, *br. ch.*). The space between the ventral part of the carapace and the base of the legs is so very small, and moreover is so well guarded by long setae that no water can enter the branchial chamber at this border, as is the case in the Macrura. There are, however, two openings into the branchial chamber—the small *posterior inhalent branchial aperture*, above the coxopodite of the last pereiopod, and the larger *anterior inhalent branchial aperture*, situated immediately in front of the coxopodite of the chela. The ventral part of the carapace turns forward in front of the latter opening, and passing around the mouth it fuses with the pre-oral cephalic sterna. The portion of the carapace which passes around the mouth is turned inwards at each side to form a chamber which lies immediately in front of the Branchial Chamber. This may be called the **Pre-branchial Chamber.** Its roof is membranous and is fused on its inner side with the epistoma and with the endopleurites of the two post-oral cephalic somites, and probably represents the epimera of the third, fourth and fifth cephalic somites. The Pre-branchial Chamber will be described in detail in the section on Respiration.

Both the dorsal and the inflected portions of the lateral region of the carapace were designated the "branchiostegite" by Milne-Edwards because they enclose the branchial cavity.

Anteriorly the dorsal surface of the carapace is bounded by a median portion between the orbits and two lateral portions. Similarly the posterior boundary consists of a median portion and two lateral portions. So that we may speak of these borders as the anterior, antero-lateral, posterior and postero-lateral respectively.

The **Anterior Border** is situated between the orbits. The *rostrum*, which occupies the median portion of this region, consists of a median and two lateral lobes. It is continued ventrally as a median plate which separates the two cavities in which are lodged the eye peduncles. Each of the lateral lobes of the rostrum passes downwards as the *supraciliary lobe*, which fuses with the anterior and inner region of the second antenna (Pl. III, fig. 20, *S.l.*). Passing outwards from the rostrum the anterior border of the carapace divides at each side into the supra-orbital and infra-orbital portions which form the boundary of the orbit. On its inner side the supra-orbital edge has the prominent *supra-orbital lobe* which is close to the lateral lobe of the rostrum. The inner boundary of the orbit is fused with the outer portion of the second antenna.

The **Antero-lateral Borders** form an arc of a circle the centre of which is at the junction of the two outer grooves bounding the epibranchial region of the carapace (see below). Each antero-lateral border is divided up into nine lobes by well-defined ridges. There is no definite distinction between the antero-lateral border and the postero-lateral border, but the latter may be said to commence at the posterior end of the ninth lobe. There is also a feebly marked lobe on the outer portion of the postero-lateral ridge.

The **Postero-lateral Border** passes backwards and inwards. This border is well rounded and not so clearly defined as the anterior and antero-lateral borders.

Immediately in front of this border there is the *postero-lateral ridge*, which is continuous on its outer side with the antero-lateral border. At its outer edge it is coincident with the postero-lateral border, but as it passes inwards it becomes quite distinct from the latter and dies away near the median line in front of the posterior border.

The **Posterior Border** of the carapace is horizontal, and is continuous behind with the tergum of the first abdominal segment.

Areas of the Carapace. (Text fig. 2.)

The dorsal surface of the carapace is divided up by means of small depressions into areas.

The *Cervical groove* (*C. gr.*) separates the cephalic region of the carapace from the thoracic region. This groove is seen as a transverse median depression a little more than half way down the carapace. The width of this median groove is almost equal to the distance between the two supra-orbital lobes.

At each of its outer edges the median groove is continuous with a well-marked depression which commences at the posterior end of the fifth lobe of the antero-lateral border. This depression is curved, the convexity being in front. The median groove and its two lateral extensions together form the cervical groove.

The Cephalic portion of the carapace is divided into the Facial and Gastric regions.

The Facial region is separated from the rest of the cephalon by a faint transverse depression near the front of the carapace. The outer ends of the depression bend forward and terminate on the second lobe of the antero-lateral border. This region is divided into a median **Frontal** region (*Fr.*) and two lateral **Orbital** regions (*Orb.*).

The Gastric region is bounded behind by the

Cervical groove, and is composed of a median triangular portion having the apex pointing backwards and two lateral portions which end at the antero-lateral border. The median portion is divided into two anterior **Protogastric** regions (*Pg.*), a median anterior **Mesogastric** region (*Mg.*), a pair of posterior **Metagastric** regions (*Mtg.*), and a median posterior **Urogastric** region (*Ug.*). The lateral portions are known as the **Hepatic** regions (*Hep.*). Each extends outwards to the antero-lateral border and is bounded behind by the outer part of the cervical groove.

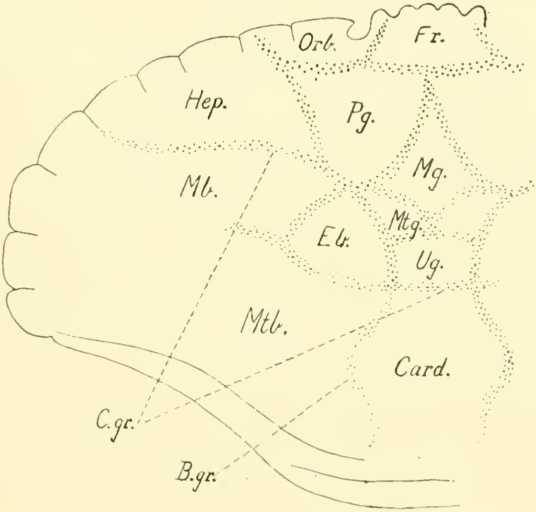


Fig. 2.—Areas of the Carapace.

Fr. = Frontal region.
Orb. = Orbital ,,
Hep. = Hepatic ,,
Pg. = Protogastric ,,
Mg. = Mesogastric ,,
Mtg. = Metagastric ,,
Ug. = Urogastric ,,
Mb. = Mesobranchial region.
Mtb. = Metabranchial ,,
Eb. = Epibranchial ,,
Card. = Cardiac ,,
C.gr. = Cervical groove.
B.gr. = Branchio cardiac groove.

The Thoracic portion comprises that part of the carapace which lies behind the cervical groove. It is divided by two longitudinal grooves—the *Branchio-cardiac grooves* (*B.gr.*)—into a median **Cardiac** region (*Card.*) and two lateral branchial regions. Each branchial region is made up of an anterior **Mesobranchial** region (*Mb.*) and a posterior **Metabranchial** region (*Mtb.*) and a small inner **Epibranchial** region (*Eb.*).

The ventral inflected portion of the carapace is divided into two parts by a well defined groove, which may be termed the *pleural groove*, as it probably marks the separation between the cephalo-thoracic terga and pleura. It is along this groove that the carapace splits during ecdysis (see section on Ecdysis). The pleural groove commences at the epistoma and passes outwards and slightly backwards until it almost reaches the posterior end of the seventh lobe of the antero-lateral border. Here it turns backward and runs parallel to the postero-lateral ridge, finally reaching the posterior border with which it becomes continuous. Thus the pleural groove divides the inflected portion of the carapace into an outer, or **Sub-hepatic** region, and an inner, or **Sub-branchial** region. The sub-hepatic region may be considered as an inflected portion of the tergum, and the sub-branchial as belonging to the pleural region. Milne-Edwards regarded the sub-branchial region as part of the cephalo-thoracic epimera, but the inner walls of the branchial chambers undoubtedly represent the epimera.

2. Pre-oral Cephalo-thoracic Sterna.

(Pl. III, figs. 19, 20.)

Ventrally the median lobe of the rostrum passes backwards as a triangular plate, the apex of which points posteriorly. This plate, which is separated at its posterior end from the first sternum [antennulary sternum] (S^1)

by a well-defined suture, forms a septum* between the articular cavities of the two optic peduncles.

From the dorsal side of the sternal region the septum between the above-mentioned articular cavities is short and broad. On a level with the posterior end of these cavities there is a well-marked suture separating the septum from the first sternum.

Immediately in front of the dorsal side of the ophthalmic articular cavities (*o.m.c.*) are two short calcareous plates near the median line, which stretch across to the roof of the carapace. These are the *Procephalic processes* (*p.e.p.*) to which are attached the anterior gastric muscles.

The **First Sternum** (S^1) lies in the segment of the first antennae (*ant^{le}.*) and separates the articular cavities of these appendages. Owing to the depth of the sternum in this region its relationship to the articular cavities is best seen from the dorsal side of the sternum.

It consists of a median piece lying between the articular cavities of the antennules, and of two lateral expansions which form the posterior boundaries of the articular cavities. Viewed laterally the sternum is seen to have a comparatively great depth. About half way down the anterior face of this sternum is a concavity into which fits a process from the septum between the ophthalmic articular cavities.

From the ventral side the first sternum bounds the posterior and inner sides of the sockets of the antennules, and the lateral prolongations extend as far as the bases of the second antennae.

---

* In the present Memoir the optic peduncles are not regarded as modified appendages, and I shall not regard the region of the body from which the eyes arise as the first segment, nor shall I speak of the septum between the articular cavities of the optic peduncles as the first sternum.

Huxley* in his short account of the crab states that the ophthalmic and antennulary sterna are fused, and that the suture is between the fused sterna and the rostrum. I am of the opinion that the whole of the sternum behind the suture belongs to the antennulary somite alone, and that the septum separating the articular cavities of the optic peduncles is a posterior prolongation of the rostrum, as described above. An examination of the sternum from the dorsal side (Pl. III, fig. 19) shows that the suture is on a level with the posterior boundary of the ophthalmic articular cavity; so that, if Huxley's view be accepted, we have the ophthalmic sternum entirely behind the articular cavity of its own somite! It is much more reasonable to conclude that the suture separates the ophthalmic septum from the antennulary sternum.

The **Epistoma** is a broad plate in front of the mouth and immediately behind the first sternum. It represents the united sterna of the second (antennary) (S^2) and third (mandibular) (S^3) somites. Its anterior border is concave in front. The two lateral borders gradually slope inwards towards their posterior ends. The posterior border is deeply concave behind and bounds the front edge of the mouth.

The middle part of the anterior border touches the posterior edge of the first sternum and the two outer portions bound the posterior edge of the second antenna. The lateral borders are in contact with the membranous roof of the pre-branchial chamber.

From the middle of the anterior border of the ventral side of the epistoma a median groove passes backwards but does not extend as far as the posterior border. From

---

* T. H. Huxley, *Manual of the Anatomy of Invertebrated Animals*, 1877, pp. 340-345.

the posterior edge of this groove a slight depression passes outwards at each side parallel to the anterior border. This depression probably marks the boundary between the antennary and mandibular sterna. This groove is better defined on the dorsal side of the epistoma.

The **Labrum** (Pl. III, fig. 20, *lab.*) is a soft fleshy lobe attached to the middle region of the posterior border of the epistoma. It is surrounded near the middle by a calcareous ring which gives off a median posterior prolongation. At each side of this median plate is a soft fold.

3. Post-oral Cephalo-thoracic Sterna (Pl. I, figs. 2, 3, Text fig. 3).

These are all fused together as a single oval-shaped plate situated between the bases of the paired post-oral cephalothoracic appendages. Transverse grooves are present which mark the division of this region into segments or somites, and which mark the places at which the sterna grow inwards to form the endosternites of the endophragmal system.

The surface of the fused sterna is concave laterally in order to accommodate the abdomen, which is always in a flexed condition. This concavity is especially well marked in the males. The surface of the sterna is, however, convex antero-posteriorly.

On the sternum of fifth thoracic somite are two small tubercles (*P.*) which fit into two concavities on the abdomen and thus form an effective locking apparatus which keeps the abdomen in position. These are especially large in the males.

The sternum of the sixth thoracic somite of the female bears a pair of large openings which are the external genital openings.

The sterna of the last four thoracic somites are characterised by a median groove which marks the place at which the "Median plate" of the endophragmal system has grown inwards. The anterior end of this median groove is marked by a very deep depression which is situated at the posterior end of the fourth thoracic sternum.

At the outer and posterior corners of each sternum are backwardly directed areas—the "episterna" (*Eps.*) which run for a short distance alongside the following sternum, from which they are separated by distinct sutures. Between each episternum and the corresponding sternum is a slight groove which is not very distinct in the edible crab. In Portunus and other crabs, however, this groove is much more distinct so as to suggest a complete separation between the sternum and episternum. This probably explains why Brooks* states

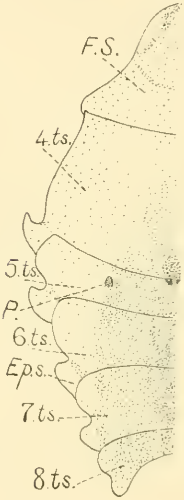


Fig. 3.—Ventral view of post-oral cephalothoracic sterna (male).

F.S. = Fused sterna of the two post-oral cephalic and the first three thoracic somites. *4.ts.*—*8.ts.* = Sterna of the 4th to 8th thoracic somites. *Ep.s.* = Episternum. *P.* = Sternal papilla of the abdominal locking apparatus.

---

* Brooks, *Handbook of Invertebrate Zoology.*

that the episternum is *anterior* to the outer end of its own sternum. He has evidently mistaken the groove mentioned above for a true suture, and has therefore concluded that the episternum belongs to the following sternum. The last thoracic sternum has no episterna.

At the anterior end of each episternum is a small concavity into which fits the ventral hinge of the coxopodite of the appendage of that somite.

The sterna of the last two cephalic and the first four thoracic somites (*F.S.*) are fused together, without any sign of separation into distinct segments as in the posterior region of the thorax.† There is, however, a slight evidence of a division in front of the fourth sternum of the thorax.

That portion of the thoracic sterna which is covered by the abdomen is characterised by the absence of setae. There are long setae along the outer edges of the episterna, and also on that portion of the fused sterna belonging to the two last cephalic segments and the first four thoracic segments.

In front of the fourth thoracic sternum the outer edges of the sterna are turned up vertically.

The first post-oral cephalic sternum has two lateral processes which project forwards and give support to the **Metastoma.** The metastoma is a fleshy lobe forming the posterior lip of the mouth.

4. Cephalic epimera.

In the first two cephalic somites it is difficult to identify the epimera, but the latter are probably represented by the region between the outer portion of the articular cavities of these somites and the carapace.

---

† The two post-oral cephalic sterna, which are represented by two narrow bars at the extreme anterior end of the fused post-oral sterna, are separated from each other, however, by transverse sutures.

The epimera of the third (mandibular) and the two last cephalic somites (maxillary) are probably represented by the membranous roof of the pre-branchial chamber at each side (Pl. III, fig. 18, *r.br.*). This is continuous behind with the thoracic epimera.

5. Thoracic epimera

(Plate III, fig. 18, *epm.* 6-12).

The thoracic epimera are represented by a continuous plate at each side forming the inner wall of the branchial chamber. This is the "flanc" of Milne-Edwards. The lower border of the epimera commences immediately above the base of the thoracic appendages. They pass upwards and inwards and are continuous above with the membranous roof of the branchial chamber. At the posterior end they extend upwards almost to the carapace, from which they are only separated by short muscles which pass from the summit of the epimera to the carapace. At the anterior end the epimera are much shallower and become continuous with the roof of the branchial chamber some distance below the carapace.

The fused thoracic epimera form an extremely convex wall which is divided up into segments by vertical sutures, which correspond to the lines of separation between the various somites of the thorax. In this way the epimera are divided up into seven portions. The epimera of the first and second thoracic somites are completely fused, and there is no groove separating them, but apart from this there is one segment of the fused epimera for each of the remaining thoracic somites. The epimeron of the fourth somite is particularly broad. That of the last thoracic somite is not bounded posteriorly by a groove, but is continuous with the sternum of the same segment.

In their natural position the gills lie upon the thoracic epimera.

THE ABDOMEN.

The abdomen is continuous with the posterior part of the cephalothorax. The connection is effected by means of an arthrodial membrane, which allows of considerable movement between the two regions. The abdomen is small and in its natural position is closely applied to the sternal region of the thorax. This region differs in the two sexes, being much broader in the female than in the male. This character provides a useful and ready method of distinguishing between the two sexes. There are other differences which require a more detailed examination.

Female.

(Pl. I, fig 2, Pl. IV, fig. 32, Pl. V, fig. 34.)

This consists of six somites and the telson, all of which are freely movable. When lying in position it extends as far forward as the posterior end of the sternum of the third thoracic somite. The locking arrangement for keeping the abdomen closely applied to the thoracic sternum is not so well developed as in the male. It consists of two extremely small tubercles on the fifth thoracic sternum which fit into two slight depressions at the postero-lateral corners of the ventral side of the sixth abdominal somite. The total length of the abdomen is $2\frac{1}{2}$ times as much as its greatest width.

There are four pairs of appendages, one pair being borne on the second and on each of the three following somites, respectively.

On the dorsal side of the abdomen the terga are separated from the pleura by two longitudinal grooves. Ventrally the median portion is covered by a thin uncalcified cuticle and the outline of the hind-gut is clearly seen.

The hind-gut opens on the ventral side of the telson at the *anus*.

Only the first somite requires any special comment. The upper side of this somite is prolonged forward as a thin triangular flap, the apex of which points anteriorly. This triangular portion is covered by the carapace, only a narrow region at the posterior end of the somite being exposed. All around the anterior edge of this somite is a thin membrane which is continuous with the posterior region of the cephalothorax.

The first two somites are hollowed out laterally to provide free movement for the last pair of thoracic legs.

Male (Pl. I, fig. 3).

When lying in position the abdomen extends slightly in front of the middle of the fourth thoracic sternum. It is slightly shorter than the female abdomen and much narrower. As in the latter, the sides of the first two somites (and also part of the third) are hollowed out and pass round the inner sides of the last pair of thoracic appendages.

The first somite has the same arrangement as in the female. The anterior part of the dorsal side is triangular and is covered by the carapace.

The third, fourth and fifth somites are fused together so that there is absolutely no movement between them. The sutures marking their separation still persist.

There are only two pairs of appendages which are present on the first and second somites respectively.

These appendages are peculiarly modified to act as copulatory organs (see sections on Appendages and Reproductive System).

The male abdomen is much more closely applied to the thorax than is the case in the female. This is partly due to the small number of appendages and also to the very effective locking apparatus. The latter is similar to that described in the female and the position of the parts is the same, but the tubercles on the thoracic sternum are much larger, as is also the case with the concavities on the sixth abdominal somite.

Below are given the measurements of the abdomen of a male and female, both having a carapace breadth of 23·5 cm.

No. of Somite.	FEMALE.		MALE.	
	Greatest length.	Greatest width.	Greatest length.	Greatest width.
	mm.	mm.	mm.	mm.
1	17	25	17	22
2	8	22	8	17
3	7	30	7	23
4	8	32	8	20
5	10	35	9	17
6	20	35	13	16
Telson	18	21	13	13
	Total length, 88 mm.		Total length, 75 mm.	

External apertures.

The external openings are as follows:—

The **Mouth**—a median aperture on the ventral side of the cephalic region between the mandibles.

The **Anus**—a median aperture on the ventral side of the telson.

The **Excretory Openings** one pair. These are situated at the base of the second antennae on the ventral side. Each is covered by an operculum.

The **Female Reproductive Openings**—one pair. These are two large apertures on the sternum of the sixth thoracic somite.

The **Male Reproductive Openings** one pair. These are situated on the ventral side of the coxopodites of the last pair of thoracic appendages.

Appendages (Plate II).

There are five pairs of appendages on the head and eight pairs on the thorax. There are four pairs of abdominal appendages in the female and only two pairs in the male. The appendages are as follows:—

Cephalon. Somite I.—1st Antennae (Antennules).
,, II.—2nd Antennae.
,, III.—Mandibles.
,, IV.—1st Maxillae.
,, V.—2nd Maxillae.

Thorax. Somite VI.—1st Maxillipedes.
,, VII.—2nd Maxillipedes.
,, VIII.—3rd Maxillipedes.
,, IX.—1st Pereiopods.
,, X.—2nd Pereiopods.
,, XI.—3rd Pereiopods.
,, XII.—4th Pereiopods.
,, XIII.—5th Pereiopods.

		Female.	*Male.*
Abdomen.	Somite XIV.	—Absent.	1st Pleopods.
	,, XV.	—1st Pleopods.	2nd Pleopods.
	,, XVI.	—2nd Pleopods.	Absent.
	,, XVII.	—3rd Pleopods.	Absent.
	,, XVIII.	—4th Pleopods.	Absent.
	,, XIX.	—Absent.	Absent.

The First Antenna or Antennule (Pl. II, fig. 4, Pl. III, fig. 20) is situated in a deep depression on the ventral side of the cephalic sternum (*s.a.*^{1}). This depression or socket is bounded in front by the rostrum (*rost.*), and behind by the lateral expansion of the first sternum (S^1). The outer boundary is formed by the inner edge of the second antenna (*ant.*), and the inner boundary by the median portion of the first sternum. The appendage consists of a broad basal joint, from which is given off on its inner side a two-jointed portion. These three pieces together form the *protopodite* (*prot.*). From the end of the distal segment of the protopodite arise two many-jointed flagella—an inner *endopodite* (*end.*) and an outer *exopodite* (*ex.*). The exopodite is the larger of the two, and bears on its inner side a tuft of long setae. The "olfactory" setae are small setae on the ventral side of the exopodite (see section on Sense Organs).

On the dorsal side of the basal segment of the protopodite is a longitudinal groove covered with long setae. This groove marks the place where the auditory sac opens to the exterior in the young animal. In the adult crab this groove is completely closed, although it remains open a short time after ecdysis.

In their natural position the three parts of the protopodite are folded on one another. The second segment is closely ăpplied to the inner side of the basal segment. The third segment is bent back along the dorsal side of the second, and its distal end lies in an excavation made for its reception in the dorsal wall of the basal segment.

Second Antenna (Pl. II, fig. 5, Pl. III, fig. 20). This consists of a large basal portion (*prot.*) which is fused to the carapace, and a distal flagellum, which consists of two long basal segments and a number of short rings.

arising from the anterior and inner region of the basal portion. At the posterior and outer corner of the large basal segment is the operculum (*op.*), which covers the external excretory opening. This operculum probably represents the *coxopodite* and the larger basal portion the *basipodite*, the two together forming the *protopodite*. The flagellum probably represents the *endopodite*.

The outer edge of the basipodite is fused to the subhepatic region of the carapace. Backward processes from the supraciliary (*S.l.*) and supra-orbital lobes fuse with the anterior end of the basipodite. The inner and posterior corner of this segment is in contact with the lateral portion of the first sternum, and the posterior border of the same segment is in contact with the epistoma.

The Mandible (Pl. II, fig. 6) lies at the side of the mouth. The main portion is an elongated strongly calcified structure which is divided into two parts—an inner part, which projects over the ventral region of the mouth, and acts as the "jaw," and an outer part, the *apophysis* (*apoph.*), to which are attached the tendons of the mandibular muscles. At the outer extremity is the tendon of the external adductor (*t.ex.ad.*). Behind this, attached to a small projection, is the tendon of the external abductor (*t.ex.ab.*). To the posterior and inner side of the apophysis is attached the tendon of the internal adductor (*t.int.ad.*). The internal abductor arises from the apophysis on the inner side of the base of the tendon of the external adductor. There is no tendon for the internal abductor. Anteriorly the mandibular palp (*md. palp.*) arises from the inner side of the apophysis. The mandible is hinged to the epistoma by means of a small projection below the palp. There is no definite hinge posteriorly, but the posterior border of the inner region of the apophysis is attached to the metastoma by means of a somewhat flexible membrane.

The First Maxilla (Pl. II, fig. 7, Pl. IV, fig. 26), which arises immediately behind the mandible, is small and is made up of a *protopodite* and *endopodite*. The exopodite is absent. The protopodite is on the inner side and is composed of two distinct pieces—a narrow proximal *coxopodite* (*C.*) and a larger *basipodite* (*B.*) which is external to the coxopodite. The *endopodite* (*end.*) arises from the outer side of the basipodite, and consists of a broad proximal leaf-like region and a narrower distal region. From the distal extremity of both parts of the protopodite arise fairly strong setae.

The Second Maxilla (Pl. II, fig. 8, Pl. IV, fig. 27) consists of an inner *protopodite*, a median *endopodite* (*end.*) and an outer *exopodite* (*Scaph.*). The protopodite is composed of a *coxopodite* (*C.*) and a *basipodite* (*B.*), each of which is bilobed. The two lobes of the coxopodite are long and slender, and are clearly separated from one another. Those of the basipodite are broader, and the separation between the two lobes is only partial. On the outer side of the basipodite is the small endopodite, which ends in a long narrow process. On the outer side of the endopodite and arising from the basipodite, is the large modified exopodite which is known as the *scaphognathite* (*Scaph.*). This is a broad plate of irregular shape which lies in the pre-branchial chamber. By means of its rapid and complicated movement it bales the water out of the branchial chamber.

In the **First Maxillipede** (Pl. II, fig. 9) the protopodite is on the inner side. The *coxopodite* (*C.*) is small and richly clothed with setae, and the *basipodite* (*B.*) is a long lamella having two rows ot setae on its outer edge. The *endopodite* (*end.*) is between the exopodite and the protopodite. It is membranous, the proximal half being flattened laterally and the distal half dorso-ventrally. The *exopodite* (*ex.*) is long and slender and consists of a long proximal segment, which is as long as the endopodite, and a distal many-jointed flagellum (*flag.*) which in its natural position projects inwards at right angles to the proximal segment. During life this flagellum is exceedingly active. From the outer side of the protopodite arises the long *flabellum* (*flab.*) (or epipodite). This is a long narrow membranous plate which passes back into the branchial chamber above the gills. The proximal portion of the flabellum is broad and leaf-like.

The **Second Maxillipede** (Pl. II, fig. 10) has the exopodite and flabellum in the same position as in the previous appendage. The flabellum (*flab.*), however, is much shorter than that of the first maxillipede, and lies along the upper portion of the thoracic epimera and below the gills. The protopodite is much reduced, but the proximal *coxopodite** (*C.*) and the distal *basipodite* (*B.*) can still be made out. The endopodite is comparatively larger than the same part in the first maxillipede. It arises from the basipodite and is divided into five movable segments. The first or proximal segment—the *ischiopodite* (*I.*) is small. The second segment or *meropodite* (*M.*) is the longest, and equal in length to the other four segments. The three distal segments are small, and between the second and third segment the endopodite turns inwards, the distal segments being at right angles to the meropodite. The names of the third, fourth and fifth segments are *carpopodite* ($C.^1$), *propo-*

---

* The following abbreviations are sometimes used:—*coxa* = coxopodite; *basis* = basipodite; *ischium* = ischiopodite; *meros* = meropodite; *carpos* = carpopodite; *propos* = propodite; *dactylos* = dactylopodite.

dite (*P.*) and *dactylopodite* (*D.*) respectively. Arising from the appendage immediately in front of the base of the flabellum is a *podobranch* (*pod. br.*) (see section on Respiratory Organs).

The **Third Maxillipede** (Pl. II, fig. 11, Pl. IV, fig. 30) is built on a similar plan to the previous appendage. The basis and the ischium are fused together to form the *basi-ischium* (*B.-I.*). The podobranch (*pod. br.*) is very small and arises from the coxopodite. The flabellum (*flab.*) lies on the lower part of the thoracic epimera below the gills. The endopodite and exopodite (*ex.*) are closely applied together and are much flattened so as to form with the same appendage of the other side an effective operculum closing over the remaining mouth parts, and preventing the exhalent current of water from the branchial chamber from passing out except in front of the scaphognathite.

The mandibles, maxillae and maxillipedes all lie around the mouth in the large depression between the anterior parts of the sub-branchial regions of the carapace. The ventral side of the third maxillipedes is on a level with the sub-branchial region. As the flabellum of this appendage passes back into the branchial cavity, it passes along the front of the anterior inhalent branchial aperture, and reduces the size of the aperture considerably. At this point the flabellum* is also richly clothed with strong setae, which probably act as a "strainer" in conjunction with the setae present on the front part of the coxa of the chela (see section on Respiratory Organs).

The **First Pereiopod** (or chela) (Pl. II, fig. 12, Pl. III,

---

* The coxopodite of the third maxillipede is prolonged outwards, and bounds the inner part of the inhalent aperture. The flabellum bounds the outer part. Both are richly clothed with setae on their posterior faces.

fig. 21) is the largest appendage in the body. It consists of seven segments (or podomeres). A comparison with the third maxillipede indicates that the two proximal segments belong to the protopodite, and the remaining five to the endopodite. There is no exopodite present. The seven segments have the same names as the similar parts in the third maxillipede. With the exception of the second and third segments, which are fused together to form the *basi-ischium* (*B-I.*), all the parts are freely movable. The basi-ischium has a thin groove running around it, which marks the separation of this fused portion into its two constituent parts. This groove is known as the *fracture plane* because it is at this point that the animal fractures the limb during the process of self-amputation (see section on Autotomy). The two distal segments of the limb are slightly modified to form the pincer which constitutes an effective prehensile organ.

Each of the movable segments swings in a different plane, so that the combined movement of the whole appendage is a very complete one. The coxopodite (*C.*) articulates with the body by means of two hinges, one being dorsal (Pl. III., fig. 21, *d.*) and the other ventral (*v.*). The dorsal hinge is attached to the antero-ventral corner of the epimeron of the fourth thoracic somite, and the ventral hinge articulates at the postero-lateral corner of the sternum of the same segment. Thus the motion of the coxopodite is in a horizontal plane, moving backward and forward. The fused basi-ischium (*B.-I.*) articulates with the coxa by an antero-dorsal (d^1) and a postero-ventral hinge (v^1), and the movement is upwards and downwards in a plane making an angle of about 45° with the vertical. The meros (*M.*) has very little movement. Its two hinges are antero-dorsal (d^2) and postero-ventral respectively (v^2), and the small degree of movement of which this segment is capable is almost in a vertical plane. The two hinges of the carpos (*C.*^{1}) are situated dorsally (*d*^{3}) and ventrally (*v*^{3}), and the segment moves forward and downward. The propodite (*P.*) has two hinges—dorsal (*d*^{4}) and ventral (*v*^{4}). The former is external to the latter, and the segment moves forward and slightly upward. In the dactylos (*D.*) the hinges are horizontal and the segment swings in a vertical plane.

The dimensions of the various segments of the chela in a female crab (carapace breadth 23·5 cm.) are as follows:—

	Anterior length.	Posterior length.
Coxopodite ...	... 7 mm.	... 11 mm.
Basi-ischiopodite	... 17 ,,	.. 6 ,,
Meropodite ...	... 19 ,,	... 32 ,,
Carpopodite ...	... 10 ,,	... 30 ,,
Propodite ...	... 50 ,,	... 20 ,,
Dactylopodite	... 20 ,,	... 30 ,,

The dorsal sides of the basi-ischium and of the meros are flattened so that they can be closely applied to the anterior portion of the sub-branchial and sub-hepatic regions of the carapace, and in these places setae are absent from the carapace.

Between the meros and the carpos the limb is capable of bending on itself, so that the anterior borders of the propodite and the carpos become closely applied to the anterior borders of the basi-ischium and the meros.

On the dorsal side of the basi-ischium and meros there are irregular grooves. These are the lines of absorption (Pl. II, fig. 12, *abs.*) (see section on Ecdysis).

Pereiopods 2-5 (Pl. II, fig. 13). These are known as the "walking legs." Their essential structure is the same as that of the chela. The one obvious difference is that in all the walking legs the propodite has not an outgrowth which, in conjunction with the dactylos, forms a pincer. In other words, the walking legs terminate in a single claw, and are not chelate.

The three terminal segments are capable of being flexed upon the proximal segments. This flexion is in a vertical plane.

Pleopods (Female) (Pl. II, fig. 17). There are four pairs of appendages on the female abdomen, one pair being situated on each of the second, third, fourth and fifth somites respectively. They are all similar in structure. Each pleopod is attached to the abdomen by a basal piece—the *protopodite* (*prot.*). From this arise two long pieces—an outer *exopodite* (*ex.*) and an inner *endopodite* (*end.*). The exopodite is almost cylindrical in section, and about half as long as the abdomen.

From the outer and inner edges of the exopodite rows of setae arise. Each seta has short fine branches given off from each side of the central stem. The endopodite is about as long as the exopodite. About one-third of its length from the base is a well-defined transverse groove. The setae are arranged, as in the exopodite, along the outer and inner edges, but they arise in small bundles. The setae are very long and do not bear offshoots except near the tip, where there are a few very fine short branches. The eggs are attached to the endopoditic setae.

Pleopods (Male) (Pl. II, figs. 14, 15, 16). There are two pairs of abdominal appendages in the male, which are situated on the first two somites. Both pairs are greatly modified and act as copulatory organs (see section on Reproductive Organs).

First pair (Pl. II, fig. 14). Each consists of two parts—a broad basal portion, probably the *protopodite* (*prot.*), and an elongated distal portion, which is rolled on itself longitudinally to form a tube. This distal portion probably represents the endopodite (*end.*). The two basal portions fuse in the middle line, thus forming a tunnel-like structure extending backward below the second somite. Below the fused basal portions of the first pleopods arise the *second pair* of appendages (Pl. II, fig. 15). Each consists of two parts—a horizontal rod (*prot.*) projecting posteriorly, and a vertical rod (*end.*) attached to the posterior end of the first portion. The vertical rod is divided into two parts by a transverse groove. The horizontal rod probably represents the protopodite, and the vertical portion is the endopodite. There is no trace of an exopodite on any of the male pleopods.

The vertical rod-like portion of the second pleopod fits into the tube of the first pleopod.

ENDOPHRAGMAL SKELETON

(Pl. III, fig. 18, Text figs. 4, 5, 6, 7).

The post-oral region of the cephalothorax has an extremely complex system of internal plates, known as the endophragmal skeleton. Essentially this system may be said to consist of a number of inwardly-projecting plates arranged transversely so as to divide up the interior of the cephalothorax into a series of irregular compartments. Each partition, or arthrophragm, arises at the junction of two somites, and is formed by an infolding of the sternal and epimeral exoskeleton between these somites. Thus, each plate of the endophragmal skeleton is double, and is composed of two flattened plates of exoskeleton which are closely applied together.

The primary function of the endophragmal system is to afford attachment for the muscles of the proximal region of the appendages in this region of the body. It is also useful in supporting and protecting certain portions of the viscera.

Although at first sight the arthrophragms of the first five post-oral cephalothoracic somites differ in a marked degree from those of the posterior thoracic region, it will be shown that all are built on the same plan.

DESCRIPTION OF A TYPICAL ARTHROPHRAGM (Text fig. 4).

The fourth thoracic arthrophragm (between the fourth and fifth thoracic somites) may be taken as a type. It is a vertical partition extending inwards at each side from the line of junction of the fourth and fifth thoracic epimera. The portion of the partition in contact with the thoracic sternum arises between the fourth and fifth thoracic sterna. Thus we may distinguish between two kinds of plates, viz., those growing inwards from the epimera—the **endopleurites** (Pl. III, fig. 18, *ep.*, also Text figs. 4, 5, 7), and those arising from the inner side of the sternum—the **endosternites.** Each arthrophragm consists, therefore, of an outer endopleurite and an inner endosternite at each side of the middle line. The two endosternites in the arthrophragm under discussion are separated from each other in the middle line by the *median plate* (fig. 18, *med. p.*), which is an ingrowth from the median suture present on the last four thoracic sterna. The plates of which the arthrophragm is composed are sometimes known as the "apodemata."

The Endosternite is irregular in shape and has five principal borders.

The *median border* is vertical, and is the part of the endosternite in contact with the median plate.

The *sternal border* (Text fig. 4, *Sb. s.*) is in contact with the sternum, and forms the ventral boundary of the endosternite.

The *articular border* (*Ab. s.*) passes upwards and outwards, and is equal in length to the sternal border. It is connected with the arthrodial membrane in contact with the coxopodites of the fourth and fifth thoracic appendages.

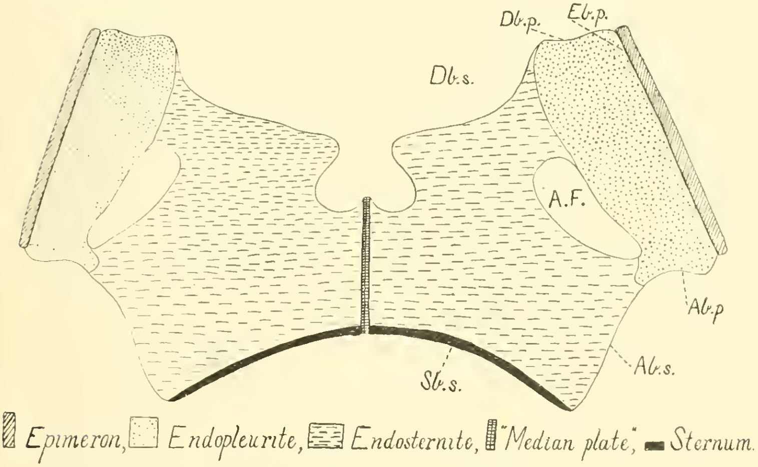


Fig. 4.—Diagram of a typical arthrophragm.

Db.p. = dorsal border of the endopleurite.
Db.s. = dorsal border of the endosternite.
Eb.p. = epimeral border of the endopleurite.
Ab.p. = articular border of the endopleurite.
Ab.s. = articular border of the endosternite.
Sb.s. = sternal border of the endosternite.
A.F. = apodemal foramen.

The *outer border* passes inwards and upwards, and at its upper and lower ends fuses with the endopleurite. This fusion is interrupted in the middle region of the border by the large *apodemal foramen* (*A.F.*) which lies between the endosternite and endopleurite.

The inner part of the *dorsal border* (*Db. s.*) passes upwards and outwards from the median line, describing almost a semi-circle. The upper edge of the semi-circle almost reaches the median line. Thus the inner portion of the dorsal border of each side surrounds an almost closed cavity, which corresponds to the "sternal canal" of the Macrura.

The Endopleurite is rectangular in shape, and its length is about twice as great as its width. Four borders may be distinguished.

The *inner border* is in contact with the outer border of the endosternite at its upper and lower ends. In the intermediate region it forms the outer boundary of the apodemal foramen.

The *articular border* (*Ab. p.*) is in contact with the upper part of the arthrodial membrane connecting the coxopodites of the fourth and fifth thoracic appendages.

The *epimeral border* (*Eb. p.*) is in contact with the fourth and fifth thoracic epimera.

The *dorsal border* (*Db. p.*) bounds the dorsal free end of the endopleurite

Above the apodemal foramen the endopleurite becomes fused on its posterior face with the following arthrophragm, and the anterior face of the arthrophragm under discussion becomes fused with the preceding endopleurite.

All the arthrophragms of the post-oral cephalothoracic region are built on the above plan, that is to say, each somite has one endosternite and one endopleurite at each side. But in some cases the homology is very much disguised.

The last five thoracic arthrophragms are very similar to the one described, but the anterior arthrophragms are extremely reduced. It is, therefore, advisable to describe the endophragmal skeleton in two parts.

(1) The last five thoracic arthrophragms, beginning in front and working backward (posterior thoracic).

(2) The two post-oral cephalic arthrophragms and the first three thoracic arthrophragms, beginning behind and working forward (anterior post-oral).

(1) POSTERIOR THORACIC ENDOPHRAGMAL SYSTEM (Pl. III, fig. 18, and text, fig. 5).

This consists of the arthrophragms of the last five thoracic somites

The *median plate* commences at the posterior end of the fourth thoracic sternum. At first it is extremely shallow, but as it proceeds posteriorly it increases in height. It is present in the last four thoracic somites.

As in other parts of the endophragmal system, the median plate is composed of two closely applied portions of the exoskeleton. In the fifth thoracic somite these two parts remain separate, and the cavity between them opens to the exterior at the posterior end of the fourth thoracic sternum.

Each endosternite is at right angles to that part of the sternum from which it arises, and similarly each endopleurite arises at right angles to the epimeron. If the sternum were horizontal throughout its entire length, and also if the epimeral wall at each side were vertical, the endophragmal system would be represented by a series of vertical partitions arranged one behind the other. This is the case in the Macrura. In the Brachyura, however, neither the sterna nor epimera follow this arrangement. The thoracic sternum is extremely convex antero-posteriorly and has an extreme upward tilt at its posterior end. The epimeral wall, instead of having a flat surface, is extremely convex on its outer face. The shape of the sternum and of the epimeral wall gives rise to much complexity in the endophragmal system of the last five thoracic somites. The endosternite and the endopleurite of the same arthrophragm instead of being in the same plane, as in the Macrura, may be situated at a considerable angle to each other, so that it is difficult to believe that they belong to the same segment. The fifth endosternite is almost vertical, but the succeeding endosternites incline more and more forward until the last arthrophragm is practically horizontal.

The endopleurites of each arthrophragm become fused with the anterior face of the following arthrophragm, and thus we have each somite divided into four chambers. There is an outer chamber at each side lying between two consecutive endopleurites, and bounded on the outer side by the epimeron and on the inner side by the backward growth of the endopleurite. These chambers may be called the *Pleural muscle chambers* (Text fig. 6, *P.*).

There is also an inner chamber at each side, lying between two consecutive endosternites, and separated from one another by the median plate. We designate these the *Sternal muscle chambers* (Text fig. 6, *S.*).

These pleural and sternal muscle chambers contain the muscles which work the two basal segments of the appendages in this region.

The muscle chamber of the last walking leg is not divided into parts owing to the absence of a separate endopleurite in this somite. Therefore this last muscle chamber may be known as the *Pleuro-Sternal muscle chamber* (Text fig 6, *PS.*). Each of these chambers has an antero-lateral prolongation, which extends forward as far as the posterior face of the fourth thoracic arthrophragm.

The **fourth thoracic arthrophragm** (Text fig. 5, *A.*) arises between the fourth and fifth thoracic somites. This arthrophragm has already been described.

The **fifth thoracic arthrophragm** (Text fig. 5, *B.*) arises between the fifth and sixth thoracic somites. All the parts are very similar to those described in the fourth arthrophragm. The sternal border is slightly more arched. The apodemal foramen is not quite so large. There is an additional cavity left in the dorsal side of the endosternite at each side (*m.*) This is formed by the

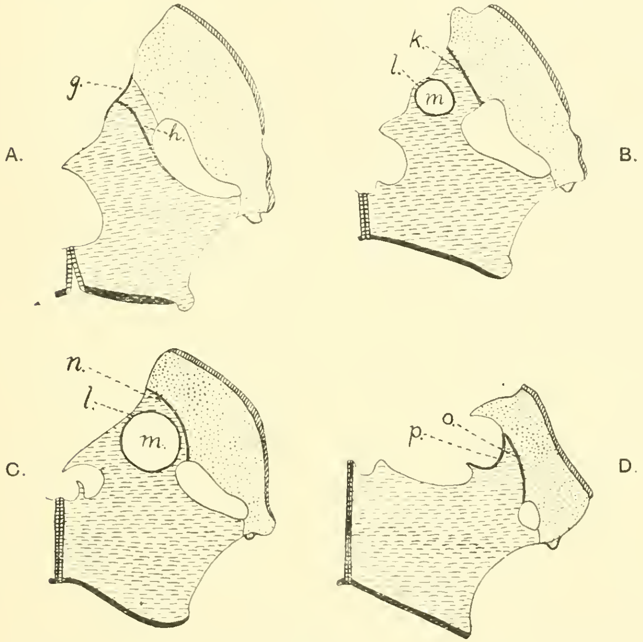


Fig. 5.—Anterior view of the left side of thoracic arthrophragms.

A. = 4th thoracic arthrophragm. B. = 5th thoracic arthrophragm.
C. = 6th thoracic arthrophragm. D. = 7th thoracic arthrophragm.
(The parts are shaded as in Fig. 4).
g. = line of fusion with the following arthrophragm.
h. = line of fusion with the 3rd thoracic endopleurite.
k. = line of fusion with the 4th thoracic endopleurite.
l. = line of fusion with posterior face of the preceding thoracic endosternite.
m. = antero-lateral extension of pleuro-sternal muscle chamber.
n. = line of fusion with the 5th thoracic endopleurite.
o. = line of fusion with the 6th thoracic endopleurite.
p. = line of fusion with the 6th thoracic endosternite.

anterior prolongation of the last pleuro-sternal muscle chamber.

The endosternite is almost vertical, but there is a slight forward tilt. The endopleurite is slightly concave on its anterior face, and its plane is slightly posterior to that of the endosternite. The border of the endosternite surrounding the sternal canal has a slight notch. Around the foramen of the pleuro-sternal muscle chamber the endosternite of this arthrophragm fuses in front with the fourth endosternite (*l.*) and posteriorly with the sixth endosternite. Similarly along the outer border of the endosternite, above the apodemal foramen, this arthrophragm is fused in front with the fourth endopleurite (*k*) and behind with the sixth endopleurite.

The **sixth thoracic arthrophragm** (Text fig. 5, *C.*) arises between the sixth and seventh thoracic somites.

The endosternite is convex on its anterior face, and its plane is inclined considerably forward. Its median border is longer than in the previous arthrophragms. The notch in the sternal canal is much more pronounced than in the fifth arthrophragm. The upper border of the sternal canal is bent posteriorly, and its inner tip becomes fused with the upper edge of the median plate in the last somite. The dorsal border is fused with the anterior (or dorsal) edge of the last arthrophragm. In this way the seventh endosternite is completely roofed over and cannot be seen clearly until the sixth endosternite is removed. As in the previous arthrophragm, there is a large foramen in the dorsal region of the endosternite through which the pleuro-sternal muscle chamber passes (*m.*).

The endopleurite is very similar to that of the fourth arthrophragm. At the junction of the endosternite and endopleurite this arthrophragm fuses in front with the fifth endopleurite (*n.*), and behind with the seventh endopleurite. Also at the edge of the foramen bounding the pleuro-sternal muscle chamber this endosternite is fused in front to the fifth and behind to the seventh endosternite (*l.*).

The **seventh thoracic arthrophragm** (Text fig. 5, *D.*) lies between the seventh and eighth thoracic somites.

The endosternite is inclined at an angle of 50° to the vertical, the upper border being anterior. It is almost completely covered by the overhanging sixth endosternite. The median border is very deep and the sternal canal is very small. The dorsal border is almost level, and partly bounds the ventral side of the pleuro-sternal muscle chamber. The endosternite does not completely surround this chamber as in the two previous arthrophragms. The sternal border is inclined at a considerable angle to the horizontal. The apodemal foramen is small.

The plane of the endopleurite is almost at right angles to that of the endosternite. At the junction of the endosternite and endopleurite this arthrophragm fuses in front with the sixth endopleurite (*o.*), and where the endosternite borders the pleuro-sternal muscle chamber there is a fusion with the sixth endosternite (*p.*).

The **eighth thoracic arthrophragm** (Pl. III, fig. 18, *e. st.* 13) lies at the posterior end of the last thoracic somite. In this somite there is no separate epimeron. It is probably fused with the sternum. The arthrophragm, therefore, shows no division into endosternite and endopleurite. It may be accepted, however, that this arthrophragm represents the fused endosternite and endopleurite. It consists of two halves, which are separated in the median line by the posterior end of the median plate. This arthrophragm is practically horizontal, and was designated the "sella turcica" by Milne-Edwards. As already stated, the last arthrophragm fuses in front with the dorsal border of the sixth endosternite. Between this arthrophragm and the seventh endopleurite there is a large foramen.

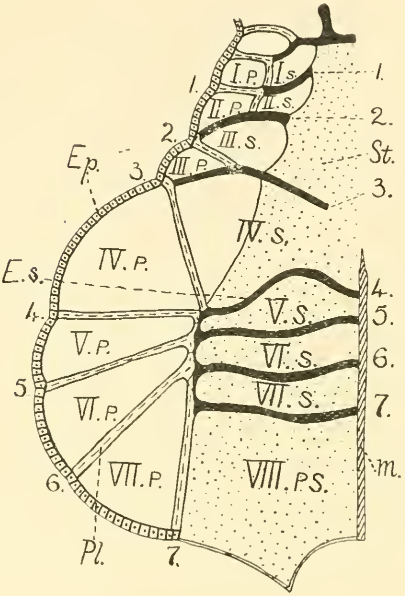


FIG. 6—Diagrammatic plan of the endophragmal system to show the muscle chambers. (The corresponding parts are shaded similarly throughout).

1—7 = thoracic arthrophragms 1 to 7.
I.P. — *VII.P.* = pleural muscle chambers of thoracic somites 1—7.
I.S. — *VII.S.* = sternal muscle chambers of thoracic somites 1—7.
VIII.P.S. = pleuro-sternal muscle chambers of last thoracic somite.
Ep. = epimeron.
E.s. = endosternite.
Pl. = endopleurite.
St. = sternum.
m. = median plate.

(2) ANTERIOR POST-ORAL ENDOPHRAGMAL SYSTEM

(Text fig. 7).

This consists of the last three thoracic and the two post-oral cephalic arthrophragms.

The nature of the epimera and sterna in this region naturally decides the form and extent of the corresponding arthrophragms.

The apparently great differences between the endophragmal system of this region and that of the posterior thoracic somites is due to three main causes.

(1) There is no median plate. This only begins at the level of the fourth thoracic arthrophragm.

(2) The post-oral sterna anterior to the fourth thoracic arthrophragm are all fused together. Consequently there can be no broad plate-like endosternites formed as in growths between the somites. The small endosternite present in each somite of this region is rod-like, and represents merely the articular border of the typical endosternite. (The third thoracic endosternite has the form of a fairly broad and deep plate, and is therefore an exception to this rule.)

(3) The epimera in front of the second thoracic arthrophragm are fused together, so that the endopleurite in these somites are extremely reduced and represent only the articular border of the typical endopleurite.

Here, as in the posterior thoracic region, each endopleurite gives off a posterior out-growth, which fuses with the following arthrophragm. So that pleural muscle chambers and sternal muscle chambers may be made out, but owing to the rod-like nature of their constituent parts, they have a very different appearance from the muscle chambers of the posterior somites of the thorax (see Text fig. 6, also Pl. III, fig. 18).

The **third thoracic arthrophragm** (Text fig. 7, *E.*) arises between the third and fourth thoracic somites.

Each endosternite (Pl. III, fig. 18, *e.st.*8) differs from that of the typical arthrophragm described above. It arises merely from the outer edge of the sternum, so that the two endosternites are separated from each other by the entire width of the sternum in this region. The endosternite is a broad and deep plate facing downwards and backwards. The dorsal and inner corner is prolonged inwards and backwards and almost meets the similar part from the other side.

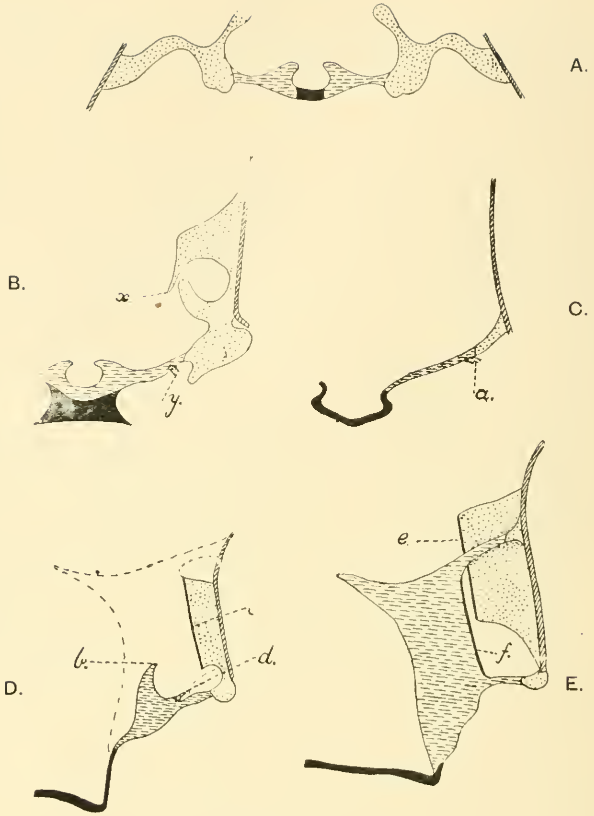


Fig. 7.

A. = anterior view of 1st post-oral cephalic arthrophragm.
B.—*E.* = anterior views of the left side of the following arthrophragm.
B. = 2nd post-oral cephalic arthrophragm.
C. = 1st thoracic arthrophragm.
D. = 2nd thoracic arthrophragm. *E.* = 3rd thoracic arthrophragm.
(The parts are shaded as in Fig. 4).
a. = junction of 2nd cephalic endopleurite with 1st thoracic endosternite.
b. = point of fusion between 2nd thoracic endosternite and 2nd cephalic endopleurite.
c. = line of fusion between 2nd thoracic endopleurite and 3rd thoracic endosternite.
d. = point of fusion with the 1st thoracic endopleurite.
e. = line of fusion between 3rd thoracic endopleurite and the 4th thoracic endosternite.
f. = line of fusion between 3rd thoracic endosternite and the 2nd thoracic endopleurite.
x. = point of fusion between the 2nd cephalic endopleurite and the 2nd thoracic endosternite.
y. = point of fusion with 1st cephalic endopleurite.
(The dotted line in Fig. D represents the 3rd thoracic endosternite.)

On its anterior face the endosternite is connected with the narrow plate-like second thoracic endopleurite (*f.*). Near the point of junction of these two plates the dorsal and articular borders are prolonged backwards as rod-shaped pieces, each of which comes into contact with anterior rod-like outgrowths from the corresponding borders of the third thoracic endopleurite.

The endopleurite arises betwen the third and fourth epimera. It gives off two short anterior rod-like prolongations from the dorsal and articular borders which fuse with the rod-like extensions of the endosternite mentioned above. The main part of the endopleurite, however, consists of a broad plate, which passes backwards and fuses with the fourth thoracic arthrophragm (*e.*).

Second thoracic arthrophragm (Text fig. 7, *D.*). The endosternite is much more reduced than that of the third thoracic arthrophragm. It arises from the upturned edge of the sternum in this somite, and has a very irregular shape. Its inner portion passes upwards, and fuses with a narrow membranous process projecting downwards from the last cephalic endopleurite (*b.*).

The articular border is prolonged outwards as a rod-like process, which fuses with the extremely small articular border of the endopleurite of the same arthrophragm. About half way along the articular border the endosternite fuses with a posterior rod-like extension of the first thoracic endopleurite (*d.*).

The endopleurite of this arthrophragm is a deep narrow plate arising at the junction of the second and third thoracic epimera. From its lower end it sends forward a short process which fuses with the outer part of the endosternite. The main part of the endopleurite passes backwards and becomes fused with the third thoracic endosternite (*C.*), as described above.

First thoracic arthrophragm (Text fig. 7, *C.*). The endosternite arises from the upturned edge of the sternum. It consists of a simple rod which passes backwards, upwards and outwards parallel to the articular border of the second thoracic endosternite. It fuses with the endopleurite of the same arthrophragm, but immediately before doing so it comes into contact, on its anterior side, with a posterior prolongation from the last cephalic endopleurite (*a.*).

The epimera of the first and second thoracic somites are fused together, and the endopleurite of this arthrophragm arises from the ventral edge of the fused epimera immediately in front of the origin of the second thoracic endopleurite. It is rod-like, and passes forwards and inwards in precisely the same plane as the first thoracic endosternite, with which it fuses. Near its fusion with the latter, the endopleurite gives rise to a posterior process which fuses with the second thoracic endosternite.

Last cephalic arthrophragm (Text fig. 7, *B.*). The endosternites of the two post-oral cephalic arthrophragms are fused together, but there is a distinct longitudinal suture present, which assists in the identification of the two parts.* The fused endosternites pass outwards and backwards parallel to the first thoracic endosternite. After a short distance the last cephalic endosternite becomes distinct from the anterior endosternite, and at the point of separation a prolongation from the first cephalic endopleurite fuses with the endosternites (*y.*). From this point the posterior endosternite passes outwards and fuses with the lower border of the last cephalic endopleurite.

The last cephalic endopleurite is an irregular

---

* There is also a well-marked groove separating the sternum of these two cephalic somites.

membranous plate divided into a dorsal and a ventral portion. The dorsal portion has on its inner side a downwardly projecting process which fuses with the upper part of the second thoracic endosternite (*x.*) as described above. The ventral portion of the endopleurite has an upper crescent-shaped region and a lower part which fuses with the endosternite.

From the posterior side of the lower portion of the endopleurite is given off a rod-like process which fuses with the first thoracic endosternite.

First post-oral cephalic arthrophragm (Text fig. 7, *A.*). In addition to the portion fused with the last cephalic endosternite, the endosternite of the above arthrophragm has an anterior process at each side which form the skeleton of the metastoma (Pl. III, fig. 18, *met.*) or posterior lip of the mouth.

The endopleurite arises from the soft membranous epimeron immediately behind the insertion of the external abductor muscle of the mandible. It passes backwards and gives rise to a small upwardly directed process, and afterwards becomes joined to the fused endosternites.

INTEGUMENT (Text fig. 8).

The crab is covered by a continuous chitinous exoskeleton, which serves partly as a protective covering and also as a means of attachment for the muscles. The main portion of this exoskeleton is strongly calcified. Between the movable somites of the abdomen, however, and also between the articulating segments of the appendages, the exoskeleton remains uncalcified in order to allow of free movement, and has the appearance of a thin chitinous membrane. known as the "arthrodial membrane."

The exoskeleton of the ventral region of the abdomen is but feebly calcified. The outer walls, the floor and roof of the branchial chamber and the roof of the pre-branchial chamber are also extremely thin and membranous. The chitinous linings of the fore-gut and hind-gut, which are continuous with the exoskeleton, are uncalcified, except in those regions of the fore-gut where the ossicles are present. The gills, also, are covered by an extremely fine chitinous layer.

The integument of the crab consists of an epidermis, below which lies the dermis. On the outer side of the epidermis is a chitinous layer, the thickness of which differs considerably in various parts of the body. This outer chitinous layer is a product of the epidermis, and constitutes the exoskeleton already referred to. The chitinous layer may be impregnated with calcareous salts.

The **epidermis** [Chitogenous epithelium, Vitzou*] (Text fig. 8, *e.*) consists of a single row of columnar cells resting upon a *basement membrane* (*f.*). These cells differ in their appearance in various parts of the body, and also show marked changes during the interval between one act of ecdysis and the next. In the dorsal integument of the hard crab, for example, the cells of the epidermis are only moderately columnar, but in the oesophagus of the same animal the cells are extremely elongated. In the soft crabs the cells are of much greater length comparatively than in the hard crabs.

In some regions where we have two parts of the integument coming close together, such as at the edge of the carapace and also the gill lamellae, the cells of the epidermis sometimes become extremely elongated and pass across the dermis to fuse with similar cells from the

---

* Vitzou, A. N. "Recherches sur la structure et la formation des téguments chez les Crustacés Décapodes." *Arch. de Zoologie expér. et gén.*, T. X. [1882], p. 451.

epidermis of the opposite side. Vitzou has termed such cells " colonnades de soutien."

The cells of the epidermis are also elongated at the point where the muscle fibres arise.

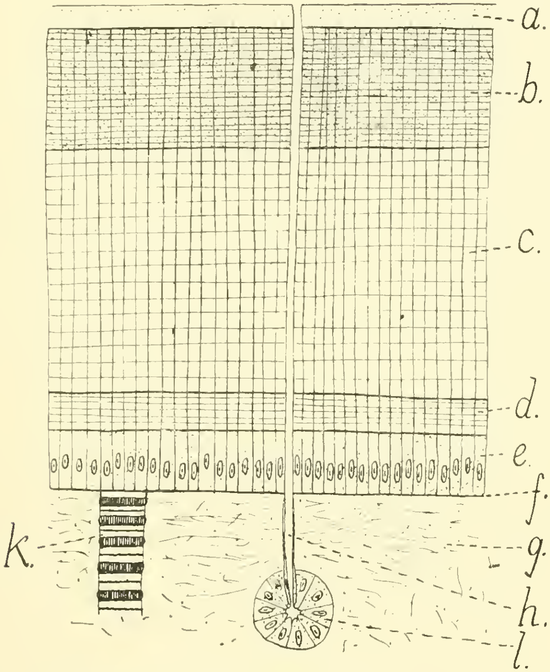


FIG. 8.—Diagrammatic section through the integument of a hard crab.

a. = cuticle.
b. = pigmented layer.
c. = calcified layer.
d = non-calcified layer.
e. = epidermis.
f. = basement membrane.
g. = dermis.
h. = duct of the cutaneous gland.
k. = muscle attached to the basement membrane.
l. = cutaneous gland

The **dermis** (*g.*) lies below the basement membrane, and varies in thickness. It consists mainly of a network of connective tissue fibres and scattered cells. There is a layer of pigment cells close to the basement membrane.

As pointed out by Cuénot,* there are two kinds of cells present in the connective tissue which contain reserve material. These are the "cellules de Leydig" and the "cellules protéiques." The former contain glycogen, and are present in great numbers, especially when the period of ecdysis approaches. The latter are also present in great abundance, and contain proteid material.

The cutaneous glands are also embedded in the dermis. The muscle fibres stretch across the dermis, and are attached to the inner side of the basement membrane. The muscles when dissected appear to be attached to the exoskeleton, but an examination of sections reveals the fact that they do not extend farther than the basement membrane.

The **chitinous layer** of the integument is situated on the outer side of the epidermis, and consists of several layers. Commencing from the outside, these are as follows:—

(1) The *cuticle* (Text fig. 8, *a.*) is an extremely thin structureless layer covering the whole of the chitinous exoskeleton. Its continuity is interrupted at intervals where the ducts of the cutaneous glands open to the exterior. From the cuticle there arise numerous small papillae, which are only seen when examined under the microscope. These must not be confused with the setae, which are visible to the naked eye and which have an entirely different structure (see below).

(2) The *pigmented layer* (*b.*) is a moderately-thick layer containing pigment. In the hard parts of the exoskeleton this layer is calcified. It has a laminated structure, and the numerous layers of which this portion of the exoskeleton is composed are parallel to the surface.

(3) The *calcified layer* (*c.*) is the broadest layer of all

---

* Cuénot, L. "Études physiologiques sur les Crustacés Décapodes." *Archives de Biologie*, T. XIII, p. 245.

in the fully-formed exoskeleton. It is colourless and richly impregnated with calcareous salts. Like the previous layer, it exhibits striations parallel to the surface, but the laminae are generally broader than in the pigmented layer. It is to this layer that the great thickness and hardness of the shell in a hard crab are due, as new laminae are constantly being added to this region until the exoskeleton attains its maximum thickness.

(4) The *non-calcified layer* (*d.*) is a very thin layer composed of delicate laminae parallel to the surface. This layer remains in a very soft condition, and is not formed until the calcified layer has attained its maximum width.

Vertical sections through the integument reveal the fact that there are striations in the chitin at right angles to the surface, as well as the horizontal lamellae already referred to. Also, as Vitzou has pointed out, in horizontal sections the chitinous integument is divided up into small hexagonal areas, and in each of these areas small pores are present. Vitzou determined that these areas were of the same size and shape as the horizontal sections through the cells of the epidermis. He concluded, therefore, that the exoskeleton is composed of innumerable hexagonal prisms packed side by side, having their long axes at right angles to the surface of the body. Furthermore, each of these chitinous prisms is in contact with the outer end of an epidermal cell. So that for every cell of the epidermis there is a corresponding prism forming a unit of the chitinous exoskeleton. Such an explanation accounts for the presence of the vertical striations in vertical sections, and for the polygonal areas in the horizontal sections. The small pores in the middle of these areas are due to the presence of numerous fine canals traversing each prism from the epidermis to the exterior.

Mode of Formation of the Exoskeleton.

Originally the exoskeleton was believed to be produced by a secretion from the cells of the epidermis. Vitzou, however, claimed that the process is effected in a different manner. According to him the new shell is produced in the following way. The contents of each epidermal cell becomes modified at the outer margin. This outer part becomes cut off from the rest of the cell. Thus at this stage the epidermis is covered by a thin layer, which, however is not one homogeneous whole, but is divided up into numerous polygonal areas, each area corresponding in shape and position to an epidermal cell. The process is repeated; the outer part of each cell is again cut off, and at this stage we have a two-layered polygonal cylinder above each cell. This process is repeated until we have built up over each cell a multilayered cylinder. Since the cells of the epidermis lie close together, the chitinous cylinders are also tightly packed and form what appears to be a continuous exoskeleton. The striations parallel to the surface of the integument represent the successive lines of growth. Thus, according to Vitzou, the process of formation of the chitinous integument consists in the successive thickening of the outer walls of the epidermal cells.

Setae.

These are long hair-like processes which project from the exoskeleton in various regions of the body. In sections each seta is seen to arise from the region of the epidermis as a narrow tube enclosing a cavity. This tube passes through the chitinous layers and projects from the exterior as a long narrow process. Its walls are cuticular and are continuous with the thin structureless cuticle covering the chitinous integument. So that wherever a seta arises the continuity of the thick exoskeleton is broken in order to allow this tube-like prolongation to reach the exterior. The contents of the setae are protoplasmic and are connected with the epidermis. In some regions of the body the setae have nerve fibres passing to their interior. These are the *sensory setae*, of which there are several kinds (see section on Sense Organs). The setae may be simple prolongations, or they may consist of a central axis, from which arise off-shoots. In the latter case the cavity of the central axis is not continued into the lateral out-growths. In addition to the setae described above, there are small papillae on the surface of the shell, which are merely thickenings of the cuticle and do not contain a cavity. Vitzou states that in Portunus these cuticular processes are comparatively long. In Cancer, however, they are extremely small, and can only be detected under the microscope. Vitzou affirms that the long "setae," present in the walls of the fore-gut, have no central cavity, and are probably merely extremely large cuticular prolongations and not true setae. These "setae" in the fore-gut act as strainers. Where the sub-branchial region of the carapace is closely applied to the bases of the thoracic legs there is a rich growth of setae. These probably assist in preventing the water from entering the branchial chamber at the base of the thoracic legs.

The inhalent branchial opening is also well guarded by long setae, both on the flabellum of the third maxillipede and on the anterior border of the coxopodite of the chela. The setae on the endopodites of the pleopods in the female are used for the attachment of the eggs.

Cutaneous (or tegumentary) glands.

Scattered throughout the connective tissue, near the basement membrane, are globular masses of cells, each cellular clump being connected with the exterior by a fine duct. These are the cutaneous glands. Each cell of the globular mass is in contact with a small cavity on its inner side. This central cavity of the glandular mass receives the secretion from the various cells. The cavity is connected with the duct, and thus the glandular secretion is enabled to pass to the exterior. The duct is lined by a fine protoplasmic wall. The wall of the duct probably represents a single cell, in which case the cavity of the duct is intracellular. The gland cells and the duct cell are all modified epidermal cells.

The cutaneous glands are scattered throughout the integument, and in some regions are extraordinarily abundant. The glands present in the mandibles and in the walls of the oesophagus, and also those in the hindgut, have a similar structure to the ordinary glands on the surface of the body. They are, in fact, modified cutaneous tegumentary glands.

Immediately in front of the mouth there is a compact mass of cutaneous glands at each side, which open on the surface of the epistoma. These glands have the structure of the typical cutaneous glands, but are extremely large. They are about four times as large as those present in the walls of the oesophagus (see section on Alimentary Canal). Similar glands are found also in the metastoma, packed very closely together. Herrick* has also observed them in the same regions in the lobster. (See fig. 60.)

In the floor of the branchial chamber there is a well-defined transverse ridge lying in front of the inhalent

---

* Herrick. "The American Lobster." *Bull. U.S. Fish Com.*, Vol. XV., 1895.

branchial aperture. The epidermis in this region presents a very interesting condition, and there appear to be numerous modified cutaneous glands.

There are also great numbers of cutaneous glands present on the endopodites of all the maxillipedes.

On the endopodites of the pleopods of the female there are closely-packed tegumentary glands. According to Herrick, these secrete the cement which attaches the eggs to the endopodites of the abdominal appendages.

The function of the various tegumentary glands in various parts of the body is not clearly known. Lang* states that some have an excretory function. There is little doubt that the functions of these glands differ in various regions of the body. Those, for example, on the pleopods are extremely specialised. It is not inconceivable that the glands in the integument of the epistoma and metastoma may produce a secretion which is poured on the food as it enters the mouth.

The glands in the walls of the oesophagus are probably salivary glands. Herrick thinks that this explanation of their function no longer holds good, since glands of similar structure have been found in the walls of the hind-gut. This argument, however, does not carry much weight, if we recognise that *all* the tegumentary glands (both on the surface and in the walls of the alimentary canal) have the same essential structure, and yet are capable of performing different functions in various regions of the body.

ECDYSIS.

The epidermis of all Arthropods is covered by a continuous layer of chitinous integument, which may become calcified in certain regions. This outer integu-

---

* Lang. *Text-book of Comparative Anatomy*, Part I.

ment is continuous with the chitinous lining of the fore-gut and hind-gut. The body, therefore, may be said to be enclosed in an inflexible coat, which prevents the tissues from expanding. The growth of the animal cannot be gradual, but can only take place when the animal breaks through the stiff outer covering. Immediately after exuviation, the animal, which is then only covered by an extremely thin flexible membrane, will increase in size. This process of casting, or **ecdysis,** is characteristic of all Arthropods. Ecdysis takes place periodically, and growth can only take place while the animal is in a "soft" condition.

In Cancer, when ecdysis is about to take place, the carapace opens along the pleural groove at each side. These two longitudinal splits become connected posteriorly with a transverse opening, which makes its appearance between the posterior border of the carapace and the tergum of the first abdominal somite. Thus the tergal region of the carapace is free from the remainder of the exoskeleton, except along a line marking the posterior boundary of the first cephalic sternum. The carapace, therefore, acts like a lid of a box, and is hinged anteriorly. The first part of the body to be withdrawn from the old shell is the abdomen, which is followed by the various legs. When all the parts are completely free the crab emerges from beneath the hinged carapace.

On the dorsal sides of the basi-ischium and meros of the chela there are faint grooves (Pl. II, fig. 12, *abs.*). These are the "lines of absorption," and at the time of ecdysis the exoskeleton of the chela loses its calcification at these points. In this way the withdrawal of the large claw is effected, as it would be extremely difficult for the chela to be withdrawn if the integument at the base of the limb remained hard.

As pointed out by Vitzou,* the method of ecdysis in the Macrura differs from that found in the Brachyura, because in the latter the abdomen is withdrawn first. In the Macrura the thorax is first withdrawn, and the abdomen leaves the old shell last.

The tissues of the animal become greatly changed immediately before ecdysis. The blood increases enormously in volume, and Witten† suggested that the increase is due to the absorption of water by means of the digestive gland. He presumed that this excess of blood plasma produced the internal pressure necessary for ecdysis and growth. The muscles become very soft and semi-fluid, and the fibres lose their well-defined outlines and cross-striations.

The digestive gland probably increases in size during ecdysis. The fat cells are stocked with glycogen, the ferment cells are much bigger, and the colour of the ferment vesicle is of a deep brown colour, thus giving the digestive gland a deeper colour at this period. The reproductive organs are generally in an immature condition at the time of ecdysis.

Immediately before and after ecdysis the crabs are unfit for food. They are "watery" and have a bitter taste. Reference is made in the Economic section to the "Granny" crabs, which are considered by the fishermen to be diseased crabs. I have reason to believe that they are merely crabs preparing for ecdysis.

One of the most interesting changes which accompany ecdysis is probably the formation of the new integument, as a result of the extreme activity of the epidermal cells. This new exoskeleton is already formed when the hard shell is discarded.

---

* Vitzou. *Arch. zool. exp. et gén.*, T. X, 1882.

† *Report on the Scientific Investigations, Northumberland Sea-Fisheries Committee*, 1903.

Before ecdysis the cells of the epidermis become greatly elongated, and in the underlying dermis the cells of Leydig, which are rich in glycogen, become extremely numerous. The supply of reserve food material in these cells is evidently of the utmost importance at a time when growth and regeneration of the tissues is taking place. At the time when the crab is preparing to cast, a new chitinous layer is formed by the epidermis. This new layer is separated from the old shell by a gelatinous fluid. The chitinous layer, which is the first appearance of the new exoskeleton, consists of two parts--an outer structureless cuticular layer, and an inner chitinous layer containing pigment. This inner layer represents the pigmented layer. The calcified and non-calcified layers are not produced until after ecdysis. The calcified layer grows throughout the greater part of the period until the next ecdysis, and it is to this layer that the hardness and increasing thickness of the shell is due.

Vitzou's theory explaining the method of formation of the exoskeleton has been described above (see section on Integument).

The frequency of casting and other problems connected with ecdysis are discussed below in the section on Economics.

Autotomy and Regeneration of Limbs.

One of the most interesting and characteristic features in the natural history of the crab is the power the animal possesses of throwing off injured limbs (**autotomy**) and of forming new limbs to replace the old (**regeneration**).

The processes associated with these phenomena may be briefly stated as follows:—

If the distal portion of one of the pereiopods be seriously injured, the crab immediately throws off part of the limb. The whole limb is not sacrificed. The self-amputation always takes place along the thin groove present on the basi-ischium representing the line of separation between the basipodite and ischiopodite. This groove, therefore, may be said to surround the **fracture plane** (Pl. II, fig. 12, *f.p.*).

When autotomy has been effected, the fracture plane is seen to be covered by a thin membrane, or **diaphragm,** which is perforated, slightly below the centre, by a small foramen. The blood flows out through this small opening, but soon coagulates, forming a clot over the mouth of the foramen and also on the outer surface of the diaphragm.

The diaphragm with its outer coating of coagulated blood assumes a dark brown colour in a few days, and ultimately becomes quite black. This black coating is worn away in course of time, and reveals a thin membrane extending across the stump.

Beneath the membrane a small papilla makes its appearance, and marks the commencement of the regeneration of the limb.*

Conditions necessary for Autotomy.

The successful performance of self-amputation in Cancer depends upon several conditions, of which the most important are discussed below.

1. *The crab must be healthy.*

This is a most important factor. Animals which are in a diseased or weak condition, or which have been kept out of water for a considerable time, and in which, as a

---

* According to Williamson, the regeneration only takes place when the crab is preparing for ecdysis. The limb does not attain its full size at the first moult after regeneration. Two or three moulting processes must take place before the limb attains its normal size.

consequence, the nerve responses are feeble, do not perform autotomy very readily.

2. *The nerve of the limb must be sufficiently stimulated.*

This appears to be a self-evident proposition. Whatever may be the cause of autotomy, and whatever may be the reason of this complex phenomenon, it is without doubt the result of nervous stimulation. But the question as to what is a " sufficient " stimulation cannot be disposed of so easily (see below under the general discussion on Autotomy).

3. *The thoracic nerve mass must remain intact.*

We are indebted to Fredericq[*] for his investigations on the physiological processes involved in autotomy. He has proved that the latter is the result of a reflex, and that the thoracic ganglion belonging to the appendage is the centre of this reflex. The brain is the seat of voluntary and co-ordinated movement in Cancer, and if the brain be removed autotomy will still take place. If, on the other hand, the thoracic nerve mass be removed or destroyed, self-amputation cannot proceed. The afferent nerve fibres which are stimulated as the result of injury to the limb are connected with the ganglion cells of the thoracic nerve mass, and from these the efferent fibres pass to the extensor muscle of the basi-ischium. This muscle is the one concerned in the autotomy, and thus we are provided with a fourth condition.

4. *The integrity of the extensor muscle of the basi-ischium must be maintained.*

The first movement after the limb has been injured is the extension of the basi-ischium; i.e., it moves in a dorsal direction. This movement continues until the

---

[*] Fredericq, L. "Nouvelles recherches sur l'autotomie chez le crabe." *Archives de Biologie*, T. XII, 1892.

distal portion of the limb comes into contact with the carapace or with some other fixed object, when the limb breaks at the fracture plane. That this upward movement, or extension, of the basi-ischium is necessary for autotomy may be proved by cutting the extensor muscle (or muscles), and then injuring the limb. No self-amputation will then take place. If the flexor muscle be cut, and the extensor remain uninjured, autotomy will proceed.

5. *The distal portion of the limb must come into contact with some point of resistance.*

This condition has been emphasised above. As soon as that part of the limb on the distal side of the fracture plane comes into contact with some point of resistance (e.g., the carapace) the upward movement of this portion is stopped. The proximal portion of the basi-ischium, however, still continues to move upwards under the influence of the extensor muscle. Thus there are two forces acting on the fused basi-ischium—a force at the proximal end tending to move the segment upward, and a force at the distal extremity preventing this upward movement. A great strain is produced on the basi-ischium and it snaps at its weakest point, which is the fracture plane.

6. *The stimulation to produce autotomy must be applied between the fracture plane and the distal end of the propodite.*

The nerve does not pass into the dactylopodite, so that if the latter segment be wounded the nerve will not be stimulated. It is equally futile if the limb be damaged on the proximal side of the fracture plane.

Amongst the Brachyura two kinds of autotomy have been recognised.

(1) If the crab is captured by means of one of its limbs it will throw off the limb in order to escape from its enemy ("evasive autotomy").

It is evident that all Decapods do not act similarly under such conditions. It does not appear to be the case in Cancer or Carcinus. Fredericq's researches led him to believe that crabs did not throw off legs in order to escape from enemies, but his experiments were confined to a few species. Taking all the evidence available, it would appear that autotomy does take place under the above conditions in some crabs, such as the Maiidae and the Grapsidae.

(2) If one of the legs of a crab be severely wounded, the limb will be thrown off. This probably occurs without exception in the Brachyura.

It is well to remember that in both cases we are probably dealing with essentially similar physiological conditions. In both cases the autotomy is produced as the result of the stimulation of the nerve of the leg, and the difference appears rather to be one of degree than of kind. In both the above cases the autotomy is produced as the result of a reflex, and the seat of this reflex is in the ganglion of the somite to which the autotomised leg belongs.

Quite recently, Piéron* has concluded that there is still another kind of autotomy which is purely voluntary, and will not take place after the commissures connecting the cerebral ganglia with the thoracic mass have been cut. One of his experiments with Grapsus was as follows:—A leg of the crab was tied to a stake within view of a

---

* Piéron, H. *C.R. Soc. Biol.*, 11th May, 1907. *Ibid.*, T. LXIII (1907), Nos. 33 and 34.

sheltered crevice in the rocks. The crab discarded the imprisoned limb as a conscious effort in order to reach the inviting shelter. This did not happen if the brain were destroyed or if the commissures were cut ("psychic autotomy").

It is difficult at the present juncture to accept Piéron's explanation, as Mlle. Drzewina† has also performed similar experiments with Grapsus, and has obtained entirely different results. But so far as Cancer is concerned, the "psychic autotomy" does not appear to be present.

It is not possible in the present state of our knowledge to arrive at a definite conclusion with regard to the full significance of the processes involved in autotomy. But whatever may have been the lines along which autotomy has been evolved, there is no doubt that one of its most important objects is the prevention of bleeding. If the arthrodial membrane between an appendage and the body be cut, the crab will probably bleed to death, and this appears to be one of the greatest dangers with which the animal has to contend. The limbs, on account of their position and size, are continually in danger of being torn or crushed. If the limb were seriously injured, and autotomy did not take place, the crab would bleed to death, because the wounded surface would probably be too large to allow coagulation to take place. This difficulty is surmounted by the limb being thrown off at the fracture plane, across which, as we have already seen, a membrane is stretched. This membrane is perforated by a small foramen through which pass the nerve and blood streams connecting the proximal and distal parts of the appendage. Over this foramen a clot may readily be formed, and thus the excessive bleeding may be prevented.

---

† Drzewina, A. *C.R. Soc. Biol.*, T. LXIII (1907), Nos. 33 and 34.

Histology. (Text fig. 9).

Before autotomy. A longitudinal section through the basi-ischium of a pereiopod in which autotomy has not been effected displays the following structure (9*A*.).

In the region of the fracture plane the exoskeleton is discontinuous, the plane of the discontinuity being at right angles to the longitudinal axis of the basi-ischium. The break is not always easily detected, as the two parts fit very closely together.

On the inner side of the exoskeleton is the normal layer of epidermis (*ep.*). At the plane of breaking the epidermis turns inward both at the distal extremity of the basipoditic region and also at the proximal end of the ischiopodite. These ingrowths extend as far as the central nerve and blood vessels, where the epidermal ingrowth of the basipodite (*i.*) becomes continuous with that of the ischiopodite (*o.*). In other words, across the plane of fracture the epidermis underlying the exoskeleton is not directly continuous, but becomes turned inward as far as the central nerve of the leg.

Thus there is a double diaphragm stretching across the leg in the fracture plane, and near the centre of this double membrane there is a small opening which permits of the passage of the nerve (*n.*) and blood vessels from one side to the other. The walls of this narrow opening are composed of a cellular membrane, which connects the proximal and the distal diaphragms.

After autotomy. The ischial portion of the exoskeleton is broken away at the fracture plane, and the underlying structures belonging to the ischium have also been torn away. These include the epidermis of the ischium and also the distal portion of the diaphragm. Stretching across the broken end of the stump (Text fig. 9, *B.*) is a membrane representing the proximal portion of the double diaphragm (*i.*). Near the centre of this is a small foramen. In sections taken immediately after autotomy there is a layer of coagulated blood (*b.*) on the outer side of the diaphragm.

The torn edge of the diaphragm in contact with the foramen appears to grow over the latter. Thus, shortly after the autotomy has been effected, there is a continuous membrane or diaphragm covering the broken stump (9 *C.*). This membrane is composed of a single layer of epidermal cells, which is continuous with the epidermis underlying the exoskeleton of the basipodite. On the outer side of the membrane is a layer of coagulated blood. On the inner side of the ectoderm of this membrane, and lying close to it, there appears to be a continuous layer of connective tissue fibres. Miss Reed* describes also the presence of a dense mass of blood cells immediately beneath the membrane.

Regenerative process. Shortly after autotomy has taken place the cells of the diaphragm begin to degenerate (Text fig. 9, *D.*). Ultimately there is on the outside of the stump a layer of dead tissue, formed of an outer layer of coagulated blood, beneath which is the layer of degenerate epidermal cells. According to Miss Reed, there is also an inner layer of degenerate blood cells. The dead epidermal cells of the diaphragm become disconnected from the epidermis underlying the exoskeleton of the limb, and this epidermis grows inward beneath the dead outer layer. This takes place from all sides, and the in-growing cells meet in the centre and form a single

---

* Unfortunately I did not have access to Miss Reed's paper on the histological processes in connection with autotomy until after my own observations had been made. My results, in the main, however, bear out the conclusions arrived at in her paper (*Bryn Mawr College Monographs*, Reprint Series, Vol. V, 1905).

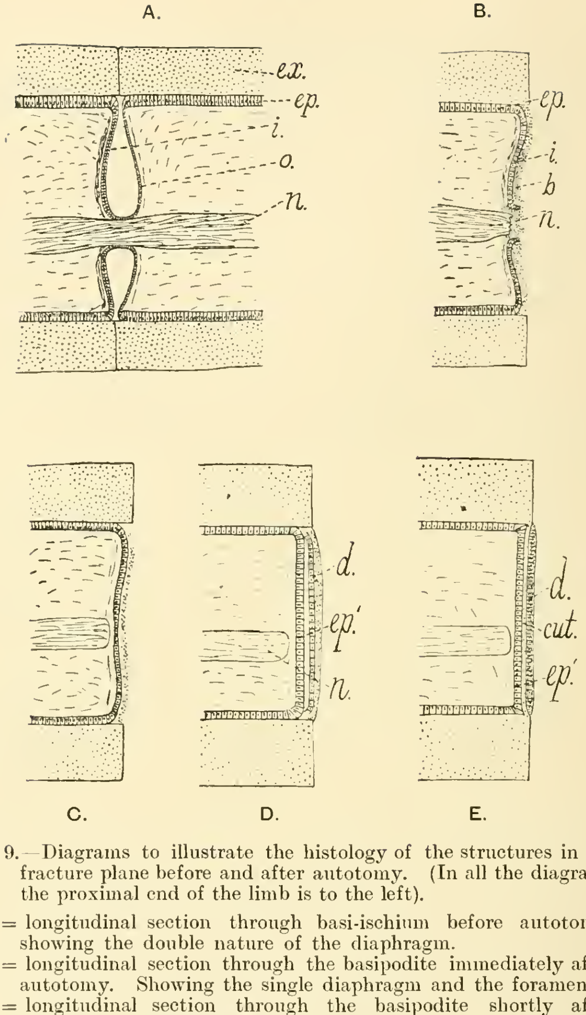


Fig. 9.—Diagrams to illustrate the histology of the structures in the fracture plane before and after autotomy. (In all the diagrams the proximal end of the limb is to the left).

A. = longitudinal section through basi-ischium before autotomy, showing the double nature of the diaphragm.
B. = longitudinal section through the basipodite immediately after autotomy. Showing the single diaphragm and the foramen.
C. = longitudinal section through the basipodite shortly after autotomy. The epidermis of the diaphragm has grown over the foramen.
D. = the degeneration of the diaphragm and the formation of a new layer of epidermis beneath.
E. = Formation of a thin cuticle (which is continuous with the exoskeleton) by the new epidermis.

ep. = epidermis.
ex. = exoskeleton.
i. = proximal part of diaphragm.
o. = distal part of diaphragm.
ep′. = new epidermis.
n. = nerve of the appendage.
b. = coagulated blood.
d. = degenerated diaphragm and blood tissue.
cut. = new cuticle formed by the new epidermis.

layer of cells beneath the outer dead layer. Eventually a thin layer of chitin is secreted on the outer side of these cells (Text fig. 9, *E.*), and this layer of chitin is continuous with the exoskeleton. The old membrane, which is now almost black, becomes worn off, and this new chitinous membrane is exposed.

The cells in the new layer of epidermis become extremely active, and increase in number internally. At first an undifferentiated mass of cells is formed beneath the membrane, but gradually differentiation takes place and the new parts of the limb are laid down in miniature. As they increase in size they grow outward, and form a small papilla on the stump.

MUSCULAR SYSTEM.

(Pls. III, IV).

Muscles of the Cephalothorax.

I. Eye. The ocular peduncle consists of two parts—an inner rod-like portion extending inwards as far as the middle line, and an outer swollen portion at the free end of which is the visual organ. The outer portion articulates with the inner, and is connected with the latter by means of a flexible membrane. The movement of the outer portion is effected by two small muscles—a ventral flexor and a dorsal extensor.

II. First antenna. The muscles are extremely small. The basal segment of the protopodite has a dorsal extensor and a ventral flexor. In their natural condition the second and third segments are flexed. In both cases the extensor is on the inner side and the flexor muscle is on the outer side.

III. Second antenna. The basal region of this appendage is fused with the carapace, and the muscles have degenerated. The operculum, which probably represents the coxopodite, is still freely movable, but its extensor and flexor muscles have now another function in connection with the raising and closing of the operculum. The whole question of the homology of the opercular muscles has been fully discussed by Marchal.* The flagellum has not much movement, and its muscles are very small.

IV. Mandible (fig. 31). There are two sets of muscles—the adductors for closing the mandibles and the abductors for opening the mandibles.

External adductor muscle (*e.a. md.*). Arises as a broad band from the anterior and outer portion of the sub-hepatic region of the carapace. It passes inwards and upwards, and is inserted on a long tendon attached to the outer part of the mandibular apophysis.

Internal adductor muscle (*i.a. md.*). Arises from the urogastric region of the carapace. It passes downwards and forwards as a short broad muscle, and is inserted on an extremely long narrow tendon attached to the posterior margin of the mandible.

External abductor muscle (*e.b. md.*). Arises from the posterior and inner corner of the hepatic region of the carapace. It passes directly downwards, and is inserted on a narrow tendon attached to the posterior side of the apophysis. This muscle is comparatively small.

Internal abductor muscle (*i.b. md.*). Arises from the top of the vertical rod-like portion of the first post-oral endopleurite. It passes outwards and forwards, and is attached to the outer part of the apophysis.

---

* Marchal. "Appareil excréteur des Crustacés Décapodes." *Archives Zool. exp. et gén.* (Ser. 2), T. X, 1892.

V. First maxilla (fig. 26). There are two extensors and two flexors.

Flexors. One outer (*o.e.m.*) and one inner (*i.e.m.*) muscle, which run together and arise from the outer portion of the protogastric region of the carapace. They pass directly downwards together, and when near the maxilla the two separate and are inserted on the outer and inner parts of the coxopodite respectively.

Extensors. One outer (*o.f.m.*) and one inner (*i.f.m.*) The tops of the two pillar-like portions of the first post-oral endopleurites are joined by a strand of tissue. Beneath the arch thus formed the two muscles arise near the middle line. They pass downwards and slightly inwards, diverging somewhat as they approach the appendage. They are inserted on the coxopodite at the same point as the corresponding flexor muscle.

VI. Second maxilla. There are two extensors and two flexors.

Extensors. The inner extensor arises from the posterior face of the first post-oral endopleurite. It s a short muscle which passes downwards and slightly outwards, and is inserted on the outer side of the coxopodite.

The outer extensor is a long narrow muscle. It arises from the epimeron of this somite just in front of the last cephalic endopleurite. It passes inwards and downwards across the anterior face of the flexors of the scaphognathite, and is inserted close to the small inner extensor.

The two *flexors* are small, and arise close together near to the origin of the outer extensor. They pass directly downwards, and are inserted near together on the inner side of the coxopodite.

The **Scaphognathite** (figs. 27, 28) has a complex movement, and the plane of motion is roughly at right angles to its long axis. There are two sets of muscles—extensors which pull the organ downwards, and flexors which draw it up again to its natural position. In the upward movement the scaphognathite does not remain flat, as when in a position of rest, but it becomes curved so that the upper side is concave. This is effected by a set of accessory muscles. The latter extend into the leaf-like portion of the scaphognathite, and do not stop at the edge of the organ, as do the other muscles.

All the flexors arise from the anterior face of the last cephalic endopleurite. Their names have been given according to the position of insertion on the scaphognathite. The flexors are inserted on the anterior wall of the base of the scaphognathite.

Inner flexor (*i. e. s.*) A long narrow muscle arising from the upper part of the endopleurite. It passes down the latter and, turning slightly inwards, it is inserted on the innermost part of the base of the scaphognathite. It has a small branch which arises from the side of the epimeron.

Outer flexor (*o. e. s.*) An extremely broad muscle, which arises immediately beneath the origin of the previous muscle and also on its inner side. It passes down the endopleurite parallel to the epimeron, and is inserted on the extreme outer edge of the base of the scaphognathite.

Outer median flexor (*o. m. e.*) A long and fairly broad muscle, arising from the extreme inner border of the endopleurite above the large foramen of the latter. It passes downwards and outwards across the front of the foramen, and is inserted on the base of the scaphognathite on the inner side of the previous muscle.

Inner median flexor (*i. m. e.*) A very short muscle arising from the endopleurite near the middle of the base of the foramen. It passes downwards below the other flexors and is inserted at the base of the scaphognathite on the outer side of the inner flexor.

The extensor muscles are situated beneath the flexors, so that it is necessary to cut away the latter in order to expose the extensors. There is one extensor corresponding to each flexor, and the insertion of each extensor is near to that of the corresponding flexor All the extensors arise at the base of the anterior face of the last cephalic endopleurite. They are all short muscles, and are inserted on the posterior wall of the base of the scaphognathite.

Inner extensor (*i. f.*) Arises at the base of the endopleurite. It passes inwards and is inserted close to the inner flexor.

Inner median extensor (*i. m. f.*) It lies immediately below the inner median flexor, and above the three other extensors. It arises about the middle of the base of the endopleurite and passes downwards and forwards. Its insertion is close to that of the inner median flexor.

Outer median extensor (*o. m. f.*) Its origin is on the inner side of the previous muscle. It passes obliquely outwards and forward beneath the previous muscle, and is inserted close to the insertion of the outer median flexor.

Outer extensor (*o. f.*) A very short and broad muscle arising on the outer side of the origin of the inner median extensor. It passes outwards and downwards and is attached to the scaphognathite close to the insertion of the outer flexor.

The last two muscles have their insertions situated in the thickened bulb-like portion of the scaphognathite.

The accessory muscles are situated entirely within the scaphognathite itself. Their function is to bend the scaphognathite during the process of lifting up or extending the latter.

There are two muscles which arise close together on the inner side of the insertion of the inner flexor of the scaphognathite. They extend outwards into the middle and inner portions of the scaphognathite.

The *anterior accessory* (*a. acc.*) divides into two parts, each of which is attached to the anterior wall of the scaphognathite.

The *posterior accessory* (*p. acc.*) also divides into two parts. One division appears to be inserted on the posterior wall and the other on the anterior wall.

VII. First maxillipede (fig. 29). Only the extensor and flexor of the **Coxopodite** need be noted here.

The *extensor* (*e. C.*) arises on the epimeron of this somite. It passes downwards and inwards between the two flexors of the flabellum and behind the extensor of the latter (see below). It is inserted near the outer and posterior margin of the coxopodite.

The *flexor* (*f. C.*) arises at the upper side of the posterior face of the last cephalic endopleurite on the inner side of the point where the latter fuses with the second thoracic endosternite. It passes directly downwards as a narrow muscle, and is inserted on the anterior margin of the coxopodite.

The muscles of the exopodite have the same arrangement as the similar parts in the third maxillipede.

The muscles of the **flabellum** are large and powerful. The flabellum lies on the dorsal side of the gills, and by repeated rhythmical movements keeps the surface of the gills free from sand and mud.

The *extensor* (*ex. fl.*) is a short broad muscle arising from the upturned edge of the sternum in this somite. It passes outwards across the mouth of the cavity of the coxopodite, and is inserted on the inner side of the base of the flabellum.

The *anterior flexor* (*a.f.fl.*) is a fairly broad muscle arising from the posterior face of the last cephalic endopleurite, immediately above the foramen of the latter. It passes downwards, and is inserted on the anterior edge of the base of the flabellum.

The *posterior flexor* (*p.f.fl.*) is an extremely broad muscle arising from the last cephalic endopleurite, above the origin of the previous muscle. It runs downwards behind the extensor of the coxopodite, and is inserted on the posterior edge of the base of the flabellum.

VIII. Second maxillipede. This appendage is similar to the third maxillipede in structure, and its muscles have the same arrangement (see below).

The extensor muscle of the coxopodite arises from the inner side of the second thoracic epimeron, and the flexor arises from the upper end of the anterior face of the second thoracic endosternite. All the muscles of the basi-ischium are attached to the lower end of the anterior face of the second thoracic endosternite. The muscles of the flabellum are quite small, but have the same parts as described in the first maxillipede.

IX. Third maxillipede (fig. 30).

Coxopodite. There is a small extensor and a larger flexor.

The *extensor* muscle arises on the inner side of the third thoracic epimeron, and is inserted on the outer side of the coxopodite by means of a narrow tendon (*ex. C.*).

The *flexor* muscle is attached to the anterior wall of the third endosternite. It passes outwards, and is inserted on a broad tendon (*f. C.*) at the inner side of the coxopodite.

Basi-ischium. There are two chief muscles.

The *extensor* is a small muscle arising from the anterior wall of the third thoracic endosternite. It is inserted on the ventral side of the basi-ischium by means of a small tendon (*ex. B.*).

The *flexor* is a larger muscle arising near the origin of the extensor. It is inserted on a long tendon (*f. B.*) on the dorsal side of the basi-ischium. There is also a small accessory flexor inserted on the outer side of the larger flexor.

There is one flexor and one extensor for each of the remaining segments of the endopodite. The muscles of the meropodite and carpopodite are fairly large. Those of the propodite and the dactylopodite are small.

The **exopodite** has two small muscles—a dorsal extensor and a ventral flexor.

The **flagellum** of the exopodite is flexed in its natural position. There is a large *extensor* muscle (*ex. fl.*) running the whole length of the exopodite, which is attached to the outer edge of the flagellum and by its action raises the latter. I have not been able to make out a flexor muscle. Probably the flagellum falls back into its natural flexed condition by means of the elasticity of the arthrodial membrane.

The flagellum in each of the maxillipedes is very active, and is constantly moving with great rapidity.

X. Chela.* (fig. 21, Text fig. 10).

Coxopodite. There are two muscles—a posterior

---

* In all the pereiopods it is probable that those muscles which are situated in the dorsal region of the pleural muscle chambers arise, not only from the walls of the latter, but also from the carapace in this region (Pl. IX, fig. 56, *fl.m.*)

extensor pulling the coxopodite backward and an anterior flexor pulling it forward.

The *extensor* is situated in the outer and posterior region of the fourth thoracic pleural muscle chamber. It arises from the anterior and posterior walls of the latter and passes forward and downward. Its insertion is on a long narrow tendon arising from the posterior side of the coxopodite (fig. 21, *ex. C.*, Text fig. 10, *d.*).

The *flexor* is a much larger muscle than the extensor, and lies in the fourth thoracic sternal muscle chamber. It arises from three parts of the endophragmal system—(1) from the posterior face of the third thoracic endosternite; (2) from the inner side of the third endopleurite; and (3) from the anterior face of the fourth thoracic endosternite. It passes downward and forward, and is inserted on an extremely broad tendon on the anterior side of the coxopodite (fig. 21, *f. C.*, Text fig. 10, *c.*).

Basi-ischiopodite. There are two extensors and three flexors inserted on the proximal region of this segment.

The *anterior extensor* is situated in the anterior and ventral portion of the fourth thoracic pleural muscle chamber. It arises from the ventral part of the anterior and inner walls of the chamber. It runs outward, and is inserted on a long and narrow tendon situated immediately above the anterior hinge (fig. 21, *a. ex. B*, Text fig. 10, *f.*).

The *posterior extensor* is a small muscle situated almost entirely in the base of the coxopodite. It is attached to the ventral part of the wall of the fourth pleural muscle chamber. It passes outward, and is inserted on a small tendon which is immediately above that of the anterior extensor (fig. 21, *p. ex. B.*, Text fig. 10, *e.*)

The *anterior flexor* lies in the ventral region of the fourth sternal muscle chamber, and arises from the fourth thoracic sternum. Its course is outward, upward and backward, and at its outer extremity it is inserted on a broad tendon lying on the ventral side of the basi-ischium, mid-way between the two hinges (fig. 21, *a. f. B.*, Text fig. 10, *k.*).

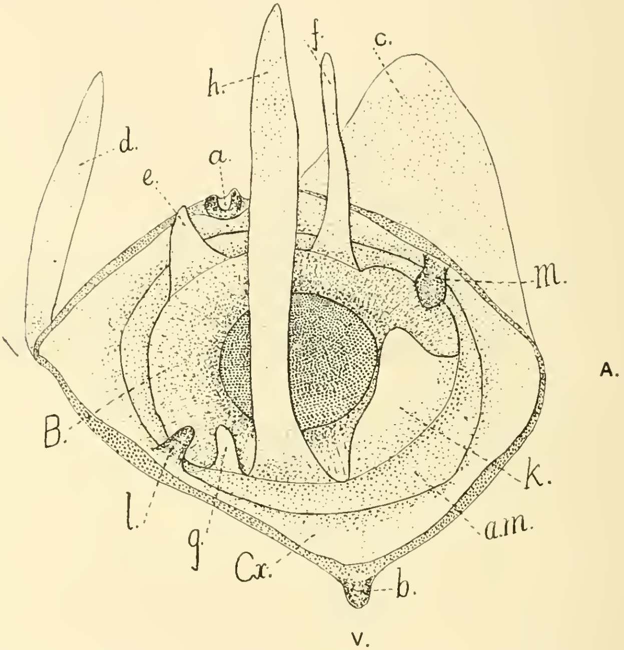


FIG. 10.—The proximal end of the chela, after all the soft tissues have been removed. The tendons of the muscles moving the coxa and basi-ischium are shown. (The upper side of the figure is dorsal, and the right side is the anterior end.)

Coxopodite.—*a.* = dorsal hinge ; *b.* = ventral hinge ; *c.* = tendon of flexor muscle ; *d.* = tendon of extensor muscle.

Basi-ischium.—*e.* = posterior extensor muscle ; *f.* = anterior extensor muscle ; *g.* = lesser posterior flexor muscle ; *h.* = greater posterior flexor muscle ; *k.* = anterior flexor muscle ; *l.* = posterior hinge ; *m.* = anterior hinge.

The *greater posterior flexor* lies in the outer and anterior portion of the fourth pleural muscle chamber, and its origin is on the anterior wall of the latter. It passes downward behind the anterior extensor, and is inserted on an extremely long tendon which arises from the joint immediately behind the tendon of the anterior flexor (fig. 21, *p. f. B.*, Text fig. 10, *h.*).

The *lesser posterior flexor* is situated on the inner and anterior region of the fourth pleural chamber. It passes outward, and is inserted on a small tendon in front of the posterior hinge (Text fig. 10, *g.*).

The **Meropodite** has very little movement, and the muscles are extremely small.

The *extensor* is a small muscle arising from the posterior wall of the ischium. It passes downward and backward, and is inserted on a small tendon on the ventral side of the meros (fig. 21, *t. ex. M.*).

There does not appear to be a definite flexor muscle, but when the extensor muscle relaxes, the weight of the distal portion of the limb is sufficient to produce the small amount of flexion necessary.

Carpopodite. There is an anterior flexor and a posterior extensor muscle.

The *extensor* arises from the posterior walls of the meros throughout its entire length. The insertion of the muscle is on a long tendon situated near the dorsal hinge of the carpos. This tendon lies in the dorsal part of the meros and extends almost to the proximal end of the latter (*ex. C.*^{1}).

The *flexor* has its origin on the anterior walls of the meros. Its tendon is similar in size to that of the extensor. It lies in the ventral region of the meros, and arises from the antero-ventral border of the carpos (*f. C.*^{1}).

Propodite. There is a posterior extensor and an anterior flexor muscle.

The *extensor* arises from the posterior walls of the carpos, and is inserted on a broad tendon at the posterior side of the propodite (*ext. P.*).

The *flexor* has its origin on the anterior wall of the carpos, and is inserted on a large tendon at the anterior side of the propodite (*f. P.*).

Dactylopodite. There is a dorsal extensor and a ventral flexor.

The *extensor* is comparatively small, and arises from the dorsal or posterior walls of the propodite. It is inserted on to a narrow tendon which is situated immediately above and between the two hinges of the dactylos (*ext. D.*).

The *flexor* is an extremely large muscle which occupies the greater portion of the propodite. It arises from the ventral and anterior walls of the latter, and is inserted on a very broad tendon which is attached to the ventral side of the dactylopodite (*f. D.*).

XI. First walking leg (Pl. III, fig. 22).

Coxopodite. There is a posterior extensor and an anterior flexor.

The *extensor* is situated in the fifth pleural muscle chamber. It passes downward, and is inserted on a long narrow tendon immediately behind the dorsal hinge (*ex. C.*).

The *flexor* is a large muscle situated in the anterior and upper portions of the fifth sternal muscle chamber. Its origin is partly on the anterior wall of the chamber and partly on the median plate. It passes outward and downward, and is inserted on a broad tendon on the anterior portion of the coxopodite (*f. C.*).

Basi-ischiopodite. There is one dorsal extensor and one ventral flexor muscle.

The *extensor* occupies the dorsal and posterior portion of the fifth sternal muscle chamber. It arises from the anterior face of the fifth thoracic endosternite, and passes outward and downward, and is inserted on a long tendon on the dorsal side of the basi-ischium (*ex. B.*).

The *flexor* lies in the ventral and posterior part of the fifth sternal muscle chamber. It arises from the median plate, and passes downward and outward. Its insertion is on a fairly broad tendon on the ventral side of the joint (*f. B.*).

In addition to the above flexor there is a small accessory flexor muscle on each side of the former. They are probably comparable to the anterior flexor and lesser posterior flexor of the corresponding segment of the chela.

The muscles of the other segments of this limb are very similar to those described above in the chela. The two muscles of the dactylopodite, however, are extremely small, and almost equal in size.

XII. Second walking leg.

The muscles here are similar to those of the first walking leg.

Coxopodite. The *extensor* arises from the sixth pleural muscle chamber. The *flexor* arises from the sixth sternal muscle chamber.

In the **Basi-ischiopodite** both muscles arise from the sixth sternal muscle chamber.

XIII. Third walking leg.

The muscles are similar to those of the two previous appendages.

Coxopodite. The *extensor* arises from the seventh pleural muscle chamber. The *flexor* arises from the seventh sternal muscle chamber.

In the **Basi-ischiopodite** both muscles arise from the seventh sternal muscle chamber.

XIV. Fourth walking leg (Pl. III, fig. 23).

In the coxopodite and basi-ischium there are the same muscles as in the other walking legs. There is, however, an additional extensor of the coxopodite. This *ventral extensor* is inserted on a small narrow tendon (*v. ex. C.*) immediately below the insertion of the dorsal extensor.

The muscle chamber in this somite is not divided into pleural and sternal regions. Hence it may be designated the pleuro-sternal muscle chamber (see section on Endophragmal System). All the muscles of the coxa and the basi-ischium arise from this chamber.

The dorsal extensor of the coxopodite arises from the anterior wall of the chamber; the ventral extensor from the median plate: the flexor of the coxopodite from the anterior end of this muscle chamber. The extensor of the basi-ischium arises from the anterior and inner corner of the chamber, and the flexor has its origin on the median plate.

The muscles of the remaining parts of this appendage are similar to those of the other walking legs.

In the chela the coxa swings horizontally. In the first walking leg the coxa is slightly tilted, so that it swings forward and slightly downward. In each of the succeeding walking legs the corresponding part is more tilted, and in the last walking leg the ventral hinge of the coxa is more posterior and the dorsal hinge anterior. So that, instead of swinging horizontally as in the chela, the coxa swings in a plane inclined at a considerable angle to the vertical, and during the movement of extension the limb is capable of being turned almost on to the dorsal side of the carapace. The presence of the additional extensor muscle undoubtedly aids such a movement.

This freedom of movement is probably not of much value in Cancer. In the swimming crabs, however, where the last thoracic appendages are flattened and oar-like and are utilised as an effective rowing organ, such an arrangement is of no mean importance.

Muscles of the fore-gut. These are described in the section on the Alimentary Canal.

The Dorso-ventral muscles are described in the section on Respiration.

It is of interest to note in passing that in the case of those muscles arising from the carapace, there are definite marks on the outside of the shell corresponding in shape and size to the areas of the origin of these muscles. It has been stated above (section on Integument) that the muscle is not directly attached to the chitinous exoskeleton, but arises from the basement membrane underlying the epidermis. How, then, can the marks of the muscle attachments be duplicated on the outer side of the exoskeleton?

The most probable explanation is that in those regions where the muscles are attached to the basement membrane the cells of the epidermis are in some way affected by the underlying muscles. In this manner the rate of secretion of the integument may have been slightly reduced in these localised areas, thus producing the marks on the outer side of the carapace.

MUSCLES OF THE ABDOMEN.

On account of the third, fourth and fifth somites being fused together, the abdominal muscles of the male abdomen differ from those of the female.

Female abdomen (Pl. IV, figs. 32, 33).

There are two sets of muscles working each somite, a pair of dorsal extensors, and a pair of ventral flexor muscles.

Somite I. Each *extensor* (*ex.* 1) arises as a broad band of muscle from the top of the epimeral region of the last two thoracic somites. It passes inward and backward, and is inserted on the side of the anterior triangular portion of the tergum of the first somite.

Each *flexor* (*f.* 1) muscle arises from the "sella turcica" in the thorax, and passes backward near the median line. It is inserted on a small ingrowth of the sternum immediately in front of the arthrodial membrane separating the first sternum from the second.

Somite II. Each *extensor* (*ex.* 2) is inserted on a small concavity in the tergal region of the first somite. It passes backward, and is inserted near the middle line on a tendon which is attached to the anterior extremity of the second somite.

Each *flexor* (*f.* 2) arises from the posterior face of the ingrowth, or tendon, at the posterior end of the first sternum. It passes backward near the median line, and is inserted on the anterior face of a similar tendon at the posterior extremity of the second sternum.

Somite III.-VI. and Telson. The muscles in the succeeding abdominal somites have the same arrangement as those of the second somite. The flexor of the last abdominal somite is not inserted on a well-marked tendon. The same applies to both the origin and insertion of the flexor muscle of the telson.

Uropod of female (Pl. IV, fig. 25).

In their natural position the uropods are extended and lie almost horizontal, with their distal extremities pointing toward the posterior end of the abdomen.

The **Protopodite** is capable of two kinds of movement. First there is a movement in an antero-posterior plane. The flexor muscle, which has very little power, moves the protopodite forward, and the extensor acts in the opposite direction.

The *extensor* (*ex. prot.*) arises from the posterior region of the tergum of the somite to which the uropod belongs. It passes forward and downward, and is inserted on a small tendon on the anterior wall of the protopodite, some distance below the proximal border of the latter.

The *flexor* (*f. prot.*) arises from the anterior region of the tergum. It passes downward and inward, and its insertion is on a tendon arising from the outer border of the protopodite.

The protopodite also has a slight movement from side to side. The flexor muscle draws the appendage toward the middle line and the extensor pulls it outward.

The *lateral extensor* (*l. ex. prot.*) arises from the outer region of the tergum, and passes downward and inward. Its insertion is on a tendon arising from the outer border of the protopodite.

The *lateral flexor* (*l. f. prot.*) arises from the inner part of the tergum. It passes downward and outward, and is inserted on a tendon arising from the inner border of the protopodite.

Exopodite. The movement of the exopodite is lateral. There is one extensor and two flexors.

The *extensor* (*ext. ex.*) arises from the outer edge of the protopodite. It passes downward, and is inserted on the inner wall of the exopodite some distance below the arthrodial membrane.

The *flexors* (*d. f. ex.*, *v. f. ex.*) arise from the inner wall of the protopodite. They pass outward, and converge to a single insertion on the inner edge of the exopodite.

The **endopodite** is fused to the protopodite, and has no muscles.

Male abdomen.

There are no extensors between the third and fourth somites, and also between the fourth and fifth somites.

According to Williamson, there are only two long flexors at each side arising from the thorax. One is inserted on the sternum of the united third, fourth and fifth somites, and the other is inserted on the telson.

Uropods of Male. These muscles have been described by Williamson.* In the first appendage the endopodite has a strong flexor muscle. The extensor is extremely small, and probably the flexion is effected by the elasticity of the arthrodial membrane. The protopodite has two small muscles, one of which flexes and the other rotates the limb. In the second appendage there is also a strong flexor in the endopodite. The protopodite has a system of small muscles which rotate, extend and flex the appendage.

Histology of Muscle.

The muscles of Cancer are composed of striated fibres. Each fibre is an elongated multi-nuclear cell which reveals, in longitudinal sections and in stained preparations, two kinds of striations longitudinal and transverse. As a rule, the cross striations are the more obvious, and produce the "striped" appearance so characteristic of Arthropod muscle fibres.

Each fibre is composed of numerous longitudinal fibrils, which give rise to the longitudinal striations. In a transverse section across a fibre it is seen that the fibrils have an unequal distribution, and are usually grouped together into polyhedral areas (Cohnheim's areas). The bundle of fibrils constituting a single area is known as a *muscle column*. The various muscle columns are separated

---

* Williamson, H. C. *Twenty-second Annual Report of the Fishery Board for Scotland*, p. 104.

from one another by the sarcoplasm (protoplasm), which varies in quantity in different kinds of fibres.

In stained preparations the muscle fibre reveals alternate light and dark cross-striations. At its centre, each light band is interrupted by a transverse line (Krause's membrane). There is also a transverse line stretching across the middle of the dark band (Hensen's line). The latter is only seen with difficulty. Each portion of a fibril between two adjacent Krause's membranes is known as a "sarcomere."

Haycraft's* experiments led him to believe that the cross striations are due to regularly-occurring varicosites, and some of the preparations made in the course of the present work appear to show this. It is doubtful whether this structure (even if admitted) is alone sufficient to account for the fact that the cross-striations seen in fresh tissue are accentuated under the action of various staining reagents. It is highly probable, as suggested by Schäfer, that the cross striation of the fibrils is due to the heterogeneous nature of the latter.

An examination of the fresh muscles of a crab reveals the interesting fact that—as in the vertebrates some of the muscles are of a darker colour than others. Sections across the muscle fibres show that, generally speaking, the "dark" muscles have much more sarcoplasm than the "light" ones. Hence Knoll distinguished between *plasmic* (dark) and *aplasmic* (light) fibres. Biedermann† has shown that there is a definite relationship between the amount of sarcoplasm present in a fibre and the nature of the work performed by the fibre. He has, furthermore, stated that "the elements of those muscles which serve

---

* Haycraft, J. B. "Cause of Striation of Voluntary Muscular Tissue," *Q.J.M.S.*, Vol. XXI (1881).

† Biedermann, W. *Electro-physiology*, Vol. I.

the most persistent or most strenuous action are richest in sarcoplasm."

In Cancer the muscles present all grades of colour, from an opaque yellowish brown (muscles of scaphognathite) to a transparent white (muscles of appendages). Undoubtedly, the most active muscles of the body are those of the scaphognathite, and probably the flexors and extensors of the abdomen are the most sluggish (in the Macrura the abdominal muscles are very strenuous). I append a list of muscles, commencing with the most strenuous and darkest in colour and finishing with the least active. In all cases the position of a muscle on the list for colour agrees with its position regarding its activity.

1. Muscles of the scaphognathite.
2. Muscles of the heart.
3. Mandibular muscles.
4. Anterior cardiac muscles.
5. Extensor muscles of flagella of maxillipedes.
6. Gastric muscles (other than the anterior cardiacs).
7. Muscles of the appendages.
8. Extensor and flexor muscles of the abdomen.

COELOM AND BODY CAVITY.

Arthropods in general are characterised by the presence of a greatly reduced coelom in the adult. This reduction of the coelom is the result of the increase in the blood-holding spaces or sinuses. This system of swollen sinuses, which contain the venous blood, has produced a series of cavities lying between the various organs of the body, and has been termed by Lankester a *haemocoel*. The theory of Phleboedesis formulated by Lankester to account for the development of the haemocoel is as follows:—

"The system of blood-containing spaces pervading the body in Mollusca and Arthropoda is not, as sometimes supposed, equivalent to the coelom or perivisceral space of such animals as the Chaetopoda and the Vertebrata, but is in reality a distended and irregularly swollen vascular system—the equivalent of the blood-vascular system of Chaetopoda and Vertebrata."*

In Cancer the only remnants of the true coelom are the gonadial sacs and the end sacs of the antennary glands. The labyrinth and bladder of the excretory system are lined by cells derived from epiblast.

ALIMENTARY CANAL

(Pls. V, VI, VII).

The alimentary canal extends from the *mouth*, which is situated on the ventral side of the cephalic region between the mandibles, to the *anus* on the ventral side of the telson. The nature of the development of the alimentary canal suggests a natural division into three parts:—(1) The *fore-gut*, which is the embryonic stomodaeum, (2) the *mid-gut*, the archenteron of the embryo, and (3) the *hind-gut*, which is the embryonic proctodaeum.

Fore-gut.

The fore-gut commences at the mouth and is formed of the embryonic epiblast. It is lined throughout by a cuticle which is continuous with the exoskeleton around the mouth. The mouth leads into a short *oesophagus* (Pl. VI, fig. 40, *oe.*) which opens into the so-called "stomach," which is continuous behind with the mid-gut.

The mouth is situated on the ventral surface of the

---

* Lankester, E. Ray. "The Enterocoela and the Coelomocoela," *A Treatise on Zoology*, Part II.

cephalic region, and is bounded in front by a fleshy lobe—the *labrum* (Pl. III, figs. 18, 20, *lab.*) or anterior lip—and behind by the *metastoma* (*met.*) or posterior lip. On each side of the mouth are the mandibles.

Both the labrum and metastoma have closely packed glands which have the appearance and structure of the "salivary glands" found in the walls of the oesophagus. It is not inconceivable that they have the same function as the oesophageal glands. The mandibles also have at their base a mass of glands which are continuous with those in the ventral portion of the oesophageal walls.

In the **oesophagus** (Pl. V, fig. 35) the epidermal cells (*ch. ep.*) are of great length. In a soft crab with a carapace 25 mm. in width these cells are 90 μ in length and only 3 μ wide. On the outer side of the epidermis is a thin chitinous layer about 8 μ in width. This consists of two layers—a thin outer structureless layer, the cuticle, and a broader inner layer showing evidences of longitudinal striations. On the inner side of the epidermis is a well-marked basement membrane. Below the basement membrane is a layer of connective tissue (*der.*) about 370 μ in width. This is composed of a dense reticulate mass formed of intercrossing connective tissue fibres. There are also small connective tissue cells scattered about. Embedded in the connective tissue are numerous glands which may conceivably be salivary glands, but which I designate the *oesophageal glands* (*sal. g.*).

On the outer side of the connective tissue of the oesophagus is a layer of circular muscles—the *constrictors of the oesophagus* (*c. oe.*)—and passing through the connective tissue and attached to the basement membrane are numerous muscle bundles—the *dilators of the oesophagus* (*oe. l.*).

Each oesophageal gland is globular and consists of numerous large conical cells, the apex of each cell pointing to the centre of the mass. Each cell has a well-defined nucleus near its outer side. In the centre of each gland mass is a small cavity into which the secretion from the individual cells is poured. This small central cavity is connected with the lumen of the oesophagus by means of a long narrow duct which passes between the cells of the epidermis. The duct and its walls is probably formed of a single cell, in which case the gland duct is intra-cellular. These glands are scattered through the connective tissue of the oesophageal wall. They take the stain distinctly, and have a diameter of 25 μ to 35 μ in the small crab mentioned above. From the above description it would appear that the oesophageal glands are merely modified cutaneous glands.

At the extreme ventral end of the oesophageal wall at each side there is an additional mass of such glands which are very closely packed together (*v. oe. g.*). As mentioned above, these glands are continuous with those of the mandible.

The large and spacious region of the fore-gut which follows the oesophagus is generally termed the "stomach,"* and is divided into a large anterior portion —the *cardiac chamber* (*card.*)—and a smaller posterior portion—the *pyloric chamber* (*pyl.*).

The **Cardiac fore-gut** (Pl. V, fig. 34, Pl. VI, fig. 40, *card.*) is a large simple sac roughly spherical in shape. The cuticle lining this part of the alimentary canal

---

* The term "stomach" is an unsatisfactory one, as this part of the fore-gut is neither embryologically nor physiologically what is generally recognised as a stomach. Also the terms "cardiac" and "pylroic" have no meaning when applied to the Malacostraca, seeing that the cardiac region—as pointed out by Huxley—is the farthest from the heart. It would be inconvenient, however, to reject the terms "cardiac" and "pyloric," as such a change would also involve an alteration in the names of numerous ossicles and muscles connected with the fore-gut. The terms "cardiac fore-gut" and "pyloric fore-gut" will be used in the present Memoir.

presents numerous thickenings to form an elaborate system of plates and teeth known as the "Gastric Mill." This will be described below.

The posterior wall of the cardiac fore-gut is invaginated on its ventral surface to form the *cardio-pyloric valve* separating the cardiac region from the pyloric region.

The **Pyloric fore-gut** (Pl. V, figs. 34, 36) presents a very complicated arrangement.

In the posterior two-thirds of the pyloric region the chitin of the ventral wall is thickened at each side to form the *pyloric ampullae* (*amp.*). These are clearly seen from the outside as swellings on the floor of the pyloric region. The ampullae have their chitinous lining thrown into well-defined longitudinal parallel ridges. From the summits of the ridges there are numerous fine setae projecting into the cavity of the pyloric chamber. Each seta has numerous small hook-like branches. The two ampullae meet in the mid-ventral line in a well-defined ridge—the *inter-ampullary fold* (Pl. V, fig. 36, *i. a. f.*).

The ventro-lateral walls immediately above the ampullae have the chitin enormously thickened at each side to form cushion-like pads projecting into the cavity of the pyloric chamber immediately above the ampullae. These are the *supra-ampullary ridges* ["voûte ampullaire," Mocquard] (*amp. c.*). Each cushion has a convex surface which faces inwards and downwards, and the upper parts almost meet in the middle line. The presence of the supra-ampullary ridges and the inter-ampullary fold causes the cavity and the ventral part of the pyloric chamber to be reduced to a narrow two-rayed fissure. The supra-ampullary ridges are covered with numerous fine setae, which stretch across the narrow lumen of this portion of the pyloric chamber, so as to form—as Huxley suggested—a very effective filtering apparatus.

The dorsal part of the pyloric chamber has a comparatively large cavity. In transverse sections through the pyloric region the lateral walls of the dorsal portion are roughly at right angles to one another.

The supra-ampullary wall (fig. 36, *s. amp.*) is immediately above the supra-ampullary ridges, and is almost horizontal, thus forming the floor of the upper region.

The pleuro-pyloric wall (*pp.*) is on the outer side of the supra-ampullary wall and turns upwards almost at right angles to the latter. This portion of the wall may be complicated by the presence of folds (*up. f.*).

The dorsal wall is simple in structure.

Thus in the posterior two-thirds of the pyloric region the lumen is divided into a wide dorsal portion and a narrow ventral portion, the two parts being capable of complete separation by the concrescence of the inner portions of the supra-ampullary ridges.

The anterior third of the pyloric region is comparatively simple, and shows no such division into dorsal and ventral portions.

It is probable that in the anterior part of the pyloric region the contents undergo a certain amount of separation. For instance, any hard shell-like structures belonging to the creatures taken in as food will be separated from the soft and nutritious parts. The hard parts pass backwards along the wide dorsal chamber, and by means of an elaborate system of valves they are carried directly into the hind-gut without coming into contact with the unprotected walls of the mid-gut (fig. 40, *val.*). The valves are flap-like structures projecting backwards from the upper side of the posterior end of the fore-gut.

As suggested by Huxley and Mocquard the function of these valves may be partly to prevent the waste matter from passing back into the fore-gut, but Cuénot has claimed that the valves are also used, as described above, for carrying the hard waste pieces directly into the hind-gut. The mid-gut is not lined with chitin, and consequently the sharp pieces present amongst the food in the alimentary canal would be liable to tear the walls of the mid-gut.

The soft parts of the aliments are passed through the narrow ventral portion of the pyloric region, where they are sieved by the setae stretching across the lumen, and near the posterior region of this region the food comes into contact with the secretion from the digestive glands. The latter open into the ventro-lateral wall of the mid-gut immediately behind the ampullae, and the digestive fluid flows forward and mixes with the food in the ventral part of the pyloric region.

In the cardiac and pyloric regions we have essentially the same histological arrangements as in the oesophagus. The epidermis consists of columnar epithelium of much less length than the cells of the oesophageal epidermis. The chitinous layer is very thin except in the regions of the ossicles of the gastric mill, which are merely thick portions of the chitin which have become strongly calcified. The basement membrane is well marked and the connective tissue is a very thin layer. Embedded in this layer are very thin bands of circular and longitudinal muscles.

Mid-gut (or Mesenteron) (Pl. V, fig. 34, *m. g.*).

The mid-gut is an extremely short portion of the alimentary canal, being only about 10 mm. long in a full-grown crab. This is the only part of the alimentary canal which is derived from the archenteron and is lined by cells formed from the hypoblast.

From the mesenteron arise a pair of caeca—the so-called "pyloric caeca." This is an unfortunate designation, as they do not arise from the pyloric region of the fore-gut. I therefore propose to substitute the name of **Mid-gut caeca** (fig. 34, *caec.*). Each caecum arises from the side of the anterior part of the mid-gut. It passes forward as a narrow tube alongside the pyloric chamber, and is closely applied to the postero-lateral region of the cardiac chamber of the fore-gut. On a level with the widest part of the latter the caecum terminates in a much convoluted portion.

The digestive glands (fig. 34, *di. gl.*) arise at each side from the ventro-lateral region of the mid-gut, immediately behind the origin of the mid-gut caeca. These will be described more fully below.

The epithelium lining the mid-gut (Pl. X, fig. 61) consists of columnar cells having a length of 55 μ in an adult crab. There is no cuticular lining to the epithelium of this region, but each cell has an outer striated border from 1 μ to 2 μ in thickness. This is similar to the "Härchensaum" present in the mid-gut of Anurida* and in the duodenum of many vertebrates. It is very probable that this striated border is characteristic of the mid-gut epithelium of arthropods in general, and probably the thin cuticle lining the mid-gut of Ligia described by Hewitt† is a similar structure.

In many of the epithelial cells are refractive bodies, probably the fat globules mentioned by Cuénot. Beneath the epithelium is a thick basement membrane. In the comparatively broad layer of connective tissue beneath the basement membrane are thin layers of circular and longitudinal muscles.

* Imms. *L.M.B.C. Memoir*, "*Anurida.*"

† Hewitt. *L.M.B.C. Memoir*, "*Ligia.*"

Hind-gut (Pl. V, fig. 34, *h. g.*)

The hind-gut or intestine is a long narrow tube extending from the posterior end of the mid-gut to the anus which opens on the ventral surface of the telson. Near to the mid-gut it passes below the median bridge-like portion of the reproductive organs; passing further back it runs beneath the pericardium, and a short distance behind the latter it enters the abdomen, along which it pursues a straight course. Just before entering the abdomen the hind-gut gives off from its right side a long coiled tube—the **hind-gut caecum** (fig. 34, *i. caec.*).

The caecum lies above the hind-gut, and the coils, which are packed very closely together, extend into the first segment of the abdomen.

The hind-gut has very pronounced columnar epithelium (Pl. X, fig. 62). This is lined by a thin chitinous layer, consisting—as in the fore-gut—of an outer cuticle, and a layer longitudinally striated which appears to be continuous at the anus with the pigment layer of the exoskeleton. The epithelium rests upon a basement membrane outside of which are thin layers of circular and longitudinal muscles.

In the walls of the hind-gut immediately behind the mid-gut there are closely packed glands very similar in structure to those present in the walls of the oesophagus.

There are also glands, having a similar structure to the above, present in the walls of the hind-gut in the abdominal region. They are not closely packed (fig. 62).

DIGESTIVE GLAND.

The digestive gland ("liver," "hepato-pancreas") (Pl. V, figs. 34, 37, 38, 39) is a large yellowish-brown*

---

* This colour is due to lipochrome. (Miss Newbigin, *Journ. Physiol.*, Vol. XXI., p. 237, 1897.)

organ occupying nearly the whole of the ventral side of the anterior region of the cephalothorax. It is a lobulated structure composed of a large number of digitate tubular outgrowths, and arises from the mid-gut at each side. The front edge of the gland sweeps backward close to the antero-lateral border of the carapace and resembles the latter in having a notched edge. The posterior border of the gland is generally on a level with the anterior region of the branchial chamber: in other words, the branchial chamber is only covered by the digestive gland at its anterior end. Posteriorly the gland occupies the ventral part of the region between the muscles of the thoracic walking legs, and below the pericardium and hind-gut. Throughout the digestive gland is covered by the gonads (Pl. VIII, fig. 51). The gland does not extend into the abdomen.

Arising from the mid-gut at each side there are three main ducts which communicate with smaller ducts. These branch repeatedly, and ultimately end in the cavities of the tubules of which the main part of the gland is composed. Thus the tubules have a cavity which is continuous with that of the mid-gut, and both the ducts and the tubules are lined by cells derived from the embryonic hypoblast. Each of the main ducts mentioned above receives the digestive ferments from one of the three main lobes into which each half of the gland is divided. These lobes are as follows (fig. 34): (1) An antero-lateral lobe having its outer border marked by notches which correspond to the markings of the antero-lateral border of the carapace; (2) a postero-lateral lobe lying above the anterior part of the branchial chamber; and (3) a posterior lobe which lies between the muscles of the thoracic walking legs.

Histology of the Digestive Gland
(Pl. V, figs. 37, 38, 39).

In sections the tubules are seen to be closely packed together, generally being separated only by a very thin layer of connective tissue (fig. 37, *c. t.*) or a small blood sinus. Sometimes, however, the walls of the tubules are not separated from each other by any tissue. The lumen of the tubules has four angles in transverse section, and the cells at the angles are much shorter than the others.

The *ducts* are lined by a single layer of large columnar and non-glandular cells. In the sections stained with methyl-blue eosin these cells take the stain more readily than the cells of the tubules.

The *tubules* (fig. 37) have three kinds of cells.

(1) **Fat cells** (fig 37, *f. c.*, fig. 38). These are columnar cells from 70 μ to 120 μ in length and 15 μ wide. The contents of the cells are vacuolated, due to the presence of fat globules (fig. 38, *g. f.*). The border of each cell in contact with the lumen of the tubule is striated (*sb.*). The nucleus (*n.*) is generally situated in the inner portion of the cell.

(2) **Ferment cells** (fig. 37, *fm. c.*, fig. 39). These are not quite as long as the fat cells, but they are about four times as broad. Each cell contains a large globular mass (fig. 39, *f. v.*) which nearly fills the whole cell. These masses are yellowish-brown and are responsible for the characteristic colour of the digestive gland. According to Frenzel each mass is enclosed in a bladder, and the vesicles are more abundant during feeding time than during the fasting periods. On the side of the cell in contact with the lumen of the tubule there is a small amount of vacuolated protoplasm which exhibits striation. The border of the cell in contact with the lumen was

described by MacMunn as being ciliated. This is highly improbable, and it is more likely that we have in both the ferment cells and the fat cells a striated hem (Härchensaum) (*sb.*) similar to that already described in the mid-gut epithelium. The nucleus is situated in that portion of the cell farthest removed from the lumen.

(3) **Young cells** (fig. 37, *y. c.*). These are small cells found between the larger cells near the periphery of the tubules. These young cells stain deeply and will eventually give rise to the fat cells or ferment cells.

Physiology of the Digestive Gland.

As pointed out by Cuénot, the digestive gland has many functions, which may be summarised as Digestion, Absorption, Excretion, Elimination and Regulation.

Digestive function. According to MacMunn, Frenzel and others the gland is a pancreas, and the ferments produced (proteolytic and amylolytic) are poured into the ducts of the gland and thence into the mid-gut. The ferments are produced entirely in the ferment cells.

The fat cells have the power of forming and storing fat.

Roaf* found that the action of the extract of the digestive gland was as follows:—

It does not digest coagulated white of egg. It digests fibrin most actively in alkaline solution, but not actively in acid solution. It converts starch into sugar, and inverts cane sugar. It does not hydrolise olive oil, but it hydrolises methyl acetate.

Function of absorption. According to Cuénot the digestive gland is of great importance as an accessory organ for absorbing the products of digestion. The

---

*Roaf, H. E. "A Contribution to the Study of the Digestive Gland in Mollusca and Decapod Crustacea." *Bio-Chemical Journal*, Vol. I, Nos. 8 and 9.

mid-gut is the only portion of the alimentary canal not lined with chitin, and therefore the absorption of the soluble products of digestion can only take place in this region. It is inconceivable that the short mid-gut, even with the mid-gut caeca, can be the *only* region where the process of absorption is carried on. The digestive gland, which is merely an outgrowth from the mid-gut, is richly supplied with blood, and it is an easy matter for the fluids to pass from the mid-gut into the tubules and through the cells into the blood stream. Thus the digestive gland becomes an accessory absorptive organ of no mean importance.

Excretory function. It was observed by Cuénot and MacMunn that when a Crustacean was injected with certain colouring matters, the latter were discovered in the ferment cells of the digestive gland as well as in the cells of the recognised excretory organ. Cuénot is of the opinion that the pigment contained in the excretory cells is of an excretory nature, and that when the contents of these cells ultimately find their way into the alimentary canal, the excretory pigment becomes separated from the ferments and passes down the hind-gut to the exterior.

Function of elimination. During the process of absorption, Cuénot states that the cells of the digestive gland keep back many useless products which are afterwards carried to the exterior together with the excretory products. This is quite distinct from the excretory function.

Function of regulation. In addition to the other functions it is probable that the digestive gland is capable of regulating the composition of the blood, especially with regard to the quantity of water contained in the blood.

Summary. As the food enters in at the mouth it will come into contact with the secretion from the oesophageal glands. In the cardiac region of the fore-gut the food is broken up in a very effective manner. Passing back into the pyloric chamber, the food encounters the cardio-pyloric valve. Here the large pieces are prevented from passing into the pyloric chamber. The food which passes into the latter chamber probably undergoes a further process of sifting, the useless material passing along the dorsal portion of the pyloric chamber and the food being passed along the ventral portion. In this ventral region the food first comes into contact with the digestive ferments. Both are well mixed by the action of the muscles of the pyloric chamber.

As already stated, the probable regions of absorption are the mid-gut, mid-gut caeca and the tubules of the digestive gland. The waste products pass down the long hind-gut to the exterior.

OSSICLES OF THE FORE-GUT.

(Pl. VI, figs. 40, 41, 43, 44.)

In certain regions of the fore-gut the chitinous lining is thickened and strongly calcified to form *ossicles.* These ossicles give attachment to muscles. One set of ossicles in the dorsal and lateral walls of the cardiac region are connected with three tooth-bearing ossicles. This system of plates which is worked by the anterior and posterior gastric muscles (see section on Muscles of the Fore-gut) forms a very effective apparatus for breaking up the food which has passed into the cardiac fore-gut. Hence the name *gastric mill.*

In addition to the ossicles of the gastric mill there are " supporting ossicles " in both the cardiac and pyloric regions. To these supporting ossicles are attached the various muscles of the fore-gut.

Ossicles of the Gastric Mill.

The **Mesocardiac Ossicle** (*m.c.*) is a small median ossicle in the dorsal wall of the cardiac region. It is triangular in shape, with the apex pointing forwards. It is not clearly separated from the urocardiac ossicle which passes posteriorly, and it is only partially separated from the pterocardiac ossicle which extends laterally. The ossicle is thicker dorso-ventrally at its posterior end, and to the thickened posterior edge the anterior ends of the cardio-pyloric muscles are attached. In the Macrura and the Anomura the mesocardiac ossicle is much larger than in the Brachyura, and the pterocardiac pieces are much smaller.

One pair of **Pterocardiac Ossicles** (*pt.c.*). They are situated to the right and left of the mesocardiac piece and in contact with it. The posterior border is almost straight, and the anterior border is curved. Each ossicle is broadest on its inner side, and tapers towards its outer extremity. Near the inner border of each ossicle is a smooth area where the anterior gastric muscle is inserted. Each ossicle extends outwards, and its outer extremity articulates with the zygocardiac ossicle by means of the *antero-lateral ligament* (*lig.*).

One pair of **Zygocardiac Ossicles** (*z.c.*) lying in the supero-lateral wall of the cardiac region of the fore-gut. Each passes backwards and inwards, and comes into contact at its posterior end with the exopyloric ossicle, thus forming a connecting link between the ossicle of the cardiac and the pyloric regions. The zygocardiac ossicle is irregular in shape. The anterior part is rod-like, but the ossicle becomes gradually broader as it passes backwards, and the posterior portion is a broad rectangular plate which bears the lateral tooth. One side of the ossicle points inwards, and the other faces outwards. The inner face is concave and the outer face is convex. The inner edge of the ossicle folds outwards so as to produce a deep groove on the outer side below the convexity. The ossicle has four borders. The *anterior border* is concave and terminates at its posterior extremity in the large anterior tooth. The *dorsal border*, which can be seen through the dorsal wall of the stomach, is also concave. It passes backwards and inwards and ends at the posterior border. The *posterior border* has a large indentation into which the anterior border of the exopyloric ossicle fits. The *inner border* lies obliquely, being nearer the middle line at its anterior end. The ossicle appears to be much thicker at its inner border than in any other region. This thickness is not real, but is merely due to the ossicle folding outwards at its inner border. This inner border bears the *denticles.* Anteriorly there is a large single denticle, which is followed by about seven smaller denticles, which point inwards and decrease in size from before backwards. The folded edge of the inner border is crossed by about twenty-four transverse ridges. This system of denticles and ridges on the zygocardiac ossicle is known as the **lateral tooth** (*lat. t.*).

The **Exopyloric Ossicles** (*ex. py.*) are a pair of small triangular plates, each of which lies between the posterior border of the zygocardiac ossicle and the pyloric ossicle. The superior border gives support to the posterior end of the outer part of the cardio-pyloric muscle, and on its external face it provides insertion for the external part of the posterior gastric muscle.

The **Urocardiac Ossicle** (*u.c.*) is a median plate more or less fused with the mesocardiac ossicle in front. It passes backwards and downwards as a broad, thin rectangular plate. At its posterior end, which articulates with the propyloric ossicle, it bears the large blunt **median tooth** (*med. t.*) on its ventral surface.

The **Propyloric Ossicle** (*pr.p.*) is a small median plate situated almost vertically. When the gastric mill is at rest the lower end of this ossicle is considerably behind its upper end. Its upper end articulates with the front portion of the pyloric ossicle, and its lower end is in contact with the posterior end of the urocardiac ossicle. The plate is roughly triangular in shape and its apex, which points downwards, is bifurcated. The base of the triangle is dorsal and is extremely concave. The ossicle is highly calcified around the edges, but in the centre it is almost membranous.

The **Pyloric Ossicle** (*o.py.*) is a median ossicle lying between the two exopyloric ossicles which articulate with it at each side. It covers the anterior part of the pyloric region of the stomach. Its central portion is membranous, but laterally it is slightly calcified. These lateral calcifications indicate that the pyloric ossicle is really a paired structure. In the Macrura all signs of the double origin disappear.

Cardiac "Supporting Ossicles."

The **Pectineal Ossicles** (*pec.*) are a pair of irregular hammer-shaped ossicles, each lying in the lateral wall of the fore-gut beneath the posterior portion of the zygocardiac ossicle. The curved " handle " of the hammer points anteriorly. On the inner side of the " head " of the hammer are three claw-like teeth. These are the **lateral accessory teeth** (*a.t.l.*). [" Infero-lateral cardiac teeth," Huxley.]

The **Prepectineal Ossicles** (*p.pec.*) are a pair of long narrow rod-like ossicles, each being concave on its inner border and extending upwards from the pectineal ossicle to the outer edge of the zygocardiac ossicle with which it articulates by means of a ligament.

One pair of **Post-pectineal Ossicles** (*pt. pec.*) Each is a narrow rod-like ossicle which passes backwards from the pectineal ossicle to the posterior wall of the stomach. It then suddenly turns downwards and runs down the posterior wall of the cardiac fore-gut as a straight rod. At its lower end the ossicle turns forwards for a short distance. On the internal border of the ossicle there is a row of setae projecting into the stomach.

The **Infero-lateral Cardiac Ossicles** (*i.l.*) are a pair of long rod-like ossicles, each of which lies immediately behind and parallel to the rod-like portion of the post-pectineal ossicle. Dorsally the ossicle is in contact with the sub-dentary ossicle, and ventrally it terminates on a level with the lower end of the post-pectineal ossicle. The ossicle is broader at its upper end and tapers gradually towards its lower extremity.

There is one pair of **Sub-dentary Ossicles** (*s.dt.*) At its anterior end each ossicle is in contact with the inner border of the zygocardiac ossicle. The ossicle passes downwards and backwards as a somewhat curved rod, and its posterior end touches the upper end of the infero-lateral cardiac ossicle.

The **Lateral Cardio-pyloric Ossicles** are a pair of small ossicles articulating with the posterior and upper end of the infero-lateral cardiac ossicles.

Postero-lateral Cardiac Plates (*cd. pl.*). These are a pair of broad plates roughly quadrangular in shape, each lying in front of the post-pectineal ossicle. It is a membranous area having no decided calcification, but being distinctly thicker than the ordinary wall of the stomach. There are two rows of long setae arranged along the posterior edge of each plate and projecting into the cavity of the stomach.

The **Antero-lateral Cardiac Plates**(*cd.al.*) are a pair of thickened areas in the side walls of the stomach in front of the postero-lateral cardiac plates, but they are not so well defined as the latter.

The *Cardio-pyloric valve* (*c.p.v.*) is the thickened median portion of the posterior wall of the cardiac fore-gut. Its upper end is invaginated into the floor of the fore-gut so as to form an incomplete partition between the cavities of the cardiac and pyloric regions of the fore-gut. The top of the cardio-pyloric valve is richly clothed with setae.

Pyloric "Supporting Ossicles."

In the *dorsal wall* of the pyloric fore-gut there are three pairs of ossicles.

The **Anterior Mesopyloric Ossicles** (*a.mes*) are a pair of small ossicles lying immediately behind the pyloric ossicle near the median dorsal line.

The **Posterior Mesopyloric Ossicles** (*p.mes.*) are a pair of small ossicles lying behind the anterior pair.

The **Uropyloric Ossicles** (*u.py.*) are a pair of small ossicles lying in the roof of the posterior part of the pyloric region and immediately behind the posterior mesopyloric ossicles.

In the *ventral wall* of the pyloric fore-gut the main supporting ossicles are as follows:—

The **Antero-inferior Pyloric Ossicle** (*a.i.p.*) is a median plate shaped somewhat like a truncated triangle. The base of the triangle points forwards and comes into contact with the cardio-pyloric valve. This ossicle lies in front of the inter-ampullary groove.

The **Pre-ampullary Ossicles** are a pair of small plates. Each lies at the side of the antero-inferior pyloric ossicle and immediately in front of the pyloric ampulla.

The **Postero-inferior Pyloric Ossicle** is a median curved rod-like ossicle. It is concave anteriorly, and is situated behind the pyloric ampullae.

In the *lateral walls* of the pyloric fore-gut there are the following principal ossicles:—

On the supra-ampullary walls there are three pairs of ossicles, viz., the **Anterior** (*a.s.a.*), **Middle** (*m.s.a*), and **Posterior** (*p.s.a.*) **Supra-ampullary Ossicles.**

There are also three pairs of ossicles in the pleuropyloric walls, viz., the **Anterior, Middle** and **Posterior Pleuropyloric Ossicles.**

The positions of these six pairs of ossicles are indicated by the names.

MUSCLES OF THE FORE-GUT. (Pl. VII.)

Mocquard* has divided the muscles of the fore-gut into two kinds. The *extrinsic muscles* are those muscles which have points of origin on some part of the skeletal system outside the fore-gut, and which are inserted on to ossicles lying in the walls of the fore-gut. The *intrinsic muscles* are attached at both ends to ossicles lying in the walls of the fore-gut.

Extrinsic Muscles.

Anterior Gastric Muscles (*g.a.*)—one pair. Each muscle has its origin on the procephalic process. Both pass directly backwards near the median line, being only slightly separated from one another, and are inserted on the front of the pteroeardiac ossicles near the middle line.

Inner Posterior Gastric Muscles (*g.p.i.*)—one pair. They arise from two small calcareous projections, almost median in position, situated on the under side of the mesogastric region of the carapace. Each muscle passes

---

* Mocquard, *Annales Sciences Naturelles*, 6 ser., t. 16, 1883, p. 238.

downwards and forwards, and is inserted on the front part of the pyloric ossicle.

Outer Posterior Gastric Muscles (*g.p.e.*)—two pairs. The two muscles at each side run together so that they may be mistaken for a single muscle. They arise from the under side of the mesogastric region of the carapace, some distance in front of the origin of the dorsal pyloric dilator muscles, but not so near the middle line. They pass downwards, forwards and inwards, and are inserted on the external face of the exopyloric ossicle.

The above three sets of muscles are concerned in the working of the gastric mill. In addition to these the intrinsic muscles—the cardio-pyloric muscles—to be described later, are also used in connection with the gastric mill.

The following muscles serve to dilate the fore-gut:—

Upper Anterior Dilator Muscles (*a.s.*)—one pair. Each arises from the inner side of the cephalic sternum immediately behind the orbit. The muscle is not a compact one, but passes backwards, upwards and inwards as a series of muscular strands which gradually diverge. They are inserted on the anterior and outer corner of the fore-gut.

Lower Anterior Dilator Muscles (*d.ai.*)—one pair. These are a smaller pair of muscles than the preceding. They are very close to the middle line so as to appear almost as a single median muscle. Each arises on the upper side of the epistoma near the middle line and passes backwards and slightly upwards, being inserted on the lower part of the front wall of the fore-gut near the median line. As in the preceding case, the muscle is composed of several separate strands which diverge as they approach the point of insertion.

Antero-lateral Dilator Muscles (*d.la.*)—one pair.

These are narrow muscle bands each arising about half way along the outer edge of the roof of the pre-branchial chamber. Each passes inwards and downwards parallel to the front edge of the carapace and is inserted on the lateral wall of the cardiac region of the fore-gut, above the oesophagus.

Postero-lateral Dilator Muscles (*d.lp.*)– one pair. These are broad muscles arising near the point of origin of the preceding muscles. Each passes directly inwards and slightly backwards and downwards. The muscle broadens considerably as it approaches the fore-gut. Its insertion is on the anterior edge of the postero-lateral cardiac plate.

Dorsal Pyloric Dilator Muscles (*d.sup.*)—two pairs—anterior and posterior The two muscles at each side run close together so that it is difficult to distinguish the separate muscles. They arise close together from the under side of the carapace just behind the origin of the outer posterior gastric muscles. They pass downwards and slightly forwards and are inserted on the ossicles of the dorsal wall of the pyloric region of the fore-gut. The anterior muscles are inserted on the posterior mesopyloric ossicles and the posterior muscles on the uropyloric ossicles.

Ventral Pyloric Dilator Muscles. Two pairs—outer and inner. Each of the *inner pair* (*i.py.i.*) is a long narrow muscle arising near the base of the mandibular apophysis. It passes upwards and slightly backwards on the inner side of the posterior oesophageal dilator muscle and runs very close to the posterior wall of the cardiac region. It is inserted on the antero-inferior pyloric ossicle in the ventral wall of the pyloric region. Each of the *outer pair* (*i.py.e.*) is much shorter than the inner pair. Its origin is on the endopleurite of the first maxillary segment. From this the muscle passes upwards and is inserted on the ventral pyloric wall on the outside of the insertion of the inner pair.

The following muscles dilate the oesophagus:—

Upper Anterior Oesophageal Dilator Muscles (*oe.as.*)—one pair. Each of these muscles arises from the epistoma close to the origin of the upper anterior dilator muscle. Passing backwards and slightly upwards below the latter muscle, it is inserted on the anterior wall of the oesophagus. The muscle is not compact, but is made up of separate strands which diverge as they approach their insertion.

Lower Anterior Oesophageal Dilator Muscles (*oe.ai.*). One pair of very small muscles. Each arises from a small eminence on the posterior part of the epistoma near the middle line. These eminences are behind the origin of the previous muscle. The muscle passes backwards below the previous muscle, and its insertion on the anterior wall of the oesophagus is immediately below that of the previous muscle.

Lateral Oesophageal Dilator Muscles (*oe.l.*)—one pair. Each of these muscles is made up of three distinct bands of muscle fibres. Near its origin the muscle is compact, but the fibres diverge as they approach the oesophagus. Each muscle arises near the extreme posterior angle of the epistoma and passes inwards below the upper muscle. Its insertion is on the lateral wall of the oesophagus.

Posterior Oesophageal Dilator Muscles (*oe.p.*)—one pair. Each muscle arises from the top of the pillar-like portion of the endopleurite of the first maxillary segment and passes inwards and downwards. It runs external to the inner ventral pyloric dilator, and crossing over that muscle it is inserted on the posterior wall of the oesophagus.

Intrinsic muscles.

Cardio-pyloric Muscles (*c.py.*) These consist of one median and two lateral muscles. The *median* muscle extends from the thickened posterior border of the mesocardiac ossicle to the upper edge of the propyloric ossicle. The *lateral* muscles extend from the mesocardiac ossicle to the exopyloric ossicle. These muscles are used in connection with the gastric mill and are concerned in bringing the ossicles of the mill back to their original position after each series of complicated movements effected by means of the gastric muscles.

Lateral Cardiac Muscles (*c.lat.*)—three pairs. The three muscles at each side may be distinguished as the *upper*, *middle* and *lower* muscles respectively. The *upper muscle* arises from the upper edge of the infero-lateral cardiac ossicle and passes upwards and forwards as a broad sheet of muscle to the dorsal border of the zygocardiac ossicle. The *middle muscle* also arises from the upper edge of the infero-lateral cardiac ossicle below the origin of the upper muscle and passes upwards and forward parallel to this muscle. It is inserted on the prepectineal ossicle, and also on the anterior part of the dorsal border of the zygocardiac ossicle. This muscle is much narrower than the previous one. Both sheets of muscle are broader at their insertion than at their origin. The *lower muscle* is a short broad sheet arising from the side of the infero-lateral cardiac ossicle, and passing across the upper portion of the postero-lateral cardiac plate. Its insertion is on the antero-superior border of this plate. According to Mocquard, these muscles raise the cardio-pyloric valve.

The **Postero-inferior Cardiac Muscle** (Fig. 48, *c.i.*). This is a median broad sheet of muscle covering the posterior wall of the cardiac region of the fore-gut. It is attached at each side to the posterior border of the infero-lateral cardiac ossicle.

Anterior Cardiac Muscle (*c.ant.*). This is a median muscle extending as a broad and thin sheet down the front wall of the fore-gut. It arises in the median line on the front of the mesocardiac ossicle and passes forwards. As it passes downwards along the front wall of the fore-gut it divides into two main branches, which are attached separately to the front wall of the fore-gut.

The above muscle must not be confused with the muscle of the same name described by Mocquard. The latter muscle is on the antero-lateral wall. I therefore designate it the **Antero-lateral Cardiac Muscle** (*c.al.*). There is one pair of these muscles, each being situated on the antero-lateral wall of the fore-gut immediately above the oesophagus. It is attached to the anterior border of the membranous antero-lateral cardiac plate, and passes upwards almost to the median line.

The above two sets of muscles act as constrictors of the cardiac portion of the fore-gut.

Circular Oesophageal Muscles (*c.oe.*). These are present as a broad band running around the oesophagus and acting as constrictors of the oesophagus.

Lateral Pyloric Muscles (*py.lat.*). There are several pairs of muscles—some broad and others very small—arising at each side from the upper part of the post-pectineal ossicle and the infero-lateral cardiac ossicle. They pass upwards and are inserted on the various ossicles of the lateral and dorsal walls of the pyloric region of the fore-gut. These muscles serve as constrictors of this region of the fore-gut.

THE MECHANISM OF THE GASTRIC MILL.

According to Huxley* the movement of the gastric mill is effected by means of *both* the anterior and posterior gastric muscles. By the contraction of these muscles the urocardiac tooth is thrown forward, and simultaneously the zygocardiac teeth are rotated inwards and the three teeth meet in the middle line.

Mocquard has been fortunate enough to observe the movements in a living Stenorhyncus having a remarkably transparent carapace. He states that the active movement is brought about *almost solely* by means of the anterior gastric muscles. If the posterior muscles act at all, it is only very feebly and spasmodically. When the anterior gastric muscles contract, the urocardiac ossicle and the median tooth are thrown forward. The movement is slightly complicated because of the connection between the posterior part of the urocardiac ossicle and the lower part of the propyloric ossicle. When in a state of rest the lower part of the latter ossicle lies considerably behind its upper border. As a result of the contraction of the anterior gastric muscle the lower part is drawn forward so that the ossicle takes up a vertical position. The median urocardiac tooth, if not in contact with the propyloric ossicle, would have a simple backward and forward movement. But the connection between the two ossicles causes the median tooth to move in an arc the convexity of which points downwards.

Since the anterior gastric muscles are inserted on the inner ends of the pterocardiac ossicles, the latter are also drawn forward when the muscles contract. This movement causes the outer ends of the ossicles to turn downwards and inwards. Because of the connection between

---

* Huxley, T. H. *The Crayfish.* [*International Science Series.*]

the pterocardiac and the zygocardiac ossicles the anterior handle-like portion of the latter are also drawn downwards and inwards. Posteriorly the zygocardiac ossicles are in contact with the exopyloric ossicles, which in their turn articulate with the pyloric ossicle. Therefore if we consider the zygocardiac and the exopyloric ossicles as a single rod, we have a lever of the second order, the fulcrum being at the anterior end and the weight in the region of the zygocardiac tooth. Thus, the application of the force at the anterior end rotates the tooth downwards and inwards, and the three sets of teeth meet in the middle line. When the muscles relax the ossicles spring back into their original position, partly because of the elasticity of their joints, but mainly by means of the action of the cardio-pyloric muscles.

THE BLOOD VASCULAR SYSTEM

(Pl. VII, figs. 49, 50; Pls. VIII, IX).

Briefly stated the scheme of circulation is as follows. The pure blood returning from the gills passes into the Pericardium by means of the Branchio-cardiac veins. From the Pericardium the blood enters the heart through the ostia. From the anterior end of the heart there arise five arteries carrying the blood to the gonads, digestive glands, fore-gut, and the front part of the body. From the posterior region of the heart two median arteries arise which supply the abdomen and the appendages. The impure blood returning from the system does not pass to the gills along definite vessels, but flows through irregular spaces or *sinuses* between the various organs. The blood from the sinuses eventually reaches the gills and passes along the Afferent Branchial Sinuses on the outside of the gills. The blood is distributed to the various gill lamellae where it is oxygenated. The pure blood leaves the gills by the Efferent Branchial Veins, running along the inside of the gills and which pass into the Branchio-cardiac veins.

The Pericardium (Pl. IX, figs. 54, 56, *Per.*) is a closed cavity surrounding the heart and having thin transparent walls. It is situated immediately beneath the cardiac region of the carapace, and between the "flancs." It lies above the hind-gut and covers the posterior portions of the digestive gland and gonads. When viewed from above the shape of the pericardium is roughly pentagonal (fig. 54). The base of the pentagon is anterior and the apex is posterior.

The Branchio-cardiac veins (Pl. IX, fig. 54, *bc* 1-5) enter each side of the pericardium by means of three wide openings which have no valves. The *first* opening is situated at the anterior corner of the pericardium and receives the first and second branchio-cardiac veins. The *second* opening is situated a little behind the first and receives the third branchio-cardiac vein. The *third* opening is situated at the postero-lateral corner, and at this point the fourth and fifth branchio-cardiac veins enter the pericardium.

The Heart (Pl. VII, figs. 49, 50) is a white semi-transparent body, pentagonal in shape when seen dorsally and having a rectangular shape when viewed from the side. Two angles of the pentagon are anterior and the other three are posterior. The heart is suspended in the pericardium by means of the *alae cordis* (fig. 49, 50, *cd.*1-6), which are bands of fibrous connective tissue stretching across from the angles of the heart to the wall of the pericardium. Each ala cordis appears to have a short band of muscle fibres attached to its outer extremity.

The alae cordis are eleven in number (fig. 49, 50).

Dorsal Antero-lateral (*cd.*1)—one pair. Stretching from the dorsal side of each of the antero-lateral corners of the heart to the corresponding corner of the pericardium.

Ventral Antero-lateral (*cd.*2)—one pair. Immediately beneath the dorsal antero-lateral band. Extending from the ventral side of each of the antero-lateral corners of the heart to the corresponding corner of the pericardium.

Dorsal Postero-lateral (*cd.*3)—one pair. Extending from the dorsal side of each of the postero-lateral angles of the heart to the corresponding angle of the pericardium.

Ventral Postero-lateral (*cd.*4) one pair. Having a similar position to the dorsal postero-lateral band, but lying immediately beneath it.

Median Posterior (*cd.*5)—A single band arising from the dorsal side of the posterior angle of the heart and stretching across to the posterior angle of the pericardium.

Posterior (*cd.*6)—one pair. Arising ventrally from the postero-lateral side of the heart and crossing to the postero-lateral side of the pericardium.

The walls of the heart are also very muscular, and the cavity of the heart is crossed by numerous strands of muscle.

The blood enters the heart from the pericardium by means of the *Ostia*. There are three pairs of ostia—one pair at the anterior end of the dorsal wall of the heart (Figs. 49, 50. *a.ost.*), one pair at the posterior end of the dorsal wall (*p.ost.*), and the third pair are found in the lateral walls of the heart—one ostium at each side (*l.ost.*). Each ostium is valved so as to prevent the blood from returning to the pericardium.

The Arteries. (Pls. VIII, IX.)

The following arteries are given off from the heart: At the *anterior* end (1) the median *Cephalic artery,* and on each side of this is (2) a *Lateral artery*, and (3) a *Hepatic artery*, all passing forwards. At the *posterior* end there are two median arteries arising about the same point, (4) the *Descending artery* passing downwards, and (5) the *Posterior Aorta* passing backwards above the intestine.

At its origin from the heart each artery is valved, so as to prevent the blood from returning.

Cephalic artery [Ophthalmic artery] (Pl. VIII, fig. 51. *o.art.*). This is a median artery arising from the anterior end of the heart. From its origin it passes directly forward above that portion of the gonads situated between the internal adductor muscles of the mandibles. It pursues a straight course over the pyloric and cardiac regions of the stomach and between the anterior gastric muscles. So far the course of the artery has been entirely superficial, but near the anterior end of the cardiac fore-gut it dips downward and divides into two branches immediately above the brain. Each branch passes outward and supplies the eyes and also the various parts of the front region of the head.

Lateral artery [Antennary artery] (Pl. VIII, Fig. 51. *a.art.*) There is one pair of lateral arteries, each of which arises from the anterior end of the heart a little outside of the origin of the cephalic artery. On leaving the heart the lateral artery passes outward, making an angle of about 40° with the cephalic artery. Almost immediately it passes through the outer portion of the internal adductor muscle of the mandible (*i. a. md.*). It then curves outward, sweeping around the stomach until it reaches the external abductor muscle of the mandible (*e. b. md.*). Here it divides into two parts—(1) an outer portion, the **Ovarian** (*or. a.*) [or **Spermatic**] **artery,** which follows the course of the gonads, and (2) an anterior portion, the **Antennary artery** (*a. art.*), which passes around the front of the fore-gut and supplies the organs in the region of the head.

The main portion of the lateral artery, after leaving the heart, dips down gradually until it reaches the external abductor muscle of the mandible (*e. a. md.*). The antennary artery still continues to pursue a deeper course, but the ovarian [or spermatic] artery becomes more superficial. When the gonads are well developed the main artery and the gonadial branch are partly embedded in the substance of the gonad, but when the reproductive organs are small these parts of the artery are quite superficial.

Branches of Main Lateral artery—

Branch to the Hind-gut. This arises on the inner side of the artery just behind the internal adductor muscle of the mandible. It passes downward and inward to that portion of the hind-gut beneath the front part of the heart.

Branch to the Digestive Gland. This is a large branch arising immediately in front of the branch to the hind-gut. It passes outward and gives off numerous branches to the digestive gland and also to the hypodermis in this region.

Branch to the Cardiac Fore-gut. In front of the internal adductor muscle of the mandible a large branch is given off on the inner side. It passes through the substance of the gonad and breaks up into a complicated network on the lateral and dorsal walls of the cardiac fore-gut. This branch supplies the muscles of the fore-gut.

Branches to the Hypodermis. Throughout the whole course of the lateral artery and its branches small arteries are given off which supply the hypodermis.

The Ovarian [or *Spermatic*] *Branch* (*ov. a.*). This follows the course of the gonads, and sweeps round near to the outer edge of the carapace. Numerous branches are given off to the gonads and also to the hypodermis.

The Antennary Branch (*a. art.*). This passes anteriorly and dips downward as it sweeps around the fore-gut. It passes over the paragastric lobe of the bladder and divides into an outer and an inner portion. The *outer* branch dips downward and outward and gives branches to the external adductor muscle of the mandible. It then passes outward to the hypodermis and supplies also the hepatic lobe of the bladder. The *inner* branch passes inward and supplies the antennae and the front part of the head. It also sends branches to the anterior gastric muscles and to the main vesicle and the paragastric and oesophageal lobes of the bladder.

Hepatic artery (Pl. VIII, fig. 51, *h. art.*). Owing to the fact that this artery dips down immediately on leaving the heart, and becomes deeply embedded in the digestive gland, it is rather difficult to locate. Hence several workers at the Brachyura have neither figured nor described this artery, and some have described other arteries as the hepatic artery. Milne-Edwards,* in his description of Maia, has designated as the hepatic artery those branches of the sternal artery which supply the digestive gland. Brooks† has called the lateral (ophthalmic) artery by the name of hepatic artery.

The hepatic artery of each side arises from the ventral side of the anterior region of the heart, its origin being beneath and slightly external to that of the lateral

---

* Milne-Edwards. *Hist. Nat. des Crustacés.*

† Brooks. *Handbook of Invertebrate Zoology.*

artery. Immediately on leaving the heart it dips downward and makes an outward sweep in the deeper parts of the digestive gland. Near its origin on its inner side it gives off a branch which goes to the hind-gut. There are also other small branches which supply various parts of the gland. The main artery, however, divides into two branches, the posterior of which sweeps outward embedded in the posterior part of the digestive gland. The anterior branch passes beneath the gonad and the external adductor muscle of the mandible and supplies the anterior portion of the gland.

Posterior aorta (Superior abdominal artery) (Pl. VIII, fig. 51, Pl. IX, fig. 53, *sa. art.*). This arises as a median vessel from the posterior end of the heart. Just after leaving the heart it gives off at each side a small vessel. This passes forward and downward beneath the pericardium, and supplies those parts of the reproductive organs lying beneath the pericardium, and also some of the muscles of the Basi-Ischium of the Chela.

Immediately above the hind-gut caecum a second pair of branches arises. These are the **Postero-lateral arteries** (*pl. art.*), and have several complicated branches. The main branch passes outwards above the coils of the caecum and divides into two vessels. The anterior vessel passes forward and gives off branches to the extensor muscles of the coxopodites of the four walking legs. The posterior branch supplies the muscles extending from the "flancs" to the carapace, and also gives a rich blood supply to the coils of the hind-gut caecum.

Behind the origin of the postero-lateral arteries the posterior aorta enters the abdomen. As the arrangement in the two sexes is somewhat different, these will be described separately.

Female. The aorta passes down the abdomen above the hind-gut, but not in the median line. As it passes backward it gradually crosses over to the right side. In each of the second, third, fourth and fifth abdominal segments a pair of arteries is given off to the appendages. At the posterior end of the fifth segment the aorta divides into two branches. The right branch follows the course of the aorta. The left branch crosses over the hind-gut and is continued down the left side of the hind-gut parallel to the right branch. Both branches pass into the telson, where they break up into fine branches. Throughout the abdomen small branches are given off from the posterior aorta to the hind-gut, to the abdominal muscles and the muscles of the abdominal appendages.

Male. There are only two pairs of arteries given off from the posterior aorta. These are in the first and second abdominal segments and supply the two pairs of appendages. As the aorta passes backward it crosses over to the *left* side, and in the fifth segment it bifurcates, the right branch crossing over the hind-gut. As in the female, there are also innumerable small arteries given off to the hind-gut and to the abdominal muscles.

Descending artery[*] (Pl. IX, fig. 56, *d. art.*). This leaves the heart at the posterior end close to the origin of the posterior aorta. It is an extremely wide vessel which passes almost directly downward on the right side of the hind-gut until it nearly reaches the anterior part of the "sella turcica," where it turns suddenly forward. It continues to pass downward and forward, and between the muscles of the fourth and fifth thoracic appendages it passes through the foramen

---

[*] The term *sternal artery* is generally given to this artery, as well as to its continuation along the ventral side of the thorax. I have, however, thought it more fitting to apply the term "sternal artery" only to the ventral portion.

of the coalesced thoracic ganglia. Immediately beneath the nerve chain the artery divides into a short and broad posterior branch and a much longer and narrower anterior branch. Both these branches are continuous and horizontal, and are known together as the *sternal artery.*

Sternal artery (Pl. IX, fig. 52, *S.art.*). This is a large and well-defined median artery lying in the thorax below the nerve cord and between the muscles of the thoracic appendages. It is broadest at its posterior portion just behind its connection with the descending artery (*j.d.*). In front of this connection it is continued forward as a much narrower vessel, from which are given off arteries to each of the post-oral cephalo-thoracic appendages, and also to the digestive gland. The arteries supplying these appendages arise separately from the sternal artery, except in the case of the last two pairs of thoracic appendages. The arteries supplying these appendages arise as a single vessel at each side of the posterior part of the sternal artery, each of which divides into two branches, each branch going to an appendage.

The blood supply of the last five pairs of thoracic appendages is very similar, and the artery supplying the chela may be taken as typical of all. This artery (*art.*6.) arises singly from the sternal artery and passes outwards. A short distance from its origin it gives off a large ventral branch which supplies the muscles of the coxopodite and basi-ischium. The main artery passes to the extreme end of the appendage, giving off various small branches to the various muscles of the limb.

Each of the arteries to the maxillipedes (*art.* 5), after giving off its ventral branch, enters the appendage and bifurcates, one branch going to the endopodite and the other to the exopodite.

The arteries supplying the first and second maxillipedes (*art.* 3, *art.* 4) are not symmetrical. The origin of the artery going to the first maxillipede of the right side is posterior to that of the left. In the case of the second maxillipede the origin of the artery on the right side is anterior to that of the artery on the left.

Just in front of the branches to the first maxillipede the sternal artery bifurcates, each part passing forward and uniting again behind the mouth, thus forming a ring. From this ring arteries are given off to the mandibles and the first and second maxillae (*art.* 1, *art.* 2).

Inferior Abdominal artery (Pl. IX, fig. 52, *ia.art.*). The posterior part of the broad sternal artery is continued as a narrow vessel which runs backwards over the " sella turcica " and down the abdomen beneath the nerve cord and the hind-gut. It gives off a few small branches to the hind-gut and to the flexor muscles of the abdomen.

BLOOD SINUSES AND VEINS. (Pl. IX, figs. 54, 55, 56.)

The blood returning from the various parts of the body to the gills is not enclosed in definite vessels, but flows through irregular spaces known as *sinuses.* Generally speaking, all the main organs of the body, such as the alimentary canal, digestive gland, reproductive organs, muscles, &c., have blood sinuses in close contact with them.

Above the cardiac fore-gut there is a large sinus the **Dorsal sinus**—which is situated above the epigastric lobe of the bladder. There is also a smaller sinus between this lobe of the bladder and the fore-gut. These two sinuses are connected in front.

The dorsal sinus passes down the front of the fore-gut and is connected ventrally with a sinus which passes backward beneath the stomach. At the level of the oesophagus this sinus divides into a right and left portion.

These **Sternal sinuses** pass backward at each side of the ventral part of the thorax between the leg muscles and beneath the pericardium. The two sternal sinuses are not definitely separated from one another, but are connected here and there by irregular sinuses. On the outer side each sternal sinus sends offshoots down the pleural muscle chambers to the base of the gills (fig. 56, *br. S.* 4). These branches or branchial sinuses again unite into a long sinus which runs along the base of the gills. This is the infra-branchial sinus (fig. 55, *i. s.*). The blood sinuses from each of the thoracic legs also pass into the infra-branchial sinus.

From the infra-branchial sinus the blood passes along the afferent branchial sinuses on the outside of each gill.

At the posterior end of the thorax the sternal sinuses are connected with a small abdominal blood sinus.

The sinuses in connection with the digestive gland—the **Hepatic sinus**—and the reproductive organs—the **Ovarian** [or **Spermatic**] **sinus**—open into the sternal sinus at each side. There is a very large sinus below the posterior part of the digestive gland.

The **Branchial sinuses** (*br. s.* 1-5) connect the sternal sinus with the infra-branchial sinus at each side. They are five in number at each side. The first branchial sinus (*br. s.* 1) commences below the anterior end of the pericardium. It passes down the pleural muscle chamber of the second thoracic segment and opens into the infra-branchial sinus near its anterior end. Similarly the second branchial sinus (*br. s.* 2) passes down the third thoracic pleural muscle chamber, the third sinus (*br. s.* 3) is in the fourth pleural chamber, the fourth sinus (*br. s.* 4) is in the fifth pleural chamber, and the last branchial sinus (*br. s.* 5), which commences below the posterior end of the pericardium, passes down the pleural muscle chamber of the sixth thoracic segment. All the pleural sinuses are below the branchio-cardiac veins, which also run down the pleural muscle chambers.

The **Infra-branchial sinus** (fig. 55, *i. s.*) is a long sinus which runs along each side of the thorax at the base of the thoracic legs and the gills. Posteriorly it extends as far as the last walking leg, and anteriorly almost as far as the metastoma. Into it flow the five branchial sinuses from above, and from its outer and ventral side there enters a narrow sinus from each of the thoracic appendages. From its outer and dorsal side there is given off an afferent branchial sinus to each of the gills.

Afferent Branchial sinuses (fig. 55). These sinuses run along the outer side of each gill.

First afferent branchial sinus (*af.* 1) goes to the podobranch of the second thoracic somite.

Second afferent branchial sinus (*af.* 2) goes to the arthrobranch of the second thoracic somite.

Third afferent branchial sinus (*af.* 3) goes to the small podobranch of the third thoracic somite.

Fourth afferent branchial sinus (*af.* 4) goes to the anterior arthrobranch of the third thoracic somite.

Fifth afferent branchial sinus (*af.* 5) goes to the posterior arthrobranch of the third thoracic somite.

Sixth afferent branchial sinus (*af.* 6) goes to the anterior arthrobranch of the fourth thoracic somite.

Seventh afferent branchial sinus (*af.* 7) goes to the posterior arthrobranch of the fourth thoracic somite.

Eighth afferent branchial sinus (*af.* 8) goes to the pleurobranch of the fifth thoracic somite.

Ninth afferent branchial sinus (*af.* 9) goes to the pleurobranch of the sixth thoracic somite.

The **Efferent Branchial veins** (fig. 54) receive the pure blood from the branchial lamellae. They pass down the inside of each gill. Each efferent branchial vein is a blood vessel having a definite wall.

There are nine efferent branchial veins (*ef.* 1-9) corresponding to the nine afferent branchial sinuses—one for each gill.

The **Branchio-cardiac veins** (fig. 54) convey the pure blood from the efferent branchial veins to the pericardium. There are five branchio-cardiac veins at each side. They have definite walls.

First Branchio-cardiac vein (*bc.* 1) receives the first and second efferent branchial veins. It passes up the outer side of the pleural muscle chamber of the second thoracic segment, above the first pleural sinus.

Second Branchio-cardiac vein (*bc.* 2) receives the third, fourth and fifth efferent branchial veins. It passes up the outer side of the third thoracic pleural muscle chamber. The first and second branchio-cardiac veins enter the pericardium together through the *first* opening (see section on Pericardium).

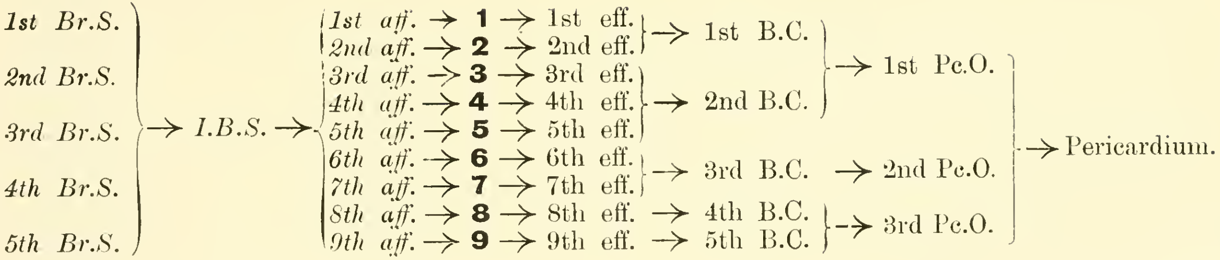
Third Branchio-cardiac vein (*bc.* 3) receives the sixth and seventh efferent branchial veins. It passes up the fourth thoracic pleural muscle chamber. It enters the pericardium by means of the *second* pericardial opening.

Fourth Branchio-cardiac vein (*bc.* 4) receives the eighth efferent branchial vein, and passes up the fifth pleural muscle chamber.

Fifth Branchio-cardiac vein (*bc.* 5) receives the ninth efferent branchial vein and passes up the sixth pleural muscle chamber. The fourth and fifth branchio-cardiac veins enter the pericardium through the *third* pericardial opening.

There are no valves between the branchio-cardiac veins and the pericardium

SCHEME OF CIRCULATION OF THE BLOOD TO AND FROM THE GILLS.



REFERENCES.

1 = Podobranch of 2nd thoracic segment.
2 = Arthrobranch ,, ,, ,,
3 = Podobranch of 3rd ,, ,,
4 = Anterior arthrobranch of 3rd thoracic segment.
5 = Posterior ,, ,, ,, ,,
6 = Anterior ,, 4th ,, ,,
7 = Posterior ,, ,, ,, ,,
8 = Pleurobranch of 5th thoracic segment.
9 = Pleurobranch of 6th ,, ,,

Br.S. = Branchial sinus.
I.B.S. = Infra-branchial sinus.
aff. = afferent branchial sinus.
eff. = efferent branchial vein.
B.C. = Branchio cardiac vein.
Pc.O. = Pericardial opening.

The Blood.

The blood is an almost transparent fluid having a slight pinkish-blue tint (due to the presence of haemocyanin). The colour deepens on exposure to air. The blood consists of an almost colourless lymph in which are found numerous small cells or *amoebocytes*. There are two principal kinds of amoebocytes:—(1) Semi-transparent cells, which are amoeboid and have finely granular protoplasm. There is a well-defined nucleus. (2) Globular cells containing refringent granules. As pointed out by Cuénot,* these granules are similar to the eosinophilous granules recognised by Ehrlich in the leucocytes of various vertebrates. Hence Cuénot designates the second kind the *Eosinophilous amoebocytes.*† They are composed of an albuminous material.

In the neighbourhood of the cephalic artery, above the fore-gut, is a cellular mass which, according to Cuénot, is a lymphatic gland in which the amoebocytes are formed.

Cuénot has recognised five kinds of amoebocytes in the blood, which are all stages in the transformation of the clear amoebocytes mentioned above. The eosinophilous amoebocytes are also formed from the clear amoebocytes, and mark a stage in the degeneration of the cell. The eosinophilous granules present in the amoebocyte are small and few in number at first. They become comparatively large in size and very numerous until the entire cell is filled with a solid mass. The cell then degenerates rapidly and finally disappears. The granules

---

* Cuénot, L. "Études physiologiques sur les Crustacés Décapodes." *Archives de Biologie*, T. XIII, 1895, p. 245.

† The granules readily take the following stains:—Picric acid, eosin, indigo-carmine, fuchsine acid and "orange G." They remain absolutely colourless under the following stains:—Methyl green, dahlia, crystal violet, methylene blue and safranin. (CUÉNOT).

are probably dissolved in the lymph. The cells themselves are eaten by the young clear amoebocytes, which thus act as *phagocytes.* The phagocytic function is limited to the young cells only. After the appearance of the eosinophilous granules they cease to act as phagocytes.

Cuénot* claims also to have discovered a phagocytic gland which is quite distinct from the lymphatic gland. It is a swollen mass of cells situated on the terminal branches of the hepatic artery. The cells resemble the free amoebocytes and probably act as phagocytes.

When the blood ceases to flow, coagulation takes place. This is effected by the clear amoebocytes. These cells become changed in their appearance, and they send out numerous fine pseudopodia which unite with those of the neighbouring cells to form a network, in which all the cells are united together. Thus a clot is formed.

The "Pericardial Pouch."

At each of the postero-lateral corners of the pericardium there is a structure which Cuénot† designated the "poche pericardiale." In Cancer each pouch lies on the upper part of the posterior thoracic epimera and projects into the branchial chamber. Externally, each pouch is covered with a cuticle which is continuous with the chitinous wall of the branchial chamber. The cavity of the pouch, which is continuous with the pericardial sinus, is to some extent broken up by connective tissue cells and by muscle fibres. The function of these pouches is unknown.

---

* Cuénot, L. *Comptes Rendus*, 1903 (No. 137), p. 619.

† Cuénot, L. "Études physiologiques sur les Crustacés Décapodes." *Archives de Biologie*, t. XIII (1895).

RESPIRATORY SYSTEM.

(Pl. X, figs. 63, 64; Pl. XI, figs. 65, 66, 67).

Respiratory Mechanism.

Respiration is effected by means of gills or branchiae, which are outgrowths from the walls of the thorax. The gills do not project directly on to the exterior, but are situated in the branchial chambers at each side of the cephalothorax.

The branchial chambers—one pair. The cavity of each chamber is morphologically a part of the exterior, and its walls are formed by the downgrowth of the carapace at each side. The sub-branchial region of the carapace is closely applied to the coxopodites of the pereiopods, and here turns inward to form the wall of the branchial chamber. In transverse section the chamber has a triangular shape (Pl. IX, fig. 56), and its walls may be spoken of as ventral, dorso-lateral and inner. The two former are membranous and are continuations of the inturned edge of the sub-branchial region.

The postero-lateral portion of the digestive gland rests upon the roof of the branchial chamber. Between the floor of the chamber and the sub-branchial region of the carapace there is a mass of connective tissue. In the anterior region of the chamber the floor is raised into a well defined transverse ridge. In a full-sized crab this groove is about $\frac{1}{4}$ inch in front of the anterior inhalent aperture. In sections through this ridge the epidermis is greatly elongated and has a glandular structure. There are also tegumentary glands below the epidermis. The podobranch of the second thoracic somite is closely applied to the posterior side of this ridge. For the sake of convenience I designate the latter the *branchial ridge*. Its probable function will be discussed below.

The inner wall is well calcified, and is formed by the thoracic epimera ("flancs"). The gills rest on the inner wall.

The development of the branchial chambers would tend to produce a stagnant layer of water around the respiratory organs. But the nature of their function requires that the gills should be in contact with water containing a normal amount of dissolved oxygen. So that, correlated with the formation of the branchial chamber, an arrangement has been effected for producing a constant stream of water over the gills. This necessitates two things (1) inhalent and exhalent openings in connection with each branchial chamber, and (2) some mechanism for producing the current of water through the chambers.

In the Macrura the inhalent opening is situated between the inner edge of the branchiostegite and the base of the thorax. In Cancer, however, this opening is considerably smaller. Between the chela and the last pereiopod the sub-branchial region is closely applied to the base of the thorax, and the line of separation between the two is guarded by a thick growth of long setae, so that it is highly improbable that any water can gain entrance to the branchial chamber in this region. Above the last walking leg, however, there is a small slit opening into the posterior region of the branchial cavity. This is the **posterior inhalent aperture.** In front of the coxopodite of the chela there is a well-defined transverse opening leading into the anterior part of the branchial cavity. This is the **anterior inhalent aperture.** The latter is guarded in front by the coxa and flabellum of the third maxillipede, which, on their posterior borders, are clothed with long setae. There are also numerous setae on the anterior face of the coxopodite of the chela. These two sets of setae probably strain the water as it passes through to the branchial chamber.

At its anterior end the branchial chamber is extremely shallow on account of the roof sloping down at a considerable angle. Above the branchial ridge, already referred to, there is an extremely narrow cavity between the top of the ridge and the roof of the chamber. This cavity is continued forward and inward into the pre-branchial chamber.

Pre-branchial chambers. One pair. They are situated at the side of the mouth, each being in front of and connected with the branchial chamber of the same side. Each chamber is produced by the ingrowth of the inner edge of the anterior part of the sub-branchial region of the carapace. Its walls, therefore, are continuous with those of the branchial chamber. The pre-branchial chamber is much smaller and shallower than the branchial chamber. On its anterior and inner side it is connected with the exterior by means of a wide opening—the **exhalent aperture.**

The current through the branchial and pre-branchial chambers is caused by the vigorous action of the scaphognathite. The latter lies in the pre-branchial chamber, and when at rest the anterior surface faces upward. Normally the scaphognathite displays the following movements:—The action of the extensor muscles tends to pull the ventral surface backward. This is followed by a sharp forward blow of the outer lobe of the scaphognathite, caused by the action of the outer flexors. This is immediately followed by an undulating movement of the inner lobe, caused by the accessory muscles and inner flexors. In this way the water is baled out of the exhalent aperture. This current from behind forward is probably assisted by the energetic action of the exopoditic flagella of the maxillipedes. The extremely active motion of these flagella is quite obvious, and they probably form an accessory current-producing organ of no mean importance.

The normal current, as we have seen, flows from behind forwards, entering at the inhalent apertures and leaving by means of the exhalent aperture. In Corystes, Atelecyclas and Portumnus, Garstang* observed that the branchial current was sometimes reversed. Bohn† has extended these observations, and finds this phenomenon is of universal occurrence throughout the Brachyura. In Cancer the habit of reversing the branchial current does not appear to be very strongly developed. Bohn suggests that the reversal takes place in order to rest the fatigued muscles of the scaphognathite, as the energetic action is performed by different muscles in the two cases.

The flabella (epipodites) of the maxillipedes pass backward into the branchial chamber. That of the first maxillipede (*f.m.*^{1}) is by far the largest, and extends backward throughout the whole length of the branchial chamber lying upon the gills. The flabellum of the second maxillipede (*f.m.*^{2}) lies below the gills towards the dorsal side of the epimera. It only extends as far forward as the middle of the epimeron of the fourth thoracic somite. The flabellum of the third maxillipede (*f.m.*^{3}) also lies below the gills and on the ventral and outer side of the second flabellum. Its proximal portion forms part of the anterior boundary of the anterior inhalent aperture. It extends backward to the posterior end of the epimeron

---

* Garstang. "The Habits and Respiratory Mechanism of *Corystes cassivelaunus*."—*Journal Marine Biological Association*, Vol. IV (N.S.), p. 223.

"The Respiratory Phenomena of *Portumnus nasutus*." *Journal Marine Biological Association*, Vol. IV (N.S.), p. 402.

† Bohn, G. "Sur la Respiration des Décapodes." *Bull. Sci. France et Belg.* T. XXXVI (Ser. 6), 1902, p. 178.

of the fifth thoracic somite. All three flabella are richly clothed with long setae.

In the living animal the flabella have a slow motion over the surface of the gills. Their main function is, undoubtedly, to keep the surface of the gills free from sand and mud which may be suspended in the water carried into the branchial chamber. In a crab from Port Erin the flabellum of the first maxillipede of the right side had been destroyed. In consequence of this the outer surface of the gills of the right side was covered with a layer of fine mud, which must have rendered the outer portions of the gills inoperative. It is doubtful whether the flabella have any function with regard to the formation or regulation of the current of water over the gills. At any rate, this function, if present, has not the importance ascribed to it by Claus.*

The description of the respiratory mechanism of the Brachyura given by Milne-Edwards has become almost classic, and has been accepted by most workers on the subject. According to this explanation, the water enters the branchial chamber at *one* place, viz., in front of the coxopodite of the chela. On entering the branchial chamber the current passes backward below the gills and then forward above the gills and out to the exterior through the pre-branchial passage.

This explanation has been disputed by Bohn,† who states that the water enters the branchial chamber throughout the entire length of the inner edge of the sub-branchial region, the entrance being especially marked at the anterior and posterior inhalent apertures ("l'orifice inspirateur antérieur et postérieur," Bohn). According to Bohn, the water entering by the anterior

---

* Claus. *Arbeit. Zool. Instit. Wien*, Bd. VI., Hft. 1.

† Bohn. *Op. cit.*

inhalent aperture does not pass backward but passes directly forward to the pre-branchial chamber, and only bathes the anterior part of the sixth gill and all the gills in front of this. The posterior gills are supplied by water entering the posterior inhalent aperture. He denies that there is a backward current caused by the flabella.

My own observations on these points are as follows: —There are two inhalent apertures—the anterior and posterior. Between these two apertures the inner border of the sub-branchial region is closely applied to the side of the thorax, and there appears to be absolutely no inflow of water along this border. Of the two inhalent apertures, the anterior is decidedly the most important. The current of water flowing in through the posterior aperture is very small. I think it extremely probable that some of the water drawn in at the anterior inhalent aperture passes backward, but I do not accept the explanation of Claus—that the backward current is caused by the flabella of the maxillipedes. The presence of the well-defined branchial ridge (see above) in the anterior part of the branchial cavity has suggested another explanation. The ridge is situated on the floor of the branchial chamber immediately in front of the anterior inhalent aperture. It arises near the inner side of the chamber, and passes in front of the aperture as a transverse wall. On the outer side of the aperture it turns backward and outward, and after extending half way down the branchial chamber, it gradually dies away. At its anterior end the branchial chamber is exceedingly shallow, so that the ridge almost extends to the roof of the chamber, leaving only a narrow slit which communicates with the pre-branchial cavity. As the water flows in through the anterior inhalent aperture, it will be drawn forward by the vigorous action of the scaphognathite.

The branchial ridge, however, will act as a formidable barrier, and although some of the water will undoubtedly pass directly over into the pre-branchial chamber, it is reasonable to suppose that some of it will have its course changed by the branchial ridge and will pass backward, following the direction of the latter.

The Gills (Figs. 63, 64).

The gills arise from each side of the thorax and lie upon the inner wall of each branchial chamber, i.e., on the thoracic epimera. According to the terminology introduced by Huxley, the gills may be placed in three categories the *podobranch* arising from an appendage, the *arthrobranch* arising between an appendage and the epimeron, and the *pleurobranch* arising from the epimeron.

In Cancer there are only nine gills at each side. The following is the branchial formula.

Thoracic somites	1	2	3	4	5	6	7	8	Total.
Podobranch	—	1	1	—	—	—	—	—	2
Anterior arthrobranch	—	1	1	1	—	—	—	—	3
Posterior arthrobranch	—	—	1	1	—	—	—	—	2
Pleurobranch	—	—	—	—	1	1	—	—	2
Epipodite	(1)	(1)	(1)	—	—	—	—	—	(3)
Total	(1)	2 + (1)	3 + (1)	2	1	1	—	—	9 + (3)

First gill. Podobranch of the second thoracic somite (figs. 63, 64, *g.* 1). It arises from the coxopodite of the second maxillipede between the exopodite and the flabellum. It lies with its outer face in contact with the posterior side of the branchial groove, and its inner face is closely applied to the basal portions of the gills 2 to 6. Its apex points backward and outward. Length 22 mm.*

Second gill. Arthrobranch of the second thoracic somite (*g.* 2). Arises from the arthrodial membrane of

---

* The measurements of the gills are taken from a crab having a carapace breadth of 12 cm.

the second maxillipede. It passes directly backward and lies upon the fused epimera of the first and second thoracic somites. Its long axis is at right angles to that of the first gill. Length 25 mm.

Third gill. Podobranch of the third thoracic somite (*g.* 3). Arises from the elongated coxopodite of the third maxillipede. It is extremely short and is wedged in between the first and fifth gills, at the base of the latter. Length 7 mm.

Fourth gill. Anterior arthrobranch of the third thoracic somite (*g.* 4). Arises, together with the fifth gill, from the arthrodial membrane of this somite. It lies on the thoracic epimera, immediately behind the second gill. Length 26 mm.

Fifth gill. Posterior arthrobranch of the third thoracic somite (*g.* 5). Arises from the same place as the fourth gill, and lies immediately behind the latter. Its base is notched in order to receive the third gill. Length 25 mm.

Sixth gill. Anterior arthrobranch of the fourth thoracic somite (*g.* 6). Arises together with the seventh gill from the arthrodial membrane between the chela and the fourth thoracic somite. It lies behind the fifth gill. Total length 37 mm.

Seventh gill. Posterior arthrobranch of the fourth thoracic somite (*g.* 7). Arises from the same place as the sixth gill and lies immediately behind it. Total length 37 mm.

Eighth gill. Pleurobranch of the fifth thoracic somite (*g.* 8). Arises from the epimeron of this somite. Total length 28 mm.

Ninth gill. Pleurobranch of the sixth thoracic somite (*g.* 9). Arises from the epimeron of this somite, upon which it lies, immediately behind the eighth gill.

Structure of a gill (figs. 65, 66, 67).

Each gill is of the phyllo-branchiate type. With the exception of the third gill, they are all pyramidal in shape, their apices pointing upward (with the exception of the first gill, in which the apex points backward). Along the outer side of each gill runs the afferent branchial vessel, and the efferent vessel is situated on the inner side. The gill is composed of numerous lamellae, which have the appearance of the leaves of a book. Each lamella is covered with a thin layer of chitin. This layer is also continued on the outside of the afferent and efferent vessels. The gills, therefore, are covered by part of the general chitinous exoskeleton, and at ecdysis this outer chitinous layer is cast with the remainder of the exoskeleton. In transverse section each gill is triangular (fig. 65). The efferent vessel is situated at the apex of the triangle, and the afferent vessel lies in the middle of the base of the triangle. Stretching across from the afferent to the efferent vessels is the *branchial septum* (*i. b. s.*), which separates the anterior from the posterior lamellae.

In the branchial septum between the afferent and efferent vessels transverse sections reveal the presence of scattered cells, generally having brown contents (fig. 67, *br. c.*). These are excretory cells, and together constitute the branchial excretory organ (see section on Excretory System). Cuénot* found that when a crab is injected with ammonium carminate or methylene green these substances are taken up by the excretory cells of the branchial septum. These cells, therefore, have the same reaction as the end-sac epithelium.

I have not been able to find any trace of the branchial glands discovered by Allen† in Palaemonetes. Cuénot,

---

* Cuénot. *Arch. de Biol.*, T. XIII, p. 245.

† Allen. *Q.J.M.S.*, Vol. XXXIV, p. 75.

however, has found them close to the efferent vessels in several of the Bracyhura. They do not appear to be present in Cancer.

In longitudinal sections through the gill (fig. 66) the lamellae are seen to be lined by epidermal cells (*ch. ep.*). There is a narrow cavity containing blood separating the upper and lower layer of cells. This cavity, or *lamellar sinus* (*l.s.*) is bridged over in certain parts by the junction of the two layers of epidermal cells. At the free edge of each lamella the lamellar sinus is continuous with the larger *outer lamellar sinus* (*o. l. s.*). This runs around the edge of the lamella, and the epidermal cells in this region are extremely flattened. Each lamellar sinus is in contact with the afferent branchial vessel on the outer side, and the efferent branchial vessel on the inner side. It is in the lamellae that the aeration of the blood is effected.

Dorso-ventral muscles (Pl. VIII, fig. 51, Pl. IX, fig. 56, *d. v. m.*).

Extending upward from the membranous roof of the branchial chamber to the carapace, is a series of muscles which may be termed the *dorso-ventral muscles.* The arrangement of these muscles will not be described in detail. There are three sets of muscles at each side (see fig. 51). The outer and middle series are arranged in two parallel lines running antero-posteriorly. The inner set is small, and is situated above the inner region of the branchial chamber. The roof of the chamber is considerably lower at the anterior end than in the posterior region, so that the anterior muscles are consequently longer than the posterior muscles.

Since the roof of the branchial chamber is soft and membranous, it is capable of considerable movement. The contraction of the dorso-ventral muscles will effect the raising of the branchial roof, and thus produce a corresponding increase in the capacity of the branchial chamber. When the muscles relax, the weight of the superimposed digestive gland and gonad will be sufficient to depress the roof and decrease the volume of the branchial chamber.

Although it is difficult to understand the precise function of these muscles, it must be conceded that their action may be of supreme importance in connection with the branchial chamber, either as a current regulator or as an accessory current-producing organ. It will not be surprising if additional investigations on this point throw new light on some of the problems discussed above.

EXCRETORY SYSTEM

(Pl. X, figs. 57, 58, 59, Text figs. 11 and 12).

Excretion is performed in three different parts of the body.

(i) by the Antennary glands and their connections.
(ii) by the Ferment cells of the digestive gland.
(iii) by the Branchial excretory organ.

(i) The Antennary Glands and Connections.

These form a complicated system of organs at each side of the body. The right and left sides, which are similar to one another are absolutely separate, although in certain places the two parts are in very close contact. This excretory organ is a coelomoduct*, and may be divided into three portions on each side. The first part, or the **antennary gland** ("green gland," "rein antennarie"), is situated in the cephalic region immediately behind the eye socket. It is a small spongy mass of a

---

* Goodrich. Various papers in *Q.J.M.S.*, Vols. XXXVII-XLV.

light green colour, having a triangular shape when viewed from above. At its posterior and inner corner it is connected with the second portion—the **bladder** ("vessie," Marchal; "nephro-peritoneal sac," Weldon). This is an extensive thin-walled sac having several large branches. It is easily made out because of the dark brown colour of its walls. Immediately in front of the antennary gland the main portion of the bladder is connected ventrally with the third part—the **ureter.** This is a spacious tube leading downwards and opening to the exterior beneath the *operculum*, which is situated on the ventral side of the basal portion of the second antenna.

(1) The Antennary Gland (Pl. X, figs. 58, 59, Text fig. 11) is made up of two portions. On the dorsal side is a small vesicle—the **end sac** ["saccule," Marchal] (fig. 58, *end. s.*, Text fig. 11, *e.s.*). From the floor of the end sac are given off numerous blind prolongations, which may either be simple or branched. The epithelium lining the end sac (*e.es.*) is composed of flattened irregularly-shaped cells, some of which project more than others into the cavity of the end sac. Many of these cells contain small yellow oil globules. Marchal speaks of the epithelium of the end sac in Maia as being columnar, but in Cancer it has a decidedly squamous appearance. Marchal also states that the walls of the end sac are more than one cell thick in places. This does not appear to be the case in Cancer. The cells of the end-sac epithelium do not stain so deeply as the epithelial cells of the lower part of the antennary gland.

The ventral portion of the antennary gland is much larger than the dorsal end sac. In sections this lower portion is seen to have a very complicated structure, and is, therefore, known as the **Labyrinth** (fig. 58, Text fig. 11, *Lab.*). The essential part of the labyrinth is the *Renal tube* (*tu.*), the cavity of which is connected in front with the end sac and behind with the bladder. The roof of the renal tube is in close contact with the floor of the end sac. It may be conceived that the lumen of the renal tube was primitively quite simple, so that in such a condition of things the ventral part of the antennary gland would show none of the complicated structure which we designate the labyrinth. The complexity has been produced in two ways. As already mentioned, the floor of the end sac sends downwards numerous branched tubes, the cavity of each tube being connected with that of the end sac, and its walls being lined by the squamous epithelium typical of the end sac. The floor of the end sac is closely applied to the roof of the renal tube, so that these prolongations push before them the epithelium of the renal tube, at the same time breaking up its lumen. Invaginations also appear in the ventral and lateral walls of the renal tube, giving rise to partitions across the lumen of the tube known as *trabeculae*. These ventral and lateral ingrowths are not caused by the extension of the end sac. In sections the dorsal ingrowths of the end sac can always be distinguished from the ventral ingrowths by the fact that the former appear to be lined by two rows of epithelial cells—the squamous epithelium of the end sac, carrying before it the epithelium of the renal tube, the two only being separated by a narrow blood sinus. The ventral ingrowths are only lined by the epithelium of the renal tube, and enclose portions of connective tissue which have been drawn in from tissue surrounding the gland. The epithelium of the renal tube (fig. 59, *e. tu.*) is distinctly columnar, and the protoplasm has a finely striated appearance. The cells are lined by a thin border, which is generally described as a cuticle.

In sections through the antennary gland the following structures may, therefore, be made out:

Dorsal. (*a*) The main portion of the end sac. This is a simple cavity lined by squamous epithelium, the cells of which do not take the stain well.

Ventral. The labyrinth made up of the following parts:—

(*b*) Numerous small spaces with an inner lining of squamous epithelium (ventral prolongation of the end sac), and an outer lining of deeply stained columnar epithelium.

(*c*) Irregular spaces surrounded by columnar epithelium which is deeply stained. On the side facing the lumen the cells are lined by a fine border. These are portions of the renal tube.

(*d*) Small spaces lined by the renal tube epithelium. In the spaces are connective tissue cells and blood. These are the trabecular ingrowths. In some parts the epithelium of the trabeculae fuses with the epithelium of the roof of the renal tube, so that the blood sinus passes right through the labyrinth.

(*e*) Between the epithelium of (*b*) and (*c*) may be made out small blood sinuses.

(2) The bladder (Fig. 57, Text figs. 11, 12) is extensive and complicated. It is a thin-walled sac readily made out on account of its deep brown colour.

The Main Vesicle is situated above the antennary gland, and its cavity is continuous with that of the renal tube at the inner and posterior end of the antennary gland In front of the gland it is connected with the ureter. From the main vesicle are given off the following lobes:—

(*a*) at the anterior end—Epigastric lobe, Progastric lobe, Antero-lateral lobe, Cerebral lobe.

(β) at the posterior end—Hepatic lobe, Suprahepatic lobe, Paragastric lobe, Oesophageal lobe.

The **Main Vesicle** [" sac vésical," Marchal] (*M.V.*) is situated below the anterior and outer corner of the stomach and above the antennary gland, with which it is connected at the posterior of the latter. On its ventral side the main vesicle is connected with the ureter immediately in front of the antennary gland.

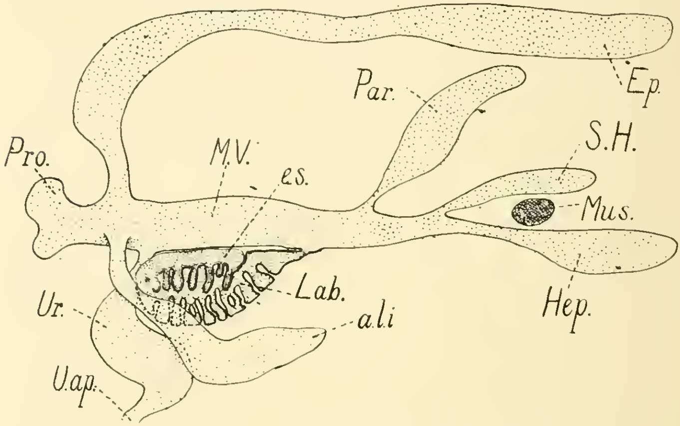


FIG. 11.—Diagrammatic longitudinal section of the excretory system.

Ep. = Epigastric lobe.
Pro. = Progastric ,,
Par. = Paragastric ,,
S.H. = Supra-hepatic ,,
Hep. = Hepatic ,,
a.l.i. = Inner part of antero-lateral lobe.

M.V. = Main vesicle.
Mus. = External adductor muscle of mandible.
e.s. = End sac.
Lab. = Labyrinth.
Ur. = Ureter.
U. ap. = External aperture of ureter.

The **Epigastric lobe** (Fig. 57, *e. lb.*, Text fig. 11, *Ep.*) is the most obvious part of the bladder when dissecting the crab from above. It arises from the anterior end of the Main Vesicle. It passes forwards and upwards along the front wall of the fore-gut and turns back along the dorsal wall, extending as far back as the pyloric region. It is clearly separated in the middle line from the corresponding lobe of the other side. It is broad anteriorly, and becomes narrower and more irregular in shape towards the posterior end. The outer part of the broad anterior portion is slightly reflected down the side wall of the fore-gut and comes into contact with the paragastric lobe.

The **Progastric lobe** (Fig. 57, *p. lb.*, Text fig. 11, *Pro.*), is, strictly speaking, part of the Epigastric lobe. It is situated close to the connection between the Main Vesicle and the Epigastric lobe. It is on the inner side of the latter, and is closely applied to the front wall of the stomach. The lobes of each side come into very close contact in the median line, and it is only by very careful dissection that they are seen to be separate.

The **Antero-lateral lobe** ["lobe du muscle adducteur," Marchal] (Fig. 57, *a. lb.*, Text fig. 11, *a. l. i.*) arises from the anterior and outer corner of the Main Vesicle. It consists of two parts:—

(*a*) An inner lobe (Text fig. 12, B, *a. l. i.*), which passes inwards beneath the antennary gland.

(*b*) An outer lobe (Text fig. 12, B, *a. l. o.*), which passes outwards beneath the digestive gland as far as the origin of the outer adductor muscle of the mandible.

The **Cerebral lobe** (fig. 57, *c. lob.*) arises from the anterior and inner corner of the Main Vesicle. It passes inwards above the cerebral ganglia, and almost meets the corresponding lobe of the other side.

The **Hepatic lobe** [" arriere vessie " (part), Marchal] (fig. 57, *h. lb.*, Text fig. 11, *Hep.*) arises from the posterior and outer corner of the Main Vesicle by a very narrow portion, which passes beneath the outer adductor muscle of the mandible close to its insertion on the mandibular apophysis. The main part of the lobe passes outwards beneath the digestive gland and follows the course of the gland to its extreme outer and posterior corner. Along the outer edge of the digestive gland the lobe turns upwards and covers the outer part of the dorsal portion of the gland. Owing to its position beneath the digestive gland the hepatic lobe is not readily seen, in spite of its large size. Near the origin of this lobe from the Main Vesicle a small inner lobe is given off, which ends blindly near the posterior oesophageal lobe.

The **Supra-hepatic lobe** (fig. 57, *s. lb.*, Text fig. 11, *S. H.*) is not well developed in Cancer. It arises from the Main Vesicle on the inner side of the origin of the hepatic lobe, and passes above the digestive gland on each side of the fore-gut.

The **Paragastric lobe** (fig. 57, *g. lb.*, Text fig. 11, *Par.*) arises from the posterior end of the Main Vesicle near to the origin of the supra-hepatic lobe. Its outer side is applied to the mandibular apophysis, and on its inner side it comes into contact with the side wall of the fore-gut. It passes up the side of the latter and touches the epigastric lobe.

The **Oesophageal lobe** arises from the inner and posterior corner of the Main Vesicle. It passes inwards and divides into anterior (*as. lb.*) and posterior (*po. lb.*) portions which wrap around the oesophagus, touching the corresponding lobe of the other side in the middle line.

In sections through a young crab (width of carapace 15 mm.) the epithelium of the bladder (Pl. XII, fig. 82) consists of columnar cells 20μ long and 15μ wide. The protoplasm is denser near the outer portion of each cell, and the inner portion of the protoplasm is greatly vacuolated. In the outer region of the cell the protoplasm is arranged in longitudinal strands, which gives rise to the

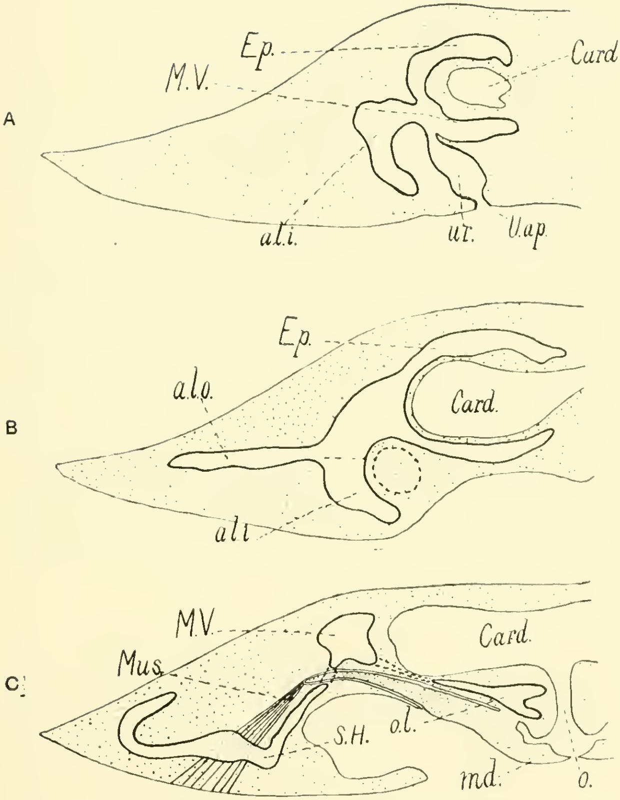


Fig. 12.—Diagrammatic transverse sections through the left half of the body to show the excretory system.

A. = at the level of the external excretory aperture.

B. = at the level of the "green gland." (The gland is shown as a dotted line.)

C. = at the level of the oesophagus. (For *S.H.* read *Hep.*)

Card. = cardiac region of the fore-gut. *o.l.* = oesophageal lobe.

o. = oesophagus. *md.* = mandible.

a.l.o. = outer portion of antero-lateral lobe.

(Other references as in Fig. 11).

striated appearance noted by Weldon and Allen. In some cases these striations are carried through to the inner region of the cell, but generally the protoplasm is divided into a deeply-stained outer portion, which exhibits the striations mentioned above, and a more lightly stained inner portion in which the strands of protoplasm are few in number, thus causing the vacuolated appearance. The nucleus of the bladder epithelial cells has a diameter of 6μ, and is situated near the centre of the cells.

(3) The Ureter (Text fig. 11, 12, A, *Ur.*) is a spacious sac situated on the inner side of the antennary gland, partly in front of and partly below the gland. The connection with the main vesicle is a narrow opening immediately in front of the anterior and inner corner of the gland. The ureter passes downwards, and opens to the exterior on the ventral surface of the proximal portion of the second antenna. It is lined with epithelial cells, which are distinctly larger than those of the bladder and take the stain more distinctly.

The relation of the parts in the neighbourhood of the external orifice is of interest. The proximal region of the ventral side of the second antenna is occupied by a small, irregularly-shaped plate—the *operculum* (Pl. II, fig. 5, *op.*), which is freely movable. The movement is possible because of its connection, by means of a flexible membrane, with the surrounding hard parts. The membrane forms a pocket-like invagination around the operculum, and is deepest on the inner and posterior side, so that the movement is greatest on this side when the operculum is raised. When the operculum is elevated it is seen that the membrane is perforated by a distinct orifice on the inner and posterior side. This is the *excretory orifice.* Hence Marchal* termed the membrane

---

* Marchal. "Appareil excréteur des Crustacés Décapodes." *Arch. Zool. exp. et gén.*, T. X (Ser. 2), 1892.

surrounding the orifice the *excretory membrane.* He states that the excretory fluid is not ejected as the result of muscular contraction around the walls of the sac-like ureter. There are no muscles in the walls of the ureter. The outflow is of a passive character, and takes place whenever the excretory orifice is opened. Although it is probable that the operculum does not fit tightly enough to prevent the outflow of the excretory fluid, yet it is when the operculum is closed that the fluid ceases to escape. When the operculum is drawn down closely into its socket, the lips of the excretory orifice are pressed together because of the contraction of the excretory membrane. On the contrary, when the operculum is raised the membrane is extended and the orifice opens. As shown by Marchal, the movements of the operculum are under the control of two muscles—an *elevator muscle* for extending the operculum membrane, and a *depressor muscle* for drawing the operculum down into its socket.

Mode of Excretion.

According to Marchal, the excretory fluid is not produced by diffusion across the epithelial cells of the antennary gland and bladder, but is the result of an actual breaking away of a part of each of the epithelial cells. An examination of the excretory fluid will show that there are numerous bladder-like vesicles and also cells floating in the fluid. In sections of the bladder, and also in teased preparations, one can see, as stated above, that the protoplasm is highly vacuolated on the inner side of each epithelial cell. Moreover, in some cells there is one large vacuole, or vesicle, projecting into the lumen of the bladder and surrounded by an extremely thin layer of protoplasm. In the interior of the vesicle is a fluid sometimes containing refringent granules. Each vesicle which contains excretory fluid and excretory granules ultimately breaks free from the cell and floats away in the excretory fluid.

In addition to this method, it is highly probable that some of the excretory fluid passes through the epithelial cells into the cavity of the bladder by the ordinary process of diffusion.

The above mode of excretion is not only performed by the cells of the bladder, but also, according to Marchal, by the cells of the labyrinth, in a slightly modified manner.

As stated above, the cells of the renal tube in the labyrinth appear to be lined by a thin cuticle. Marchal states that it is *not* a cuticle, but that the appearance is due to a row of very small vacuoles lining the inner side of each epithelial cell. These vacuoles gradually increase in size, fuse together, and the single large vesicle formed is liberated into the lumen of the renal tube, in a very similar manner to the method described above in the case of the bladder.

In the cavity of the end sac the fluid contains small vesicles containing yellow oil globules. These have been excreted from the epithelial cells of the end sac, which, as mentioned above, often contain yellow oil globules.

In addition to these, Marchal states that in Maia *entire* epithelial cells break free from the walls of the end sac.

At first Marchal believed that in Maia the wall of the end sac was composed of a single layer of cells, and he expressed surprise that it was possible for cells to break away bodily from such a layer without breaking the continuity of the walls of the end sac. Finally he decided that the wall was several cells thick in certain places, and that it was from these places that the cells found in the lumen of the end sac had broken free. Whatever may be the condition of things in Maia, there is no doubt that in Cancer the walls of the end sac are uniformly only of one cell in thickness. As in Maia, there are cells in the cavity of the end sac, and I agree with Marchal that these are epithelial cells of the end sac which have broken away. There appears to be nothing surprising that certain cells of this single layer of epithelial cells should be gradually nipped off by the activity of the surrounding cells and thus shed into the lumen of the end sac. An examination of serial sections through the end sac reveals cells in every stage of this process of shedding. This explains why certain cells of the end sac epithelium project farther into the lumen than others, as described above.

Cuénot investigated the excretory organs of Crustacea by injecting various colouring matters into the body of the living animal. He has placed these colouring matters into three groups, according to where they were eliminated.

(1) Fuchsin acid, Bismarck brown, safranin, indigo-carmine, etc.
(2) Methylene green, ammonium carminate, etc.
(3) Methylene blue.

After such injections it was found that the cells of the renal tube of the labyrinth and the cells of the bladder have a decidedly alkaline reaction and excrete the substances of the first category. The cells of the end sac, on the other hand, have an acid reaction and eliminate the substances of the second category.

By the above method of injection Cuénot discovered that in addition to the antennary gland and its connections there are two other kinds of excretory cells, viz.:—The ferment cells of the digestive gland, and the cells in the branchial septum.

Development of the Antennary Gland.

According to Waite,* who studied the development of the gland in Homarus, the end sac alone arises from the mesoderm when the embryo is only five days old, and its lumen is for a long time completely enclosed by mesodermal cells. An ectodermal ingrowth (which ultimately becomes the renal tube of the labyrinth) occurs at about the twenty-eighth day. The lumen of the end sac does not become continuous with that of the labyrinth until the embryo is nearly 300 days old. The complications in the walls of the renal tube to form the labyrinth do not occur until the third larval stage. The bladder is formed by a dorsal outgrowth of the ectodermal tube. Therefore, only the cavity of the end sac represents part of the original coelom. The renal tube of the labyrinth, the bladder and the ureter are all ectodermal in origin. Although the development of the green gland in the Brachyura has not been investigated, there is no reason to believe that it presents any striking differences from that of the Macrura.

(ii) FERMENT CELLS OF THE DIGESTIVE GLAND.

Part of the contents of the ferment cells are of an excretory nature, and when the contents of these cells pass down the digestive tubules into the mid-gut the excretory products are separated away and are carried to the exterior along with the faeces. The ferment cells of the digestive gland take up methylene blue when this colouring matter is injected into the body of the living animal. The large coloured mass inside each ferment cell is coloured light blue. Inside this mass there are small bodies, which take a dark blue stain. According to Cuénot, in five days after the experiment the blue

---

* Waite. *Bull. Mus. Harv.*, Vol. XXXV, No. 7 (1899).

stain will pass out into the lumen of the tubule and thence to the alimentary canal, where it is got rid of along with the excrement.

(iii) Branchial Excretory Organ.

This is found in the gills in that portion of the tissue situated between the afferent and efferent branchial veins. According to Cuénot, the excretory cells are continued along the sides of the branchio-cardiac veins When the crab is subject to Cuénot's system of injection, it is found that the cells of the branchial excretory organ act like the cells of the end sac They have an acid reaction and eliminate substances of the second category.

NERVOUS SYSTEM.

The nervous system of the Brachyura (*Carcinus maenas*) has been investigated in detail by Bethe.* It is proposed to give here only a short account of the nervous system of Cancer.

The nervous system may be described briefly as consisting of two main nerve masses the fused pre-oral cerebral ganglia and the fused ganglia of the post-oral region. The two are connected by a pair of commissures which pass round the oesophagus. With the cerebral ganglia are connected the nerves supplying the eye, antennules and antennae. All the post-oral appendages and somites are innervated from the posterior nerve mass which lies in the thorax. At each side of the oesophagus there is a ganglion on the commissure, from which arises the stomatogastric nerves supplying the fore-gut.

The brain is the centre of co-ordinated movement, and each ganglion of the ventral nerve mass is the reflex centre for the appendage which it supplies.

---

* Bethe. *Arch. f. Mikr. Anat.*, Bd. XLIV (1895), pp. 579-622; Bd. L (1897), pp. 460-546, 589-639; Bd. LI (1898), pp. 382-452.

The Brain.

The Brain (cerebral ganglia, *c.g.*) is situated above the anterior end of the epistoma. It is roughly rectangular when viewed from above, and is formed of a complex mass of nerve cells and fibres. The anterior half of the brain is connected with the nerve fibres supplying the eye and optic peduncle. From the posterior half arise the nerves innervating the antennules, antennae, the sense organs of the antennules, and also the nerves supplying the integument. The nerve fibres from the different parts become aggregated in the brain in definite masses or *neuropiles* ("Punktsubstanz," Leydig). Between the neuropiles there are numerous nerve cells more or less closely packed. The main neuropiles are as follows:—

Connected with the optic fibres. The *antero-superior*, *median* and *posterior optic neuropiles*, all situated in the anterior half of the brain. Also the *inferior optic neuropile* extending below the others.

Connected with the oculomotor fibres: The paired *lateral oculomotor neuropiles* situated on the outer side of the optic neuropiles, and also a *median oculomotor neuropile* lying in the middle line behind the optic neuropiles.

Connected with the first antenna (antennule). The *median neuropile of the first antenna* situated in the middle line below the median oculomotor neuropile. The *lateral neuropiles of the first antenna* situated ventrally at each side, behind the inferior optic neuropiles.

Connected with the second antenna. There are three neuropiles situated at each side of the posterior region of the brain, viz., the *median*, *posterior* and *lateral neuropiles of the second antenna.*

Connected with the tegumentary nerves. The *superior and inferior tegumentary neuropiles* situated in the posterior region of the brain, slightly anterior to the neuropiles of the second antenna.

At each side of the brain there is a globular mass of radiating fibres lying between the oculomotor and the tegumentary nerves. This is the *globulus.* There is a tract of nerve fibres extending from the globulus to the median optic neuropile. It is probable that some of the fibres of the otocyst nerve arise from the globulus.

The chief groups of nerve cells in the brain are as follows: —

The *supero-median* cells are on the inner side of the antero-dorsal region of the brain.

The *infero-median* cells are situated on the ventral side of the posterior part of the brain near the median line.

The *supero-lateral* cells are situated dorsally on the inner and anterior side of the globulus.

The *infero-lateral* cells extend along the inner side of the globulus on the ventral side of the brain.

The *anterior globular* cells are situated ventrally on the inner and anterior side of the globulus.

The *posterior globular* cells lie above and behind the globulus at its outer and posterior side.

The following nerves are connected with the brain (fig. 68): —

Optic nerve (*o. n.*). One pair. Each arises from the dorsal side of the brain at its anterior corner. The fibres are continuous with those of the various optic neuropiles. It runs outward and forward at an angle of 45° with the longitudinal axis, and passes into the distal part of the optic peduncle, where the latter articulates with the proximal part of the peduncle. In the swollen part of the peduncle the nerve becomes enlarged to form the optic ganglion (fig. 69, *o.g.*). From this ganglion nerve fibres are given off, which pass through the basement membrane and innervate the various ommatidia of the eye (see figs. 69, 70).

Oculomotor nerve (*om. n.*). One pair. These arise from the brain immediately behind the optic nerve. Each passes outward behind the optic nerve, and supplies the optic peduncle and the muscles connected with it.

Antennulary nerve (*a.*[1] *n.*). One pair. At each side this nerve appears to be single, but it is composed of two different kinds of fibres, having different functions and arising from different centres in the brain. For this reason the two nerves should be described separately, as in the case of the optic and oculomotor nerves. The main branch innervates the antennule, and is connected in the brain with the fibrils of the median neuropiles. The fibres innervating the olfactory and tactile setae are probably connected with the lateral neuropiles. The otocyst branch is connected with the lateral neuropiles, and also with the globulus. It passes out from the brain together with the fibres of the main branch, but the two kinds soon separate and those innervating the otocyst pass outwards, and the fibres are connected with ganglion cells at the base of the otocyst setae. The antennulary nerve arises from the middle of the ventral surface of the brain, but in Cancer it apparently leaves the brain near the anterior end.

Tegumentary nerve (*t. n.*). One pair of broad nerves, which leave the brain near the postero-lateral corner. Each passes outwards almost at right angles to the longitudinal axis, and divides into two main branches. The anterior branch supplies the integument in region of the rostrum. The outward branch sweeps backwards and outwards, giving off small branches to the integument.

Antennary nerve (*a.*^{2} *n.*). One pair of small nerves, which arise from the ventral side of the brain immediately behind the tegumentary nerves. They are connected with the fibres of the neuropiles of the second antenna. Immediately on leaving the brain each passes beneath the tegumentary nerve and enters the muscle chamber of the second antenna.

The **commissures** (*Com.*). One pair of rather large nerves, which arise from the posterior side of the brain. They pass posteriorly on each side of the oesophagus, and are connected with the ventral nerve mass in the thorax. At each side of the oesophagus there is a *paroesophageal ganglion* (*p. g.*), and behind the oesophagus the two commissures communicate by means of a transverse *post-oesophageal connective* (*n. po.*). From the paroesophageal ganglia arise the stomatogastric nerves, and immediately behind the ganglion there is a small nerve (*n. m.*) supplying the muscles of the mandibles.

Ventral Nerve Mass.

The ventral nerve mass (*t. g.*) is situated above the sternal artery in the third and fourth thoracic somites. It is partly supported by the median plate of the endophragmal system. It contains nerve elements representing the post-oral cephalothoracic ganglia and the abdominal ganglia. It is not possible to make out all these ganglia from dissections, but they may be distinguished in stained preparations and in sections. Slightly behind the centre of this fused ganglionic mass is a foramen (*n. f.*), through which passes the descending artery.

At its anterior end, where it is connected with the commissure, the ventral nerve mass is narrower than in its posterior portion. In this anterior portion it is possible to make out, in suitable preparations, evidences of six pairs of ganglia belonging to the last three cephalic and the first three thoracic somites. Behind this region five pairs of larger ganglia may be distinguished more readily. From these arise the nerves supplying the five pairs of pereiopods and the last five thoracic somites. Between the last two ganglia is a median swelling, which is composed of the six ganglia belonging to the abdominal somites.

The following nerves arise from the ventral nerve mass:—

First nerve (*n.* 1). One pair. Each arises close to the connections between the commissure and the ventral nerve mass. It contains fibres from the first three ganglia of the nerve mass. It passes forwards parallel to the commissure and divides into three branches, passing to the mandible, first maxilla and second maxilla respectively.

Second nerve (*n.* 2). One pair. Each arises behind the first nerve, and its fibres are connected with the cells of the fourth ganglion of the nerve mass. It passes forward and slightly outward, and supplies the various parts of the first maxillipede.

Nerves 3-9 (*n.* 3-*n.* 9). These are all paired, and are connected with the fifth and following ganglia of the ventral mass. Each nerve supplies the appendage of its own somite, and its course is very similar to that of the second nerve. Nerves 5-9, however, are larger than the others, and the posterior nerves pass outwards and backwards.

Abdominal nerve (*n. ab.*). This is a median nerve, which passes backward in the median line. It arises from the fused abdominal ganglia at the posterior end of the ventral nerve mass, and contains nerve fibres from all the abdominal ganglia. It passes backward along the median line of the "sella turcica" and along the ventral region of the abdomen. Small nerves are given off to each somite of the abdomen.

According to Jolyet and Viallanes,* the centres of the moderator and accelerator nerves of the heart are in the anterior part of the ventral nerve mass. The cardiac nerve of the Macrura does not appear to be present in the crabs.

The Stomatogastric System.

This consists mainly of nerves arising from the paroesophageal ganglia. These nerves fuse to form the stomatogastric nerve, which supplies the anterior and dorsal regions of the fore-gut. There is also the postero-lateral nerve arising behind each paroesophageal ganglion.

There are two main nerves arising from each paroesophageal ganglion. These pass below the commissure, and, passing forward, they fuse with each other and with the similar nerves of the other side to form the main stomatogastric nerve. The *ventral* nerve (*st. i.*) arises from the outer side of the ganglion, and immediately passes below the lateral dilator muscle of the oesophagus, to which it gives small branches. It passes below the commissure and innervates the anterior dilator muscles of the oesophagus. It then turns upward and fuses with the similar nerve of the other side and with the *dorsal* nerve. The latter nerve (*st. s.*) arises from the anterior and outer side of the paroesophageal ganglion. It passes immediately below the commissure, and gives off a small nerve to the anterior walls of the oesophagus. In the median line it fuses with the corresponding nerve of the opposite side, and also with the ventral nerve.

The **stomatogastric nerve** (*st. n.*) is formed by the

---

* Jolyet et Viallanes. *Comptes Rendus*, CXIV (1892), p. 189.

fusion of the two ventral and dorsal roots, as described above. It passes up the anterior wall of the cardiac fore-gut as a median nerve. About half way along this wall the nerve enlarges to form the *stomatogastric ganglion* (*st. g.*). From this point the nerve proceeds backward along the dorsal side of the fore-gut, and almost immediately gives off two large branches—the **lateral gastric nerves** (*l. g. n.*). Each lateral gastric nerve passes over the anterior cardiac muscle, which it innervates, and gives rise to a nerve plexus in the dorsal walls of the cardiac fore-gut. Both nerves also give rise to an internal branch, which passes inwards and joins again with the stomatogastric to form a large ganglion. Behind this ganglion the stomatogastric nerve bifurcates. Each branch, which is known as the **posterior gastric nerve** (*p. g. n.*), passes backward to the pyloric fore-gut. Here the two nerves join again, thus forming a ring. From the posterior end of this ring three nerves are given off—one to the hind-gut (*n. i.*), one to the digestive gland (*n. l.*) and one to the integument (*n. t.*). The muscles in this region of the fore-gut are also innervated from the posterior gastric nerves.

The **postero-lateral nerve** (*p. n.*) of each side arises from the inner side of the commissure, immediately behind the paroesophageal ganglion. It passes backward, and innervates the posterior dilator muscle of the oesophagus. It then passes upward along the posterior wall of the fore-gut, and supplies the muscles in this region.

SENSE ORGANS.

The Eye.

Each eye is situated at the distal extremity of the long optic peduncle. The peduncle is clearly divided into two portions:—(1) A long narrow proximal part, which meets the peduncle of the other side in the median line above the first cephalic sternum. This proximal portion is not seen from the exterior. (2) A shorter and broader distal portion, which is the part seen from the exterior. The two parts are separated by a region of soft chitin, which allows of considerable movement between the two parts. At the distal extremity of the peduncle is a small black area—the *cornea*—which defines the external surface of the eye. The cornea would be almost circular were it not for the presence of two small tubercles which invade the dorsal border of the black area, and thus give it a somewhat irregular shape. The cornea is composed of a thin layer of chitin, which is continuous with the thick, strongly calcified integument covering the remainder of the distal part of the peduncle.

The thick calcified integument has the usual layer of epidermis beneath, resting upon a basement membrane. In the region of the eye, the cellular layer on the inner side of the cornea is extremely thick, and is known as the *ommateum*. On the inner side of the ommateum is a well-defined basement membrane, which is continuous with that of the ordinary epidermis. The ommateum, therefore, may be regarded as a differentiation of the epidermis, with which it is continuous.

An examination of the surface of the cornea reveals the presence of numerous small hexagonal facets. Vertical sections through the eye show that this sub-division of the cornea is not merely superficial, but is continued through to the inner side of the chitinous layer. The cornea may, therefore, be said to be composed of numerous hexagonal prisms, which are packed closely together. On the inner side of the cornea the ommateum is divided into numerous elements, which correspond in number and position to the corneal facets. Each element of the ommateum is known as an ommatidium and fits below a corneal facet, and extends from the cornea to the basement membrane. All the ommatidia have the same essential structure.

Structure of an ommatidium.

Each ommatidium may be conveniently divided into proximal and distal regions. The outer parts of both these regions are defined by the presence of pigment (fig. 69, *pg. i.*, *pg. o.*).

Underlying the cornea is the flattened corneagen. Below this are the vitrellar cells, the distal region of which enclose the crystalline cone. The vitrellae are surrounded by pigment cells, which are densest on a level with the proximal region of the crystalline cone. At the proximal end of the vitrellae are the pigmented retinulae which surround the rhabdome. The retinulae are in contact with the nerve fibres from the optic ganglion, and the proximal end of the rhabdome is in contact with the basement membrane.

The **corneagen** ["corneal hypodermis," Parker] (fig. 70, *corn.*) lies immediately below the cornea, which is a product of the corneagen cells. It consits of two flattened tile-like cells.

The **vitrellae** ["cone cells," Parker] (*vit.*) lie immediately below the corneagen. Transverse sections show that there are four vitrellae in each ommatidium. Their distal extremities are applied to the base of the corneagen. Passing inward the cells become narrower. Distally they enclose the crystalline cone, which is secreted by these cells. Surrounding the vitrellae are two **pigment cells** (*pg. c.*), which are continued inward as fine processes and eventually come into contact with the retinulae. (Fig. 72 is a section through the vitrellae of a single ommatidium, and shows that there are four vitrellar cells surrounded by two pigment cells.) Between the vitrellae and the pigment cells there are intercellular spaces, which are larger at the proximal end of the vitrellae.

The **retinulae** (*ret.*) are seven pigment cells which surround the rhabdome, and extend from the proximal portions of the vitrellae to the basement membrane. Distally each retinula ends in a rounded knob, which contains a nucleus (fig. 71 shows the disposition of the retinulae around the rhabdome). At their distal ends the retinulae are extremely large, and surround the rhabdome in this region so as to completely hide it. The concentration of the pigment in this region gives rise to a well-marked pigment band (fig. 69, *pg. i.*). Proximally the retinulae are not so large, and the rhabdome can be seen quite distinctly between them. The rhabdome has a peculiarly striated appearance, which is caused by the arrangement of the pigment granules of the retinulae. The optic nerve fibres pass into the retinular cells, so that it is this part of the eye which is sensitive to light.

The **rhabdome** (*rhab.*) is a rod-like structure in the centre of the retinulae. According to Watase,* the rhabdome is a chitinous structure produced as a secretion from the retinulae. Parker† states that transverse sections show that the rhabdome is composed of four parallel rods, and he further affirms that these four rods are the inner extremities of the four vitrellae (cone cells).

The *optic nerve fibres* perforate the basement membrane and end in the retinulae.

Each ommatidium, therefore, may be said to consist

---

* Watase, S. "On the Morphology of the Compound Eyes of Arthropods," *Q. J. M. S.*, Vol. XXXI, p. 143.

† Parker, G. H. "The Histology and Development of the Eye in the Lobster," *Bull. Mus. Comp. Zool. Harv.*, Vol. XX, No. 1.

—— "The Compound Eyes in Crustaceans," *loc. cit.*, Vol. XXI, No. 2.

of a series of cells which on their outer side receive and concentrate the rays of light. These are transmitted to the retinulae by means of the transparent vitrellae. The retinulae are connected with the nerve fibres, and are, therefore, the important part of the eye. Each ommatidium is surrounded by a layer of pigment, so that the sensitive retinulae are situated at the bottom of a tube, which is completely separated from the tubes of the other ommatidia because of the presence of the pigment. Therefore, the retinulae of an ommatidium can only receive light through the small corneal facet at the distal extremity of the particular ommatidium.

The **cornea** (*cn.*) is composed of three layers. On the outside is a thin structureless layer—the *cuticle* (*cut.*). Beneath this is an outer *pigmented layer* (*pig. l.*), to which the colour of the cornea is due. Below the pigment layer is the *deeper layer.* Both inner layers exhibit longitudinal striations.

According to Watase, the corneagen, vitrellae and retinulae are all modified epidermal cells, which, in the case of the vitrellae and retinulae, have grown inward. The cornea is a chitinous secretion of the corneagen. The crystalline cone is primarily a chitinous secretion of the vitrellae, and the rhabdome is a chitinous rod secreted by the cells of the retinulae.

The otocyst.

The otocyst is found in the basal segment of the antennule. It is a sac lined with a layer of chitin, which is continuous with the outer chitinous integument. In the megalopa stage and in the young crabs the otocyst is open to the exterior, and in these stages otoliths are present in the sac. In large crabs, however, there are no otoliths, and the sac is completely closed except immediately after ecdysis, when the otocyst is connected with the exterior by means of a transverse slit on the dorsal side of the basal segment of the antennule. This slit is quite obvious in the hard crab. The walls of the sac project into the lumen at three places—(1) in the postero-lateral wall (2) in the posterior wall, and (3) the anterior part of the floor.

There are three kinds of setae situated on the walls of the otocyst and projecting into the lumen.

The **hooked setae** [" Hakenhaare," Hensen] (Pl. XI, fig. 75) are found on the convex portion of the posterior wall of the otocyst. These setae are characterised by having the distal extremity inclined at a considerable angle to the proximal portion, sometimes as much as 90°. The distal portion of the shaft has fine barbs arising from it. The base of the shaft is sunk into a socket-like depression. The total length of the hook hairs is about 55μ.

The **thread setae** [" Fadenhaare," Hensen] are found on the anterior part of the floor. They are the largest setae present in the otocyst, and are about six times as long as the hook hairs. There are well-defined barbs arising from the shaft. The base of each seta lies in a cup-shaped depression of the chitinous wall.

The **grouped setae** [' Gruppenhaare," Hensen] (fig. 76) are situated on the lateral walls of the otocyst, below the closed entrance of the sac. They are about 140μ in length, and have blunt shafts. There are no barbs present.

The three kinds of setae are innervated from the otocyst nerve, and according to Prentiss* there is one nerve element for each seta. The same author states that

---

* Prentiss, C. W. "The Otocyst of Decapod Crustacea: its structure, development, and functions," *Bull. Mus. Comp. Zool. Harv.*, Vol. XXXVI, No. 7.

the otocyst does not become functional until the megalopa stage.

Hensen and the early observers believed that the otocyst was an auditory organ. Hensen found that the "auditory" setae were individually sensitive to sound vibrations of different frequency, and concluded that in the lobster the auditory organ had a range of three octaves.

Kreidl was the first to deny that the otocysts possessed an auditory function. He substituted iron filings for the otoliths, and the experiments led him to believe that this organ served the function of equilibration.

Bethe, while accepting Kreidl's results, did not reject the idea that the otocyst was also an auditory organ.

The researches of Prentiss led him to believe that the otocyst was a static organ solely. It is probable that in the Brachyura the hooked setae and grouped setae have lost most of their functional activity owing to the absence of otoliths. The thread setae are, undoubtedly, the most important sensory organs of the otocyst. (For a further discussion of this subject the reader is referred to the paper by Prentiss.)

The sensory setae of Cancer are of two kinds.

The **tactile setae** may be present in various parts of the body. They are found on the antennules and antennae, and on most of the appendages. The setae of the otocysts are probably modified tactile setae. They are characterised by having a long tapering shaft which bears barbs, and each seta is innervated by a single nerve fibre and a single nerve cell.

The **olfactory setae** (fig. 74) are short and blunt, and are much more firmly attached to the integument than the tactile setae. Each seta is divided into proximal and distal portions by a transverse suture. At the distal end the seta is either perforated or the membranous covering is extremely thin. The olfactory setae differ from the tactile setae in having numerous nerve elements for each seta. They are present on the exopodite of the antennule on the side opposite to the long setae. They are extremely small, and there are only one or two on each ring of the exopodite. On the endopodite of the antennule there are also a few small setae on the dorsal side of each ring, which have the appearance of olfactory setae. The gustatory setae present in the region of the mouth are modified olfactory setae.

REPRODUCTIVE ORGANS

(Plate XII).

1. Male (fig. 78).

The abdomen is much narrower than in the female, and the third, fourth and fifth abdominal somites are fused together. Abdominal appendages are present only on the first and second abdominal somites, and these are modified to form copulatory organs. The external genital apertures are paired, and each is situated at the tip of a membranous papilla on the ventral side of the coxopodite of the last walking leg. The thoracic sterna are deeply concave, in order to receive the closely-applied abdomen. The locking apparatus of the male abdomen is much better developed than in the female. The dorsal side of the carapace is much flatter in the male than in the female. As Williamson has pointed out, the lobed antero-lateral border of the carapace is slightly turned up in mature males. The chela of the mature male are larger than those of mature females of the same size.

The two abdominal appendages of each side form a single copulatory organ (see fig. 16). The anterior appendage (*p.* 1) is tubular, and into the tube the posterior rod-like appendage (*p.* 2) is inserted during copulation. The copulatory organ of each side is introduced into one of the vulvae of the females during fertilisation. The genital papillae of the male are too short to reach the vulvae, and the abdominal appendages have become modified to form sexual organs in consequence of this. During copulation each genital papilla fits into the base of the tubular appendage and the spermatophores are poured into the tube. The rod-like second appendage is constantly working up and down the tube, and thus forces the male sexual products into the spermatheca of the female.

The **testes** (*test.*) are paired and symmetrical, and the two halves are connected immediately behind the fore-gut. Each testis is a compact lobulated organ situated in the antero-lateral region of the cephalothorax. It is superficial in position, and lies immediately below the dermis and above the digestive gland. The size and shape of the testis varies considerably according to the condition of the animal. In immature crabs it may be extremely small, but in the mature specimens the testis is massive and lobulated, and may cover almost the whole of the digestive gland. Its blood supply is obtained from the large spermatic branch of the lateral artery. At its inner extremity, near the cardiac fore-gut, each testis is connected with the vas deferens (*v. d.*). The main part of the testis gives off a posterior branch which passes backward beneath the vas deferens alongside the mid-gut caecum. Above the mid-gut this prolongation turns inward and joins with the similar portion from the other side to form a bridge behind the pyloric fore-gut.

The *vasa deferentia* are a pair of long convoluted tubes passing backward from the testes to the posterior region of the thorax, where each opens to the exterior on the coxopodite of the last walking leg.

In a mature crab the course of each of the vasa deferentia is as follows: Where it arises from the inner portion of the main lobe of the testis the vas deferens is an extremely convoluted and narrow tube. As it sweeps round the outer side of the cardiac stomach the tube grows broader and the convolutions become less complicated, so that in this region the course of the vas deferens may be traced without much difficulty. At the level of the pyloric fore-gut the duct turns suddenly inwards and covers the lateral walls of this region of the alimentary canal. From this point the vas deferens passes backward as a white convoluted tube above the hind-gut and below the pericardium. The maximum width is attained below the anterior region of the heart. Behind this point the duct gradually becomes narrower, and is then known as the *ejaculatory duct* (*e. d.*). At the posterior end of the pericardium the duct dips downward through the foramen on the outer side of the "sella turcica." It then passes behind the dorsal extensor muscle of the coxa of the last walking leg and in front of the extensor muscle of the basi-ischium of the same appendage. Below the latter muscle it passes beneath the flexor of the basi-ischium, and opens to the exterior at the end of a soft papilla situated on the ventral surface of the coxa of the last walking leg.

In sections through the testis the gland is seen to be composed of numerous follicles which are closely packed together. Each follicle is lined by epithelial cells which surround a central cavity, and this cavity is continuous with that of the vas deferens. In an early stage the cells of the follicles are not differentiated and are quite small.

Eventually some of these become spermatoblasts and increase greatly in size. Each spermatoblast gives rise to a large number of spermatozoa. In sections through a mature testis it is difficult to distinguish the follicles, as the cavities of the latter become almost obliterated by the growth of the spermatoblasts. When the spermatozoa are ripe they break free and are carried down into the vas deferens. Here they become collected together in small groups, and each group becomes surrounded by a capsule to form a *spermatophore.*

The spermatozoa (fig. 81) are non-motile. They consist of a central dark portion containing a nucleus and an outer clear margin. In side view the clear margin is seen to be much thinner than the central part of the cell, and has the appearance shown in fig. 81. The diameter of the cell is about 6μ.

The presence of the spermatophores gives rise to the white appearance so characteristic of the vasa deferentia of mature male crabs. In small immature crabs the vas deferens is narrow and almost transparent, due to the absence of spermatophores. As pointed out by Williamson, "the condition of maturity in the male is the presence of ripe male elements in the vas deferens." It is probable that most male crabs above $4\frac{1}{8}$ inches in width are mature, although Williamson has given instances of male crabs attaining maturity at a much smaller size.

2. FEMALE (fig. 77).

The abdomen is broad, and all the somites are freely movable. There is one pair of appendages on each of the second, third, fourth and fifth somites. After the ova are spawned they are attached to the endopodite setae of the abdominal appendages. The external genital apertures are a pair of large openings situated on the sternum of the sixth thoracic somite. The thoracic sterna are not so concave as those of the male, and the abdomen is not so closely applied to the thorax. The abdominal locking apparatus is poorly developed. The dorsal side of the carapace is well arched in the mature females, and the antero-lateral border of the carapace is not upturned as in the males.

The **ovaries** (*ov.*) are paired, and lie in a similar position to the male reproductive organs. There is, however, a considerable posterior prolongation of each ovary. As in the male, the two antero-lateral portions are connected behind the pyloric fore-gut by a strand of gonadial tissue, which forms a bridge over the mid-gut. Behind this transverse connection each ovary is prolonged backward as a narrow strip, which extends to the extreme posterior end of the thorax. At the posterior extremity the two prolongations fuse together in mature specimens. These backward extensions of the ovaries occupy a similar position to the vasa deferentia of the male; that is to say, they lie above the hind-gut and below the pericardium. Beneath the anterior end of the latter each posterior branch is connected on its outer side with a large sac, the *spermatheca** (*spt.*). Each spermatheca is continued into a short *oviduct* (*ovd.*), which opens to the exterior by means of the vulva on the sternum of the sixth thoracic somite.

The condition of the ova in the ovary naturally depends upon the degree of maturity attained by the gonads. The immature gonads are small and pale, and no evidence of the presence of eggs can be detected by the naked eye. The mature gonads, however, fill almost the

---

* In young crabs the spermatheca is extremely small, and can only be made out with difficulty.

whole of the dorsal side of the cephalothorax. They are of an orange-red colour, and the separate eggs can be readily distinguished. The red colour is due to the presence of the food-yolk. The yolk granules form the main part of the mature ovum (fig. 79). With regard to the condition of the ovaries between two processes of ecdysis, the reader is referred to the section on Bionomics.

Copulation takes place immediately after the female has cast, and while it is still in a soft condition. Apparently the spermatozoa burst free from the spermatophores as soon as they leave the vas deferens. In the spermatheca only free spermatozoa are found. After copulation the cells lining the spermatheca secrete a fluid which fills the cavity of the oviduct. This secretion hardens upon contact with the sea water, and thus the oviducts become effectively plugged, and the contents of the spermatheca cannot escape. It is a remarkable fact that the spermatozoa remain inside the spermatheca for many months before they fertilise the ova.

The eggs are spawned in the winter. Upon reaching the exterior, each egg is probably surrounded by two membranes—an inner vitelline membrane and an outer chorion. Between the two is a perivitelline space, which, according to Williamson, contains a fluid possessing adhesive properties. The eggs become attached to the endopodite setae of the abdominal appendages. The interesting question regarding the mode of attachment of the eggs to the endopodite setae is not yet conclusively settled. Some of the early observers believed that a sticky substance was secreted around the eggs as they were being shed. This, however, would not explain why the eggs become attached only to the endopodite setae. Herrick's* explanation is that the tegumentary glands of

---

* Herrick. "The American Lobster," *Bull. U.S. Fish Com.*, 1895.

the endopodites of the pleopods secrete an adhesive fluid. Williamson[*] gives a detailed explanation of the method of attachment. He suggests that the endopoditic seta penetrates the chorion of the egg in two places, and thus the egg becomes skewered on the seta. The piercing of the chorion liberates the adhesive perivitelline fluid, which assists in making the attachment more permanent. The chorion eventually becomes drawn out at the point of attachment, and the egg appears to be attached to the seta by a stalk (see fig. 80).

According to Williamson, the number of eggs attached to the abdomen may vary from half a million in a small mature female to three millions in a large crab.

DEVELOPMENT.

It is a surprising fact that the development of *Cancer pagurus* has never been satisfactorily investigated. The internal changes do not appear to have been followed in any Brachyurous embryos, and although the general characters of the larval developments in the Brachyura are well known, our knowledge of these stages in *Cancer pagurus* is extremely scanty.

The development may be divided into three stages—embryonic, larval and post-larval.

The embryonic development takes place while the embryo is attached to the pleopods of the female, and, therefore, extends over a period of about seven months. The internal development during this period has not been investigated, but it is very probable that the Brachyura do not differ from the Macrura in this respect. The early development has been thoroughly investigated in the Macrura.[†]

---

[*] Williamson. *23rd Report, Scotch Fishery Board.*

[†] See Herrick, F. H. "The Development of the American Lobster," *Johns Hopkins Univ. Circ.*, Vol. IX, 1890, No. 80.

Reichenbach, H. "Studien zur Entwicklungsgeschichte des Flusskrebses," *Ab. Senkenberg. Nat. Ges. Frankfurt*, Bd. XIV, 1886.

While working at the Biological Station, Heligoland, I was able to examine the early larval stages of Cancer. I was fortunate enough to obtain berried crabs on which the embryos were ready for hatching. The process of hatching lasted several hours, and during this time the crab assisted by moving its abdomen backwards and forwards. The last walking legs were also used for the purpose of detaching the larvae from the pleopods. Unfortunately, I was not successful in keeping the larvae alive longer than the first zoëa stage.

I give below a summary of the characters of the larval stages of the Brachyura in general. I have utilised the results of other investigators,* and have also added my own observations. The larval stages may be divided into Protozoëa, Zoëa (four kinds) and Megalopa.

Protozoea (Pl. XIII, figs. 83, 84). Hatching takes place at this stage, which is of very short duration. There are no frontal or dorsal spines present. The lateral spines (*sp. l.*) are present one on each side of the cephalo-thoracic shield. The large paired eyes are present in the head. The abdomen is well defined, but only five somites and the telson can be distinguished. The sixth somite is at this stage fused with the telson. The telson is forked, and each branch bears strong spines (fig. 84). All the cephalic and the first two pairs of thoracic limbs are present. The antennule is blunt and consists of two segments, of which the distal is the larger. The antenna consists of a broad basal joint, from which is given off a short pointed process. The mandible is a small rounded outgrowth. The first and second pairs of maxillae are

---

* Williamson, H. C. "On the Larval and Early Stages and Rate of Growth of the Shore Crab (*Carcinus maenas*)," *Twenty-first Annual Report, Fishery Board for Scotland*, p. 136.

Korschelt and Heider. *Text Book of Embryology* (Invertebrates, Part II).

similar, and are beginning to show evidences of a biramose structure. The first and second pairs of maxillipedes are large and biramose. The protopodite is large. The endopodite and exopodite have few setae. Towards the end of the protozoëa stage the cuticular covering becomes very loose, and beneath can be seen the developing organs of the first zoëa stage. Chromatophores are present at the sides of the body.

First zoea (Pl. XIII, figs. 85, 86, 87). This stage is generally seen about three or four hours after hatching, and probably lasts for at least ten days. The important difference between this and the previous stage is the presence of the large frontal and dorsal spines. The latter is about half as long as the body, and the frontal spine is about two-thirds the length of the body. Both are tipped with a red pigment. The lateral spines are well developed. The branched chromatophores are well developed. The number of appendages appears to be the same as in the previous stage, but they are more highly developed. Each antennule bears a group of setae at its tip. The antennae and both pairs of maxillae are biramose. The exopodites of the maxillipedes each bear four long setae. The third maxillipedes and the pereiopods and the associated gills are present as extremely small buds, which are hidden beneath the cephalothoracic shield. The pleopods may be seen for the first time as extremely small tubercles. In some examples of both the protozoëa and the first zoëa there was a pair of tubercles present on the second abdominal somite. The telson differs from that of the previous stage in having two extremely long posterior branches.

Zoëa stages II, III and IV. I have not been able to identify these stages in *Cancer pagurus*, but in *Carcinus maenas* they have the following essential characters. They are very similar to the first zoëa in appearance. Between the two branches of the antenna an outgrowth takes place in the second stages, and ultimately developes into the long flagellum. The maxillae are not very different from those of the first stage. The setae on the exopodites of the first and second maxillipedes increase in number at every stage. The last six pairs of thoracic appendages and their gills gradually increase in size, but never become functional during the zoëa stages. The pleopods gradually develop until at the fourth stage there are five pairs present. There is not a pair present on the sixth abdominal somite in Carcinus. At the third stage the sixth abdominal somite becomes separate from the telson. The rostral and dorsal spines gradually become shorter.

In his account of the larval stages of *Cancer irroratus*, Smith* describes the following characters in the last zoëa stage:—Rostral and dorsal spines short. The abdominal legs are seen as stumpy outgrowths. The third maxillipede is well developed, but the other posterior thoracic appendages do not project below the edge of the cephalothoracic shield. The flagellum of the antenna is present.

Megalopa stage. The main points of difference between the zoëa and megalopa are as follows:—The frontal and lateral spines disappear. According to Smith, the dorsal spine of *Cancer irroratus* persists as a small backwardly-projecting process. The carapace is broader. The pereiopods are well developed, and the gills are probably functional. The pereiopods are never biramose as in the Macrura. The abdomen is macrurous, and the pleopods are used for swimming. The telson is much shorter, and loses its spines. The megalopa is still a pelagic stage. Its pereiopods, however, may be used for

---

* Smith, S. "The Invertebrate Fauna of Vineyard Sound," *U. S. Fish Commission Report*, 1871-72 (published 1873).

walking on the bottom. The last pereiopod in *Carcinus maenas* and *Cancer irroratus* has a tuft of setae on the dactylos. According to Smith, the megalopa stage is very short, and at the first moult it changes into a young adult.

Post-larval stages. The young adult differs from the megalopa in having the abdomen tucked beneath the thorax. It is no longer a pelagic animal, but lives on the bottom, and uses the last four pairs of pereiopods for the purposes of locomotion. As pointed out by Smith* and Cunningham,† the early post-larval stages differ considerably from the larger specimens. The carapace is elongated and the rostral region is well developed. The lobes of the antero-lateral border are sharp. Cunningham pointed out that it is difficult to distinguish the early stages of Cancer from those of *Atelecyclus heterodon*. At each succeeding moult the transverse axis of the carapace increases more rapidly than the longitudinal axis.

ECONOMICS AND BIONOMICS.‡

The main features in the life-history of the edible crab may be briefly summarised as follows:—

Cancer pagurus is found all round the coasts of the British Isles, being especially abundant on the rocky coasts. The size at which maturity is attained is variable, but most crabs above five inches in breadth may be said to be mature. There appear to be no records of large

---

* Smith. *Op. cit.*

† Cunningham, J. T. "On the Early Post-larval Stages of the Common Crab (*Cancer pagurus*), and on the Affinity of that species with *Atelecyclus heterodon*," *Proc. Zool. Soc.*, 1898, Part II, p. 204.

‡ For further information on these subjects see—
Cunningham. *Cornwall County Council: Report of the Executive Committee for Fisheries*, 1897-8. Penzance, 1898.
Williamson. *Fishery Board for Scotland: 18th, 22nd, and 23rd Annual Reports.*
Wilson. *Northumberland Sea Fisheries Committee: Reports on*

edible crabs, but I have seen several specimens in shops having a carapace breadth of about twelve inches. A crab measuring nine inches would be considered a large one. The crabs are captured by means of crab-pots ("creels," Williamson; "creaves," Wilson), which are baited with fish. In Port Erin the chief fishing season is from March to September, but the crab fishery is continued throughout the winter. Generally speaking, the chief fishing season in the British Isles lasts from the early spring to the autumn. In some districts, such as the North-East of England, there is a close season.

Fishermen are not allowed to sell crabs below four and a half inches, berried crabs or soft crabs, but these restrictions do not hold good concerning crabs used for bait. Since, in some parts of the country, crabs are used for bait to a large extent, these laws for the protection of the crab fishery to some extent fail in their purpose. The size limit may be increased at the discretion of the local committees. In the Lancashire District the minimum size is five inches.

In the summer the mature crabs frequent the inshore waters, and in the winter they occur in the deeper off-shore waters. The immature crabs do not take part in this annual migratory cycle. The mature crabs cast in the autumn, and the females are fertilised when "soft." Spawning takes place in the deeper water in winter. The larvae are hatched in the following summer in the inshore waters. Wilson is of the opinion that the "berried"

---

the Crab Fishery, 1893 *and* 1895. Also *Proc. R. Soc. Edin.*, Vol. XX, 1894, p. 309.

Meek. *Northumberland Sea Fisheries Committee*, 1897-1906.

Buckland, Walpole and Young. *Reports on the Crab and Lobster Fisheries of England and Wales, of Scotland, and of Ireland* [C. 1695], 1877, p. 56.

Statistics regarding the crab fishery may be obtained from the various Annual Reports of Inspectors, Sea Fisheries (England and Wales).

crabs feed very little, and he records instances of such crabs being covered with sand. Williamson's observations appear to support this statement.

Baudouin[*] gives an interesting account of how the phenomenon of autotomy is utilised by the fishermen of Southern Spain. The common edible crab of that region is *Gelasimus tangeri.* When the crabs are captured the large claws are removed up to the fracture plane, and the crab is put back in the water. Only the claws are sent to market, the crab being returned to the sea to grow new ones.

The statistics published annually by the Fishery Inspectors for England and Wales are very scanty, and appear to have but little value in the elucidation of the numerous problems connected with the natural history of the edible crab.

I give below a summary of the figures published in the Annual Reports of the Fishery Inspectors for England and Wales since 1887, merely giving the total number of crabs caught in each year and their approximate value.

Year.	Total Number.	Approximate Value.
1887-1897 (average)	4,669,861	£55,082
1898	5,628,114	£67,895
1899	4,918,184	£62,494
1900	5,177,350	£56,822
1901	5,325,974	£58,743
1902	—	—
1903	4,923,536	£54,327
1904	4,580,318	£52,556
1905	5,106,345	£59,479
1906	—	—

---

[*] Baudouin, M. "Utilisation de l'autotomie chez un Crabe." *Revue scientifique* (Ser. V), T. VI, No. 10.

Through the kindness of Dr. Jenkins, Superintendent of the Lancashire and Western Sea Fisheries District, I am able to give the following statistics dealing with crabs landed in that Sea Fisheries District during the years 1900 to 1906, inclusive:—

Year	New Quay.		Aberdovey.		Pwllheli.		Holyhead.		Liverpool.	
	No.	£'s.	No.	£'s.	No.	£'s.	No.	£'s.	No.	£'s.
1900	—	—	—	—	6,000	180	600	6	—	—
1901	—	—	—	—	2,000	60	800	8	—	—
1902	—	—	—	—	10,204	112	1,100	11	—	—
1903	—	—	—	—	11,143	135	1,000	11	600	5
1904	50	1	—	—	10,710	125	615	6	900	8
1905	40	2	—	—	8,851	109	760	8	466	6
1906	509	11	435	7	9,347	113	—	—	800	8

The crabs returned as having been landed at Liverpool were certainly not caught in that District.

The Harbour Master of Port Erin has kindly provided me with the following figures, which give the number of crabs captured by the Port Erin fishermen during the years 1904-5-6:—

	1904.	1905.	1906.
January	?	800	1,200
February	?	3,400	2,200
March	7,000	6,500	4,000
April	7,500	8,000	6,500
May	7,500	9,400	7,000
June	6,100	5,000	4,000
July	7,000	6,500	7,000
August	6,000	2,000	5,500
September	3,000	2,000	2,500
October	1,600	1,500	2,500
November	500	400	300
December	1,200	800	300
Total	47,400*	46,300	43,000

* The figures for January and February are not given.

Fishery regulations.*

In section 8 of the Fisheries (Oysters, Crabs and Lobsters) Act (40 & 41 Vict. ch. 42), the following restrictions are imposed:—

A person shall not take or sell:—

(1) Any edible crab which measures less than four inches and a quarter across the broadest part of the back.

(2) Any edible crab carrying spawn.

(3) Any edible crab which has recently cast.

Such crabs may, however, be used for bait.

In the Lancashire and Western Sea Fisheries District the minimum legal size has been raised to five inches. (Bye-law 25*b*: "No person shall remove from a fishery any edible crab measuring less than five inches across the broadest part of the back.")

Size of crabs at maturity.

Female.—There appears to be some difference of opinion with regard to the size at which the female becomes mature. Wilson† had reason to believe that on the Northumberland Coast the size of maturity is about six inches. Williamson's‡ investigations, on the other hand, show that the crabs of the east coast of Scotland become mature when about four and a half inches in width. I have examined crabs from Port Erin which had been fertilised when about this size. It is probable that a crab is mature when it has attained a size of four and a half inches, but in many cases fertilisation may not be effected until after the next casting. There is no

---

* For a discussion on this subject read Williamson, 18*th Annual Report*, p. 134. Other literature on this point is given by him on p. 78 of the same report.

† Wilson. *Northumberland and Sea-Fisheries Committee*, 1893, 1895; *Proceedings Royal Society, Edinburgh*, 1892-3, p. 309.

‡ Williamson. *Eighteenth Report*, p. 77.

doubt that many crabs do not bear their first batch of eggs until attaining a size of six inches.

Male.—The male crabs evidently attain maturity at a smaller size than is the case in the females. Probably all males above four and a half inches are mature, and Williamson has found mature males below this size.

Fertilisation takes place in the inshore waters during the late summer and autumn, and is effected immediately after the female has cast. The one supply of spermatozoa is probably sufficient for two successive batches of eggs, and even three in the older crabs. The spermatozoa remain in the spermathecae, and the entrances to the latter are closed by plugs, which are probably formed by a secretion from the walls of the spermathecae which hardens in contact with water.

The spawning of the eggs is effected in the deeper offshore waters during the winter. The eggs are attached to the endopoditic setae of the pleopods, and remain there until the following summer, when they are hatched in the inshore waters.

The crab probably does not cast after the larvae are hatched, but a second batch of eggs are spawned in the following winter in the offshore waters. As with the first batch, the developing embryos will be retained on the abdominal appendages until the following summer, when the hatching process will again take place in the inshore waters. After the second hatching the female probably casts, and is fertilised.

The developing embryos probably remain attached to the pleopods for about seven months. The various zoëa stages and the megalopa stage may extend over a period of two months, but our knowledge of the larval stages of Cancer is remarkably scanty. It is probable that the larvae hatched at the end of June will be in the first adult stage about the end of August.

DISTRIBUTION AND MIGRATION.

According to Williamson,[*] the crabs after the larval stages may be placed in four different groups according to their distribution.

Group I includes the young stages up to $\frac{7}{8}$-inch in breadth. These are probably restricted to the shallow shore waters.

Group II includes the crabs found on the beach between tide-marks. From $\frac{7}{8}$-inch to $2\frac{1}{4}$ inches in breadth.

Group III includes the crabs living in the littoral waters beyond low-water mark. From $2\frac{1}{4}$ to 4 inches.

Group IV includes all the crabs above 4 inches in breadth. These crabs are mostly mature, and migrate from the inshore waters in the summer to the deeper offshore waters in the winter.

With regard to Group I, my own observations confirm those of Williamson. In the spring and summer, when small specimens of Cancer must be very abundant, they are very rarely found between tide-marks. On the other hand, they are frequently taken in the dredge close to the shore.

The migration of the mature crabs has been long known to fishermen, and our knowledge with regard to this subject is now fairly complete, thanks to the work of Williamson, Meek and others. Only the crabs of Group IV are concerned in the migration, which may be divided into an offshore migration in the autumn and an inshore migration in the spring. Both hard and soft crabs begin to move outward into the deeper water in September (see Text fig. 13). The extreme depth to which they travel must necessarily vary with the locality, but it is generally between twenty and thirty fathoms.

[*] Williamson. *Eighteenth Annual Report.*

The crabs probably stay in the offshore waters from December to February, and it is here that the females spawn. The inshore migration begins in February, and in May the bulk of the crabs are probably back in the inshore waters again. The hatching of the larvae takes place in the warm inshore waters, and casting process is performed, and, in the case of the females, fertilisation is effected immediately after ecdysis. In the autumn the offshore migration again commences, and the cycle is repeated.

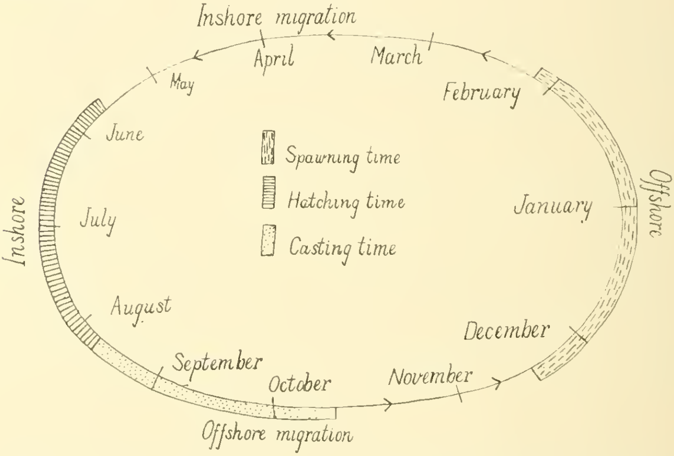


Fig. 13.—Diagram illustrating the annual migratory cycle of mature crabs. The three processes—casting, spawning and hatching—probably do not take place in one cycle.

It must be remembered, however, that in the mature female crab casting and fertilisation in the autumn is not necessarily followed by spawning in the same winter. Furthermore, casting will only take place once in two or three years. But when spawning does take place it is in the offshore waters, and the hatching is always in the inshore waters.

As suggested by Williamson, the main reason for this regular migration is the influence of temperature. In the winter the deeper layers of the offshore waters are warmer than the inshore waters, and hence the former are most suitable for the spawning time. In the summer the shallower inshore waters become much warmer, and here the young larvae are hatched. It is also reasonable to suppose that the warm water of the inshore regions is specially favourable for the somewhat critical period of casting. The necessity for food may also have an important bearing on the yearly migration.

I give below a summary of the life-history of an adult female crab between two successive processes of ecdysis. The condition of the gonads at the various stages is discussed. In the example given, it is assumed that the crab did not spawn in the winter following fertilisation. The period elapsing between fertilisation and the first spawning appears to depend altogether on the condition of the gonads. As a rule, the ovary is very small and pale when ecdysis takes place, and in such a circumstance the eggs cannot possibly be ready for spawning in the course of three or four months. Consequently the eggs are not shed until the second winter, i.e. fourteen months after fertilisation. In some crabs the ovary is fairly ripe when ecdysis takes place, and in such cases the eggs will probably be extruded in a few months.

First Year. September—*The crab casts and is fertilised.*

It then migrates to offshore waters for the winter. It returns to inshore waters in the spring of the second year. In the following autumn offshore migration again takes place.

Condition of ovary. At first it is poorly developed and pale in colour, and the eggs are without food-yolk. The ovary gradually ripens, first becoming pink in colour and finally a bright orange. This change in colour is due to the development of food-yolk. The eggs first become yolked in the spring of the second year.

Second Year. December—*Eggs extruded (first spawning).*

When the spawning takes place the crabs are in the deeper offshore waters. In the spring of the third year the inshore migration commences.

Condition of ovary. Immediately before spawning the eggs are large and of a bright orange colour, due to the food-yolk. After the extrusion of the eggs the ovary is shrunken and of a pale colour. The majority of the eggs are small and without food-yolk. There may be, however, a few ripe eggs present which have failed to escape to the exterior. As the spring advances the eggs gradually become more mature, and present a pinkish colour.

Third Year. July—*First hatching takes place.*

In the autumn of the third year the offshore migration again takes place.

Condition of ovary. At the time of the first hatching the ovary is generally of a red colour, and the eggs are about half ripe.

Third Year. December—*Eggs extruded (second spawning).**

During spawning time the crab is in the offshore waters. In the spring of the fourth year the inshore migration commences.

Condition of ovary. Very similar to the appearance at the time of the first extrusion.

Fourth Year. July—*Second hatching takes place.*

The crab is now in the inshore waters.

---

* Williamson gives instances in which the second spawning did not take place for about fifteen months after the first hatching. It is difficult to say whether this is of regular occurrence.

Condition of ovary. During the spring and summer the ovary remains unusually small, and has a pale colour. The eggs are mostly small and without yolk.

Fourth Year. September—*The crab casts and is fertilised.*

During these processes the crab is in the inshore waters. Immediately after fertilisation the offshore migration will commence, and the whole of the above history will be repeated.

Condition of ovary. Similar to that at the first casting.

BIONOMICS OF ECDYSIS.

As already seen, the growth of the crab can only take place by the exuviation of hard shell or exoskeleton. Immediately after ecdysis has taken place the body—now covered by a soft flexible membrane—increases considerably in size. In the mature female fertilisation is also effected while the crab is soft. The soft crabs are not fit for food, and it is illegal to expose them for sale when in this condition.

Season of casting.

The young crabs cast at various times of the year, but after the third year ecdysis generally takes place in the autumn. According to Williamson, the main casting period on the East Coast of Scotland is from July to September, but it may be extended to December. From August to November appears to be the chief casting time in the Isle of Man. The casting is effected in the warmer inshore waters. The hardening process in the mature crab lasts from three to five months, according to Williamson.

Rate of Growth.

From the evidence obtained by Williamson and Waddington, and also from observations taken in the course of the present work, it would appear that the rate of growth varies considerably. For example, in a series of seventeen crabs measured in Heligoland I found that the fraction of increase varied from $\frac{1}{2 \cdot 5}$ to $\frac{1}{5 \cdot 8}$ (see table on p. 382). In Waddington's series published by Williamson* the fraction varied from $\frac{1}{2}$ to $\frac{1}{6 \cdot 5}$, and in the table published by Williamson† the ratio of increase varies from $\frac{1}{3 \cdot 1}$ to $\frac{1}{9}$. But, speaking generally, it may be said that this ratio is between $\frac{1}{3}$ and $\frac{1}{4}$.

It is not surprising that this rate of growth should be a variable one. The main factors to be considered are probably the general health of the animal (i.e. the condition of the tissues) the amount of food, the purity of the water and the temperature of the water, and many other causes. Any one of these factors would alone be capable of affecting very considerably the rate of growth.

I give a table (p. 382) showing the rate of increase in seventeen different crabs. These measurements were taken from specimens in the Nordsee Museum, Heligoland, by kind permission of the Director, Professor Heincke.

Frequency of casting.

Speaking generally, it may be said that in the younger stages the moultings are frequent, but that as the crab grows older the period between each process of ecdysis and the next becomes longer.

In the earliest stages the frequency of casting differs in

---

* Williamson. *Twenty-second Annual Report, Fishery Board for Scotland*, p. 135.

† Williamson. *Eighteenth Annual Report, Fishery Board for Scotland*, p. 110 (see also Twenty-second Report, p. 122).

a marked degree in individuals of the same approximate age. As stated above, the hatching period lasts from June to August. The "early" larvae, therefore, will have a considerable advantage over the "late" larvae.

	Carapace breadth before casting. Cm.	Carapace breadth after casting. Cm.	Ratio of Increase.
1	1·55	2·05	$\frac{1}{3\cdot1}$
2	2·15	2·80	$\frac{1}{3\cdot3}$
3	2·25	2·95	$\frac{1}{3\cdot2}$
4	3·10	4·12	$\frac{1}{3\cdot0}$
5	3·12	3·82	$\frac{1}{4\cdot4}$
6	3·40	4·58	$\frac{1}{2\cdot8}$
7	4·00	5·25	$\frac{1}{3\cdot2}$
8	4·25	5·50	$\frac{1}{3\cdot4}$
9	4·45	5·55	$\frac{1}{4\cdot0}$
10	4·56	5·70	$\frac{1}{4\cdot0}$
11	5·20	6·60	$\frac{1}{3\cdot7}$
12	5·55	6·50	$\frac{1}{5\cdot8}$
13	5·55	7·20	$\frac{1}{3\cdot3}$
14	5·70	7·20	$\frac{1}{3\cdot8}$
15	6·50	9·10	$\frac{1}{2\cdot5}$
16	7·80	9·75	$\frac{1}{4\cdot0}$
17	12·80	15·50	$\frac{1}{4\cdot7}$

Consequently, the early crabs will probably cast eight or nine times before the following summer, while the late crabs may have cast only five times. There will, also, be a corresponding difference in size.

It will be realised, therefore, that it is quite impossible to state the age of a crab with any degree of certainty. The size of the crab not only depends upon the frequency of casting, but also upon the ratio of increase at each act of ecdysis. As we have already seen, both these factors are subject to a considerable amount of variation. The most valuable information on this point is to be obtained from continued observations of crabs kept in an aquarium. This has been done to a certain extent by Mr. Waddington, of Bournemouth. But, even in such cases, we are not justified in establishing any broad principles on the results obtained. In the first place, there is no doubt that captivity affects the frequency of casting. There is also the same difficulty that obtains amongst crabs living amongst natural conditions, viz., that ratio and frequency of casting vary in individual crabs. This is demonstrated quite clearly by an examination of Waddington's* three series, in which both factors vary considerably.

But in spite of the impossibility of forming any definite laws with regard to the frequency of casting, a careful examination of all the available facts and figures enables one to give a general outline of the life-history of Cancer with regard to this particular point.

I propose, therefore, to give such an outline, but, in doing so, I must emphasise what I have already said—that we are dealing with factors which are by no means constant.

I intend taking a purely hypothetical case, utilising,

---

* Williamson. *Twenty-second Annual Report*, p. 135.

however, the stages of Waddington's Series A for the first two years.

First year. The larva was probably hatched in June. During the first year the crab cast eight times, and at the end of the first year (June to June) it was 30·75 mm. broad.

Second Year. The crab cast twice (September and March), and was 45·75 mm. broad at the end of its second year. (In the first two years the ratio of increase varied considerably. It will also continue to vary throughout life, but for practical purposes I intend taking the ratio of increase to be uniformly $\frac{1}{4}$, which is an average ratio.)

Third year. There will probably be two castings, so that at the end of the year the crab will be 70·6 mm. broad.

Fourth year. There will be only one ecdysis. At the end of the year the crab will be 88 mm. broad.

Fifth year. Only one casting. Size at the end of the year, 110 mm. The crab will now be mature, and if a female will probably be fertilised while in the "soft" condition.

Sixth year. The crab will not cast.*

Seventh year. The crab will cast once, and will be 137·5 mm. in width after ecdysis. Fertilisation will again be effected when the crab is "soft."

Eighth year. The crab will not cast.

Ninth year. The crab will cast, and after ecdysis will be 171·8 mm. broad. Fertilisation will take place immediately after ecdysis.

I believe it to be highly probable that after the female crab attains a size of six inches (150 mm.) ecdysis will only take place once in three years (see below under

---

* There is every reason to believe that after attaining maturity the crabs only cast once in two years.

"Granny" Crabs). If a male, it will probably cast once in two years.

First Year.

Number of Casting	1	2	3	4	5	6	7	8
Width in mm.	4·75	5·75	8·5	10·75	14·5	19·5	24·5	30·75
Width in inches	($\frac{1}{5}$)	($\frac{1}{4}$)	($\frac{1}{3}$)	($\frac{2}{5}$)	($\frac{3}{5}$)	($\frac{4}{5}$)	(1)	($1\frac{1}{4}$)

	Second Year.		Third Year.	
Number of Casting	9	10	11	12
Width in mm.	36·5	45·75	56·5	70·6
Width in inches	($1\frac{1}{2}$)	($1\frac{3}{4}$)	($2\frac{1}{4}$)	($2\frac{3}{4}$)

	Fourth Year.	Fifth Year.	Sixth Year.
Number of Casting	13	14	Did not cast
Width in mm.	88·2	110·0	—
Width in inches	($3\frac{1}{2}$)	($4\frac{1}{2}$)	—

	Seventh Year.	Eighth Year.	Ninth Year.
Number of Casting	15	Did not cast	16
Width in mm.	137·5	—	171·8
Width in inches	($5\frac{1}{2}$)	—	($6\frac{3}{4}$)

	Tenth Year.	Eleventh Year.	Twelfth Year.
Number of Casting	Did not cast	Did not cast	17
Width in mm.	—	—	214·7
Width in inches	—	—	($8\frac{1}{2}$)

The approximate calculations given above do not lend support to Williamson's statement that "a crab of four and a quarter inches across would be not less than three years, nor probably more than four years old." Even if we take a growth ratio of one-third, which is rather high, we find that the crab would not reach the size of four and a quarter inches until the fourth year at the earliest.

There is abundant evidence to show that the adult male and female crabs do not cast every year, but probably only once in two years. There appears to be little doubt, moreover, that in the older crabs ecdysis may take place less frequently than once in two years, and Williamson has given several instances of crabs in which the shell is undoubtedly more than two years old. In the Nordsee Museum, Heligoland, there is a female Cancer, with a carapace breadth of 17 cm., having attached to the shell, an Anomia 5·8 cm. in width.

Although there appears to be a stage in the life-history of Cancer after which ecdysis is only triennial, no attempt has been made to determine at which period the change from a biennial to a triennial growth takes place.

Such an investigation presents innumerable difficulties, and the only way in which the problem can be satisfactorily solved is either by having large crabs under observation in captivity for many years, or by the careful analysis of a great number of exact measurements made for the purpose. Neither of these methods has been followed, and although Williamson has been able to gather a mass of extremely useful information, his statistics do not appear to be of much value in the elucidation of this particular problem.

Our present knowledge with regard to the frequency of casting may be briefly summarised as follows. In the early stages the young crab casts frequently. As it grows older the periods between successive castings become longer, and it is probable that after reaching maturity both males and females cast only once in two years. There is scattered evidence to show that many large crabs cast less frequently than once in two years, and a stage is ultimately reached when the crab ceases to cast.

It is my belief that after attaining a size of about six inches carapace breadth the females, as a general rule. only cast once in three years, but that the males continue to cast biennially for a considerably longer period. It must be admitted that the figures on which this suggestion is based are not sufficiently large to warrant any conclusive statements on the subject. So that, although I feel that my explanation is a reasonable one, and is, furthermore, supported by many facts, I bring it forward merely as a provisional hypothesis. I further recognise that, just as in the case of the younger stages, there can be no rigid law regarding the frequency of casting. It is quite possible that many males over six inches cast less frequently than once in two years, and that many females above this size may cast biennially.*

"Granny" Crabs.

The assumption that female crabs above six inches cast only once in three years was first suggested to me when examining into the nature of "granny" crabs. This name is given by the fishermen of Port Erin to crabs occurring in the late summer and early autumn which have dirty and discoloured shells and broken claws. These crabs, if eaten, have a bitter taste and a powerful purgative effect. The fishermen believe they are diseased crabs, and always kill such when captured. There appears to be no adequate reason for believing that these crabs are diseased. The fact that they occur in considerable numbers every year during the late summer and early autumn is sufficient to render this suggestion doubtful. The general condition of these crabs leads me

---

* Williamson has pointed out that if the soft mature female fails to be fertilised, it will probably cast again in the following year.

to believe that they are merely crabs ready for casting.*

Mr. T. N. Cregeen, of the Biological Station, Port Erin, kindly examined and measured for me a number of crabs during the summer of 1907. The table inserted below gives a summary of the results obtained.

One thousand and ninety-four crabs were examined, and of this number 318 were males and the remainder females. Of the 776 females, 112 were "grannies." It will be observed that there are no male "grannies" in the list, and that practically the whole of the female "grannies" are six inches or more in width. General information from Port Erin bears this out. Male "grannies" and small female "grannies" are almost unknown.

Crabs obtained between the Calf of Man and Bradda Head, Port Erin, during the summer (July to September) of 1907.

Greatest breadth of Carapace (in inches).	Males.	Females.		Total.
		Normal.	"Granny."	
3½—4	—	2	—	2
4—4½	27	16	—	43
4½—5	63	31	—	94
5—5½	67	90	—	157
5½—6	54	153	3	210
6—6½	38	164	18	220
6½—7	23	100	36	159
7—7½	16	58	31	105
7½—8	15	30	19	64
8—8½	13	14	4	31
8½—9	1	6	1	8
9—9½	1	—	—	1
Totals.........	318	664	112	1,094

---

* In "granny" crabs that I have examined there has been a well-defined cuticle beneath the hard exoskeleton. This condition is found in crabs preparing for ecdysis.

As already stated, mature crabs generally cast from August to November, and immediately before and after ecdysis their flesh is " watery " and has a bitter taste, and is, therefore, unfit for food. The above symptoms are also characteristic of the " granny " crab.

" Grannies " are found only amongst females above six inches in breadth. The explanation of this is that those females below this size do not retain their shells long enough for the latter to acquire the discoloured and broken appearance. An interval of two years between successive castings is evidently insufficient to produce this effect.

This diminution in the frequency of casting in the females above six inches may be due to the general rule that as the crab grows older the period between successive castings tends to become longer until a time is reached when ecdysis ceases altogether. But this explanation does not appear to be sufficient to account for the supposed difference between males and females in this respect. An important factor in determining the time of casting is the condition of the reproductive organs. Ecdysis will not take place in the female so long as there is a supply of spermatozoa in the spermathecae. The supply of spermatozoa received by the soft female is generally sufficient to fertilise at least two batches of eggs in successive winters, and it is highly probable that the older crabs will spawn three times between each moult. Williamson has emphasised this point, and has also stated that the soft female which, for any reason, does not become fertilised, will cast in the following summer. The frequency of ecdysis, then, in mature females is influenced by the condition of the spermathecae, and it is probable that on this account the older females will cast less frequently than the younger ones.

These conditions do not affect the male. In the female the casting time is of double importance, as it is at that period that fertilisation is effected. In the male, however, ecdysis would appear to be important only as a period of growth. It appears to me, therefore, from an examination of all the evidence obtainable, that male crabs above six inches in breadth continue to cast once in two years, and it is probable that this is the case until ecdysis stops. This rule cannot be an invariable one, as there are a few records of male crabs which have not undergone the casting process for at least three years.

My suggestion that the males above six inches cast more frequently than the females of a similar size, and, therefore, do not become "grannies," is borne out, not only by an examination of the statistics given above, but also by some figures which I quote from Williamson.* These figures give a comparison of hard and soft mature crabs taken off Dunbar. I have only included those figures dealing with the casting period.

Date.	Hard crabs above 4¼ ins.		Soft crabs above 4¼ ins.	
	Males.	Females.	Males.	Females.
Aug. 4, 1899	26	77	1	8
Sept. 23, 1899	76	104	235	144
Oct. 27, 1899	83	160	140	87
Nov. 5, 1898	269	206	64	32
Nov. 17, 1899	117	60	66	48
Dec. 13, 1899	196	200	56	42
Dec. 20, 1897	60	110	22	4
Totals..............	827	917	584	365

Total number of males 1,411
,, ,, females 1,282

In other words, for every 100 males (hard and soft) there are 91 females (hard and soft). For every 100 soft

---

* Williamson. *Eighteenth Report*, page 102, Table V.

males there are only 62 soft females. This points to the fact that the mature males cast more often than the females. It is probable that both males and females of between four and a quarter inches and six inches cast once in two years, so that it is in the older crabs that the males cast more frequently than the females. I do not attach too much importance to the above figures, as the numbers are too small to justify their use in the question of the frequency of casting. So far as they go, however, they confirm my statement that the female crabs over six inches do not cast so often as the males of a similar size. It is, therefore, probable that the "granny" crabs are not diseased, but are merely females ready for casting. They are only found amongst females of over six inches in breadth. The reason why smaller females and males of all sizes do not become "grannies" is because they cast at least once in two years.

I have been unable to find any reference to "granny" crabs in the literature* of the subject, but Williamson says "as a rule the shell of the old female crab is much more dirty than that of the male."† He attributes this dirtiness to the fact that the female when carrying eggs lies half buried in the mud. This explanation may have some truth in it, but it does not solve the problem as to why only female crabs above six inches in breadth become discoloured.

It is evident that the various processes which are characteristic of the life-history of the edible crab are subject to considerable variation, and it is necessary that further investigations should be made before the numerous problems can be regarded as being solved.

---

* With the exception of a preliminary notice by Professor Herdman in *Twenty-first Annual Report of the L.M.B.C. (Port Erin Marine Biological Station)*, p. 25.

† Williamson. *Eighteenth Report*, p. 110.

EXPLANATION OF PLATES.

Reference Letters.

a. acc.—Anterior accessory muscle of the scaphognathite.
a. art.—Antennary artery.
ab. 1—6.—Abdominal somites 1 to 6.
abd.—Abdomen.
abs.—Lines of absorption.
a. ex. B.—Tendon of the anterior extensor of basi-ischium of chela.
af.—Afferent branchial sinus.
af. 1.—Do. of the podobranch of the second thoracic somite.
af. 2.—Do. of the arthrobranch of the second thoracic somite.
af. 3.—Do. of the podobranch of the third thoracic somite.
af. 4.—Do. of the anterior arthrobranch of the third thoracic somite.
af. 5.—Do. of the posterior arthrobranch of the third thoracic somite.
af. 6.—Do. of the anterior arthrobranch of the fourth thoracic somite.
af. 7.—Do. of the posterior arthrobranch of the fourth thoracic somite.
af. 8.—Do. of the pleurobranch of the fifth thoracic somite.
af. 9.—Do. of the sixth thoracic somite.
a. f. fl.—Anterior flexor of the flabellum of the first maxillipede.
a. gl.—Antennary gland.
a. i. p.—Antero-inferior pyloric ossicle.
a. lb.—Antero-lateral lobe of the bladder.
a. mes.—Anterior mesopyloric ossicle.
amp.—Pyloric ampulla.
amp. C.—Supra-ampullary ridge.
a^1. *n.*—Nerve of the first antenna; *a*^{2}. *n.*—Nerve of the second antenna.
ant.—Second antenna; *ant*^{r}—First antenna (antennule).
a. oe. lb.—Anterior oesophageal lobe of the bladder.
ao. lb.—Outer portion of the antero-lateral lobe of the bladder.
a. ost.—Anterior ostia of the heart.
a. pl.—Anterior pleuropyloric ossicle.
apoph.—Apophysis of the mandible.
art. 1—*etc.*—Branches of the sternal artery supplying the first and following post-oral cephalothoracic appendages.
a. s.—Antero-superior dilator muscles of the fore-gut.
a. s. a.—Anterior supra-ampullary ossicle.
as. lb.—Anterior oesophageal lobe of the bladder.
a. t. l.—Lateral accessory tooth.

B.—Basipodite.
bc. 1—5.—Branchio-cardiac veins 1 to 5.
B-I.—Basi-ischiopodite.
bl.—Bladder.
b. m.—Basement membrane.
br.—Gills.
br. ch.—Branchial chamber.
br. e.—Branchial excretory organ.
br. s. 1—5.—Branchial sinuses 1 to 5.

C.—Coxopodite.
C^1.—Carpopodite.
caec.—Mid-gut caecum.
c. al.—Antero-lateral cardiac muscles.
c. ant.—Anterior cardiac muscles.
card.—Cardiac portion of the fore-gut.
cd. 1.—Dorsal antero-lateral muscles of the heart.
cd. 2.—Ventral antero-lateral muscles of the heart.

cd. 3.—Dorsal postero-lateral muscles of the heart.
cd. 4.—Ventral postero-lateral muscles of the heart.
cd. 5.—Posterior muscle of the heart.
cd. 6.—Lateral posterior muscle of the heart.
cd. al.—Antero-lateral cardiac plate.
cd. pl.—Postero-lateral cardiac plate.
c. g.—Cerebral ganglia.
ch.—Chela.
ch. ep.—Epidermis (chitogenous epithelium).
c. i.—Postero-inferior cardiac muscle.
c. lat.—Lateral cardiac muscles.
c. m.—Circular muscles.
c. lob.—Cerebral lobe of the bladder.
cn.—Cornea.
c. oe.—Constrictor muscles of the œsophagus.
Com.—Commissure.
corn.—Corneagen (cells of ommatidium).
c. p. v.—Cardio-pyloric valve.
c. py.—Cardio-pyloric muscles.
c. t.—Connective tissue.
ct. gl.—Cutaneous gland.
cut.—Cuticle.

D.—Dactylopodite.
d. ai.—Antero-inferior dilator muscle of the cardiac fore-gut.
d. art.—Descending artery.
Der.—Dermis.
d. cx. C.—Tendon of the dorsal extensor muscle of the coxopodite.
d. f. ex.—Dorsal flexor muscle of the exopodite.
d. g.—Duct of the gland.
di. gl.—Digestive gland.
d. l.—Deeper layer of the cornea.
d. la.—Antero-lateral dilator muscle of the cardiac fore-gut.
d. lp.—Postero-lateral dilator muscle of the cardiac fore-gut.
d. sup.—Dorsal pyloric muscle.
d. v. m.—Dorso-ventral muscles.

E.—Epistoma.
e. a. md.—External adductor muscle of the mandible.
e. b. md.—External abductor muscle of the mandible.
e. bl.—Epithelium of the bladder.
e. d.—Ejaculatory duct.
e. es.—Epithelium of the end-sac.
ef.—Efferent vessel.
ef. 1—9.—Efferent vessels of gills 1 to 9.
e. lb.—Epigastric lobe of the bladder.
end.—Endopodite.
end. s.—End sac.
ep. 4—12.—Endopleurites of somites 4 to 12.
epm. 1—19.—Epimera of somites 1—19.
e. st. 4—12.—Endosternites of somites 4 to 12.
e. st. 13.—Last thoracic arthrophragm ("sella turcica").
e. tu.—Epithelium of the renal tubule of the labyrinth.
ex.—Exopodite.
ex. 1—6.—Extensor muscles of the abdominal somites 1 to 6.
ex. B.—Tendon of the extensor muscle of the basi-ischium.
ex. C.—Tendon of the extensor muscle of the coxopodite.
ex. C^1.—Tendon of the extensor muscle of the carpopodite.
ex. fl. (Fig. 29).—Extensor muscle of the flabellum.

ex. fl. (Fig. 30).—Extensor muscle of the flagellum.
ex. prot.—Extensor muscle of the protopodite.
ex. py.—Exopyloric ossicle.
ext. D.—Tendon of the extensor muscle of the dactylopodite.
ext. ex.—Extensor muscle of the exopodite.
ext. P.—Tendon of the extensor muscle of the propodite.
ex. tel.—Extensor muscle of the telson.

f. 1—6.—Flexor muscles of the abdominal somites 1 to 6.
f. B.—Tendon of the flexor muscle of the basi-ischium.
f. c.—Fat cell of the digestive gland.
f. C.—Tendon of the flexor muscle of the coxopodite.
f. C'.—Tendon of the flexor muscle of the carpopodite.
f. D.—Tendon of the flexor muscle of the dactylopodite.
flab.—Flabellum (epipodite).
flag.—Flagellum.
fl. m.—Muscles from the top of the " gland " to the carapace.
f. m. 1.—Flabellum of the first maxillipede.
f. m. 2.—Flabellum of the second maxillipede.
f. m. 3.—Flabellum of the third maxillipede.
f. m. c.—Ferment cell of the digestive gland.
f. o.—External female genital opening.
f. p.—Fracture plane.
f. P.—Tendon of the flexor muscle of the propodite.
f. prot.—Flexor muscle of the protopodite.
f. tel.—Flexor muscle of the telson.
f. v.—Ferment vesicle.

g. 1.—First gill. Podobranch of the second thoracic somite.
g. 2.—Second gill. Arthrobranch of the second thoracic somite.
g. 3.—Third gill. Podobranch of the third thoracic somite.
g. 4.—Fourth gill. Anterior arthrobranch of the third thoracic somite.
g. 5.—Fifth gill. Posterior arthrobranch of the third thoracic somite.
g. 6.—Sixth gill. Anterior arthrobranch of the fourth thoracic somite.
g. 7.—Seventh gill. Posterior arthrobranch of fourth thoracic somite.
g. 8.—Eighth gill. Pleurobranch of the fifth thoracic somite.
g. 9.—Ninth gill. Pleurobranch of the sixth thoracic somite.
g. a.—Anterior gastric muscle.
g. f.—Fat globules.
g. lb.—Paragastric lobe of the bladder.
g. p. e.—External posterior gastric muscle.
g. p. i.—Internal posterior gastric muscle.

h.—Seta of the endopodite of the pleopod of the female.
h. art.—Hepatic artery.
h. g.—Hind gut.
h. l.—Hepatic lobe of the bladder.

I.—Ischiopodite.
ia. art.—Inferior abdominal artery.
i. a. f.—Inter ampullary fold.
i. a. md.—Internal adductor muscle of the mandible.
i. b. md.—Internal abductor muscle of the mandible.
i. b. s.—Inter-branchial septum.
i. caec.—Hind-gut caecum.
i. c. m.—Inner flexor muscle of the first maxilla.
i. ex.—Inner flexor muscle of the scaphognathite (*i. ex. s.*, Figs. 27, 31).
i. f.—Inner extensor muscle of scaphognathite.
i. f. m.—Inner extensor muscle of first maxilla.

i. gl.—Glands of the hind-gut.
i. l.—Infero-lateral cardiac tooth.
i. m. ex.—Inner median flexor muscle of the scaphognathite.
i. m. f.—Inner median extensor muscle of the scaphognathite.
i. py. e.—External inferior dilator muscle of the pyloric fore-gut.
i. py. i.—Internal inferior dilator muscle of the pyloric fore-gut.
i. s.—Infra-branchial sinus.

j. d.—Junction between the descending artery and the sternal artery.

l.—Gill lamella.
lab.—Labrum.
lat. t.—Lateral teeth.
l. ex. prot.—Lateral extensor muscle of the protopodite.
l. f. prot.—Lateral flexor muscle of the protopodite.
l. g. n.—Lateral gastric nerve.
lig.—Ligament.
l. m.—Longitudinal muscle.
l. py.—Lateral pyloric ossicle.
l. s.—Lamella blood sinus.

M.—Meropodite.
m.a^1.—Muscle chamber of first antenna.
m.a^2.—Muscle chamber of second antenna.
mand.—Mandible.
m. c.—Mesocardiac ossicle.
md. palp.—Mandibular palp.
med. p.—Median plate of endophragmal system.
met.—Metastoma.
m. ex. C'.—Extensor muscle of the carpopodite.
m. ex. M.—Extensor muscle of the meropodite.
m. ext. D.—Extensor muscle of the dactylopodite.
m. ext. P.—Extensor muscle of the propodite.
m. f. C'.—Flexor muscle of the carpopodite.
m. f. D.—Flexor muscle of the dactylopodite.
m. f. M.—Flexor muscle of the meropodite.
m. f. P.—Flexor muscle of the propodite.
m. g.—Mid-gut.
m. o.—Male genital opening.
m. py.—Middle pyloric ossicle.
m. s. a.—Middle supra-ampullary ossicle.
M. V.—Main vesicle.
mx^1.—First maxillipede.
mx^2.—Second maxillipede.
mx^3.—Third maxillipede.

n.—Nucleus.
n. 1.—*n.* 9.—Nerves arising from the ventral nerve mass of the thorax
n. ab.—Abdominal nerve.
n. c.—Nerve commissure.
n. f.—Foramen of ventral nerve mass for descending artery
n. i.—Nerve to hind-gut.
n. l.—Nerve to digestive gland.
n. m.—Nerve to the mandibular muscles.
n. po.—Transverse post-oesophageal connective.
n. t.—Nerve to the integument.

o.—Eye.
o. art.—Ophthalmic artery.
oe.—Oesophagus.

oe. ai.—Antero-inferior dilator muscle of the oesophagus.
oe. as.—Antero-superior dilator muscle of the oesophagus.
oe. l.—Lateral dilator muscle of the oesophagus.
o. e. m.—Outer flexor muscle of the first maxilla.
oe. p.—Posterior dilator muscle of the oesophagus.
o. ex.—Outer flexor muscle of the scaphognathite (*o.ex.s.*, Figs. 27, 31).
o. f.—Outer extensor muscle of the scaphognathite.
o. f. m.—Outer extensor muscle of the first maxilla.
o. g.—Optic ganglion.
o. l. s.—Outer lamellar sinus.
o. m. c.—Ophthalmic muscle chamber.
o. m. ex.—Outer median flexor muscle of the scaphognathite.
o. m. f.—Outer median extensor muscle of the scaphognathite.
om. n.—Oculo-motor nerve.
o. n.—Optic nerve.
o. n. fib.—Optic nerve fibres.
op.—Operculum of excretory opening.
op^1.—Inner side of operculum.
op. b. s.—Ophthalmic blood sinus.
o. ped.—Optic peduncle.
o. py.—Pyloric ossicle.
orb.—Orbit.
ov.—Ovary.
ov. art.—Ovarian artery.
ovd.—Oviduct.

P.—Propodite.
P. 1—4.—Walking legs 1 to 4.
p. 1—2.—1st and 2nd abdominal appendages of male.
p. acc.—Posterior accessory muscle of the scaphognathite.
p. c. p.—Pro-cephalic processes.
pec.—Pectineal ossicle.
ped.—Eye peduncle.
Per.—Pericardium.
per. gl.—" Pericardial pouch."
p. ex. B.—Tendon of the posterior extensor muscle of the basi-ischium.
p. f. B.—Tendon of the posterior flexor muscle of the basi-ischium.
p. g.—Paraoesophageal ganglion.
pg. c.—Pigment cell.
pg. i.—Inner pigmented layer of the eye.
p. g. n.—Posterior gastric nerve.
pg. o.—Outer pigmented layer of the eye.
pig. l.—Pigment layer.
pl. art.—Postero-lateral artery.
p. lb.—Progastric lobe of the bladder.
p. mes.—Posterior mesopyloric ossicle.
p. n.—Postero-lateral nerve.
pod. br.—Podobranch.
p. o. lb.—Post-oesophageal lobe of the bladder.
p. ost.—Posterior ostia of the heart.
pp.—Pleuropyloric wall.
p. pec.—Prepectineal ossicle.
prot.—Protopodite.
pr. p.—Propyloric ossicle.
p. s. a.—Posterior supra-ampullary ossicle.
pt. c.—Pterocardiac ossicle.
pt. pec.—Post pectineal ossicle.
pyl.—Pyloric region of the fore-gut.
py. lat.—Lateral pyloric muscles.

r. br.—Roof of the pre-branchial chamber.
ret.—Cells of the retinula.
rhab.—Rhabdome.
rost.—Rostrum.

S^1. —S^{19}. —Sterna of somites 1 to 19.
s. a^1. —Socket of first antenna.
s. a^2. —Socket of second antenna.
sa. art.—Superior abdominal artery.
s. amp.—Supra-ampullary wall of the pyloric region of the fore-gut.
sal. g.—Salivary (o sophageal) glands.
s. art.—Sternal artery.
sb.—Striated border of the cell.
scaph.—Scaphognathite.
s. ch.—Blood sinus from the chela.
s. dt.—Subdentary ossicle.
s. h., *s. hr.*—Sub-hepatic region of carapace.
s. l.—Supraciliary lobe.
s. lb.—Supra-hepatic lobe of the bladder.
s. mx. 2.—Blood sinus from the second maxillipede.
s. mx. 3.—Blood sinus from the third maxillipede.

s. Pi.—*s. P.* 4.—Blood sinus from the walking legs 1 to 4.
sp. a.—Frontal spine.
sp. d.—Dorsal spine.
sp. l.—Lateral spine.
spt.—Spermatheca.
st.—Stalk of the egg attached to the seta of the endopodite.
st. g.—Stomatogastric ganglion.
st. i.—Inferior root of the stomatogastric nerve.
st. n.—Stomatogastric nerve.
st. s.—Superior root of the stomatogastric nerve.

t. e. ex.—Tendon of the extensor muscle of the exopodite.
tel.—Telson.
test.—Testis.
t. ex. ab.—Tendon of the external abductor muscle of the mandible.
t. ex. ad.—Tendon of the external adductor muscle of the mandible.
t. ex. M.—Tendon of the extensor muscle of the meropodite.
t. f. ex.—Tendon of the flexor muscle of the exopodite.
t. g., *t. gm.*—Ventral thoracic nerve mass.
t. int. ad.—Tendon of the internal adductor muscle of the mandible.
t. n.—Tegumentary nerve.
tu.—Renal tubule of the labyrinth.

u. c.—Urocardiac ossicle.
up. f.—Uropyloric fold.
u. py.—Uropyloric ossicle.

v.—Globules in the epithelial cells of the mid-gut.
val.—Pyloric valves.
v. d.—Vas deferens.
v. ex. C.—Tendon of the ventral extensor muscle of the coxopodite.
v. f. ex.—Ventral flexor muscle of the exopodite.
vit.—Vitrella (cells of the ommatidium).
v. m.—Egg membranes.
v. oe. g.—Ventral oesophageal cutaneous glands.

y. c.—Young cells of the tubules of the digestive gland.
y. gr.—Yolk granules.

z. c.—Zygocardiac ossicle.

Plate I.

Fig. 1. *Cancer pagurus*, from above. Small specimen.

Fig. 2. *C. pagurus*, female, from below. Only the stumps of the pereiopods are shown. This figure shows the shape of the abdomen, and also the "pleural groove." × $\frac{1}{2}$.

Fig. 3. *C. pagurus*, male, from below. Only the stumps of the pereiopods are shown. × $\frac{1}{2}$.

Plate II.

Fig. 4. First antenna (antennule) of right side, seen from below. × 2.

Fig. 5. Right second antenna, from below. × 2.

Fig. 6. Right mandible, from below. The apophysis is also shown with the tendons of the external adductor, the internal adductor and the external abductor muscles. × 1.

Fig. 7. Right first maxilla, from below. × 1.

Fig. 8. Right second maxilla and scaphognathite, from below. × 1.

Fig. 9. Right first maxillipede, from below. × 1.

Fig. 10. Right second maxillipede, with podobranch, from below. × 1.

Fig. 11. Right third maxillipede, with podobranch, from below. × 1.

Fig. 12. Anterior view of the right chela (first pereiopod). × 1.

Fig. 13. Anterior view of the right third walking leg (fourth pereiopod). × 1.

Fig. 14. First abdominal appendage of male of right side. × 1.

Fig. 15. Second abdominal appendage of male of right side. × 1.

Fig. 16. First and second abdominal appendage of male, viewed from left side. × 1.

Fig. 17. Anterior view of a right abdominal appendage of female. × 1.

PLATE III.

Fig. 18. The endophragmal system viewed from above. On the right side the thoracic epimera have been removed in order to display the endopleurites. The following parts have also been removed:—The carapace, with the exception of the anterior portion of the sub-hepatic region; the membranous roof of the branchial chamber: the abdomen; the cephalothoracic appendages (with the exception of the mandibles); the gills; and all the soft parts of the body. × 1.

Fig. 19. The sternum of the pre-oral cephalic region, viewed from above. The dorsal part of the carapace has been removed, as well as the pre-oral cephalic appendages and the soft parts. × 2.

Fig. 20. The sternum of the pre-oral cephalic region, from below. The first and second antennae of the left side have been removed to display their sockets and muscle chambers. The long peduncle of the left eye is shown, and also the labrum. × 2.

Fig. 21. Anterior and ventral view of the right chela. The anterior wall of each segment has been cut out, and the soft parts removed in order to display the tendons. × $\frac{2}{3}$.

Fig. 22. Posterior view of the basal portion of the second walking leg (right side). The posterior wall of the coxopodite has been removed in order to display the tendons of that segment and also of the basi-ischium. × 1.

Fig. 23. Posterior view of the base of the last walking leg of the right side. The posterior wall of the coxopodite has been removed in order to display the tendons of the coxopodite and of the basi-ischium. × 1.

PLATE IV.

Fig. 24. Vertical section through the integument of a soft crab. × 550.

Fig. 25. Right abdominal appendage of female, viewed from behind. To show the muscles of the protopodite and exopodite, the posterior walls of the protopodite, exopodite and endopodite have been removed. × 3.

Fig. 26. Anterior view of the right first maxilla, in order to show the muscles. × 2.

Fig. 27. Anterior view of the right second maxilla, to show the extensor muscles of the scaphognathite. × $1\frac{1}{2}$.

Fig. 28. Anterior view of the right second maxilla, in order to show the muscles of the scaphognathite. The extensor muscles have been cut short, and the basal and inner portions of the scaphognathite have been opened in order to show the flexors and accessory muscles. × $1\frac{1}{2}$. (To see this appendage in its natural position, the figure must be rotated to the left through an angle of 45°.)

Fig. 29. Posterior view of part of the first maxillipede of the right side, in order to show the muscles of the maxillipede and flabellum. The posterior flexor and the extensor muscles of the flabellum are cut through. × 2.

Fig. 30. Posterior view of the third maxillipede of the left side. The ventral walls of the various parts have been removed in order to display the muscles. × $1\frac{1}{2}$. (The base of the appendage is to the left of the figure.)

Fig. 31. A dissection of the anterior part of the cephalothorax to display the muscles of that region. The dorsal portion of the carapace has been removed, and also the soft parts, with the exception of the muscles. × 2.

Fig. 32. Dissection of the female abdomen from the ventral side to display the extensor muscles. The ventral wall and appendages have been removed, as well as all the soft parts. × $\frac{1}{2}$.

Fig. 33. Semi - diagrammatic longitudinal section through the abdomen of the female, to show the extensor and flexor muscles. × $\frac{1}{2}$.

Plate V.

Fig. 34. A dissection from above to display the various parts of the alimentary canal. The dorsal part of the body has been removed, as well as the gonads. The gills are not shown. The digestive gland is only shown on the left side.

Fig. 35. Vertical transverse section through the oesophagus, to show especially the oesophageal glands. × 35.

Fig. 36. Transverse section through the pyloric region of the fore-gut. × 30.

Fig. 37. Transverse section through a tubule of the digestive gland. × 120.

Fig. 38. A "fat cell" of the digestive gland. × 430.

Fig. 39. A "ferment cell" of digestive gland. × 430.

Plate VI.

Fig. 40. The fore-gut from the left side, showing the ossicles. × $1\frac{1}{2}$.

Fig. 41. The pyloric region of fore-gut, dorsal view. × 3.

Fig. 41*a*. Anterior view of the pro-pyloric ossicle. × 4.

Fig. 42. Transverse section through the region of the green gland, to show the parts of the bladder. Only one side shown. × 8.

Fig. 43. The ossicles of gastric mill, from above. × 2.

Fig. 44. The ossicles of the gastric mill, from below. The fore-gut has been opened ventrally. The left zygocardiac ossicle has been rotated in order to show the lateral teeth. × 3.

Plate VII.

Fig. 45. The fore-gut from the left side, showing the intrinsic and extrinsic muscles. × 3.

Fig. 46. Anterior view of the fore-gut, to show the muscles. × $1\frac{1}{2}$.

Fig. 47. The fore-gut from above, showing the intrinsic and extrinsic muscles. × $1\frac{1}{2}$.

Fig. 48. The fore-gut from behind, showing the intrinsic and extrinsic muscles. The postero-lateral dilator has been cut near its insertion at the right side in order to show the antero-lateral dilator muscle. The right posterior dilator of the oesophagus has also been cut in order to expose the lateral dilators of oesophagus. ×3.

Fig. 49. Dorsal view of the heart. × 2.

Fig. 50. View of the heart from the left side. × 2.

PLATE VIII.

Fig. 51. General view of the blood system from above. The dorsal region of the carapace has been removed. On the right side the organs remain intact, but on the left side the ovary and digestive gland have been removed. One gill on the left side has also been turned outward in order to show the afferent branchial vein and the branchio-cardiac vein. In this region, also, the flabella of the second and third maxillipedes are seen lying beneath the gills. The course of the bladder is shown on the left side. × 1.

PLATE IX.

Fig. 52. View of ventral region of post-oral cephalothorax to show the sternal artery and its branches. All the muscles have been removed. On the right side the arteries going to the legs are cut short. The inferior abdominal artery is also cut short. × $\frac{1}{2}$.

Fig. 53. Dissection of abdomen from the dorsal side to show the superior abdominal artery. The tergal region of the abdomen has been removed. × 1.

Fig. 54. Dissection of the posterior region of the thorax to show the pericardium, heart, branchio-cardiac veins and efferent branchial veins. Only seven of the gills are shown on the left side, and on the right side only the roots of the

nine gills are shown. On the right side the epimeral wall has been removed in order to show the course of the branchio-cardiac veins, and also to show the connection between the latter and the pericardium. × 1.

Fig. 55. A dissection of the epimeral region of the thorax from the right side, in order to show the positions of the branchial sinuses, the infra-branchial sinus, the afferent branchial sinuses, and also the sinuses coming from the thoracic legs. × 1.

Fig. 56. Diagrammatic section through the thorax in the region of the heart, to show the blood system and the general arrangement of the organs. The tendons of the first walking legs are shown. × $\frac{1}{2}$.

PLATE X.

Fig. 57. Dissection of the left side to show the extensions of the bladder. The dorsal region of the carapace has been removed. The fore-gut has been cut through at the oesophagus and removed. The gonads and the digestive gland have also been taken away. The antennary gland is represented by a dotted circle. × 1.

Fig. 58. Semi-diagrammatic sagittal (vertical longitudinal) section of the antennary gland. The anterior part of the gland is to the right. × 60.

Fig. 59. Detailed drawing of part of previous figure, showing the epithelial cells of the bladder, end sac and the renal tubule. × 90.

Fig. 60. Section through the mass of cutaneous glands opening on to the epistoma. × 210.

Fig. 61. Section showing the epithelial cells of the mid-gut, with characteristic striated border. × 550.

Fig. 62. Longitudinal section through part of the wall of the hind-gut, about the middle of the abdomen, showing cutaneous glands. × 165.

Fig. 63. Dorsal view of the gills of the left side in their natural position, lying upon the thoracic epimera. The roofs of the branchial and prebranchial chambers have been removed. The scaphognathite has been turned over to the inner side, in order to show the maxillipedes. The flabellum of the first maxillipede is shown lying upon the gills (the longitudinal axis of the body is at an angle of 60° with the long axis of this plate). × 1.

Fig. 64. View of the branchial chamber of the left side. Each gill has been removed at its base, so that only the points of attachment of the gills are shown. The scaphognathite and first maxillipede (with flabellum) have been removed. By removing the gills the flabella of the second and third maxillipedes are exposed. × 1.

PLATE XI.

Fig. 65. Diagrammatic transverse section across a gill, showing the branchial septum, the afferent and efferent vessels and the lamellae. × 3.

Fig. 66. Longitudinal section through a gill in the region of the afferent vessel. × 100.

Fig. 67. Transverse section through a gill, to show especially the branchial excretory cells in the septum. × 24.

Fig. 68. A dissection of the nervous system from above. The alimentary canal has been cut through the region of the oesophagus and removed, but the stomatogastric system is shown. The nerves arising from the left side of the cerebral ganglia are alone shown. Those of the right side have been cut, only the nerves arising from the right side of the thoracic ventral mass are shown. The abdominal nerve is only shown as far as the anterior region of the abdomen. × 1.

Fig. 69. Longitudinal section through the eye. The optic ganglion is also shown. × 12.

Fig. 70. Enlarged drawing of two of the ommatidia from the previous figure. × 450.

Fig. 71. Transverse section across one of the ommatidia in the previous figure, through the rhabdome and retinulae. × 1000.

Fig. 72. Transverse section across one of the ommatidia in the previous figure, through the vitrella and the pigment cells. × 1000.

Fig. 73. Surface view of the cornea, showing one of the corneal facets. × 750.

Fig. 74. Olfactory seta taken from the exopodite of the first antenna. × 1100.

Fig. 75. Auditory seta ("hooked seta") from the auditory sac of the first antenna. × 400.

Fig. 76. Auditory seta ("group seta") from the auditory sac of the first antenna. × 300.

PLATE XII.

Fig. 77. Reproductive system of a fairly mature female, showing the double ovary, the spermathecae and the oviducts. × 1.

Fig. 78. Reproductive system of an immature male, showing the paired testes, the vas deferens and the ejaculatory duct. The fore-gut is also shown in position. × 2.

Fig. 79. Section through an almost ripe ovary, showing the eggs filled with yolk granules. The details are only inserted in one egg. × 190.

Fig. 80. A very early stage in the development of the embryo, attached to a seta of an endopodite of a female pleopod. This drawing shows the method of attachment. × 50.

Fig. 81. Ripe spermatozoon, showing the two processes. Taken from spermatheca of female. × 1400.

Fig. 82. Some of the epithelial cells of the bladder of the excretory system. The striated nature of the protoplasm is shown. × 650.

PLATE XIII.

Fig. 83. Protozoëa of *Cancer pagurus*, two hours after hatching. View from the left side. × 120.

Fig. 84. Telson of the same stage, from above. × 175.

Fig. 85. Zoëa of *Cancer pagurus*, thirty hours after hatching, showing the maximum development of the frontal and dorsal spines. × 90.

Fig. 86. Dorsal view of the cephalothorax of the same stage. The dorsal and frontal spines are cut off short. × 110.

Fig. 87. Telson of the same stage, from above. × 160.

C. Tinling & Co., Ltd., Printers, 53, Victoria Street, Liverpool.

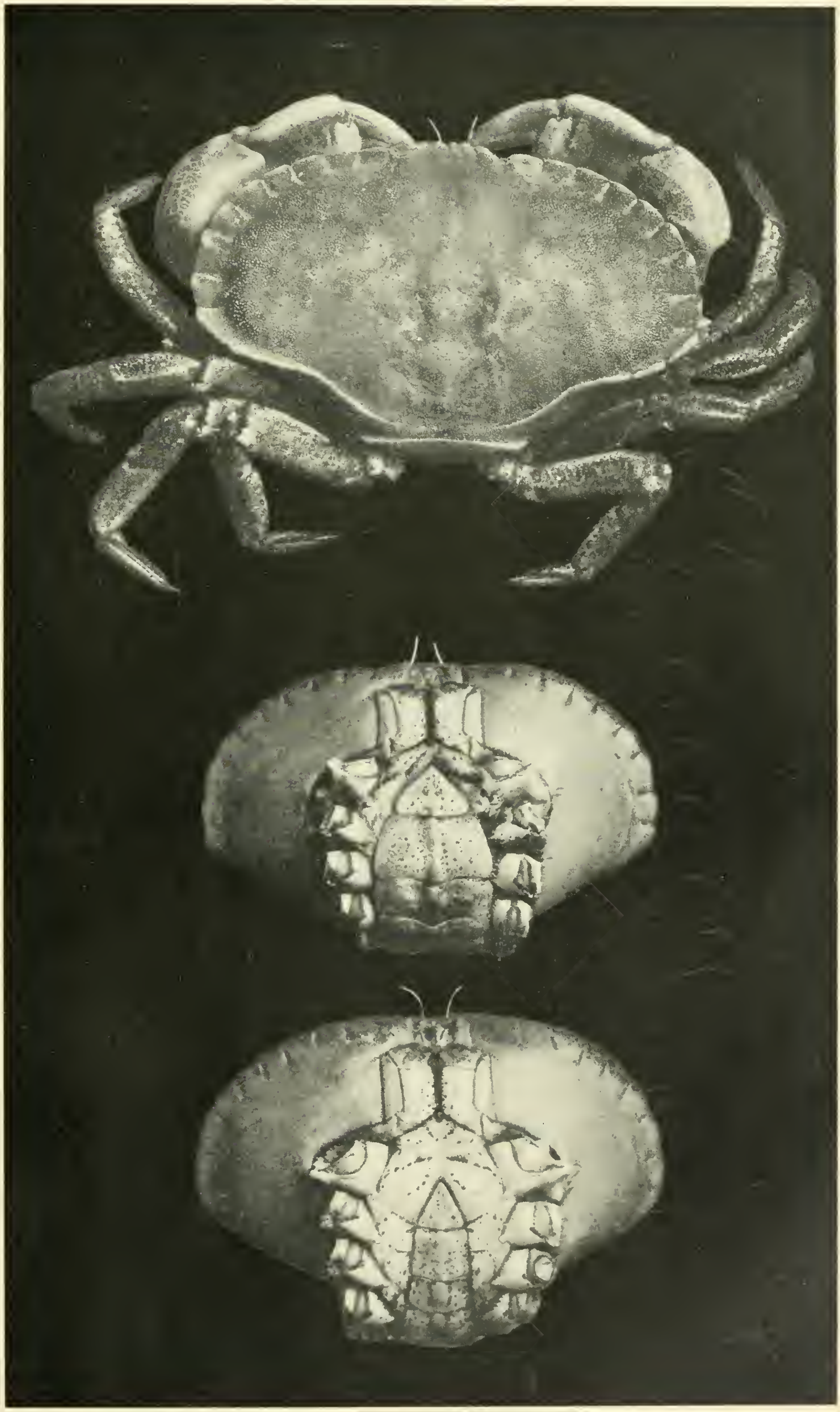
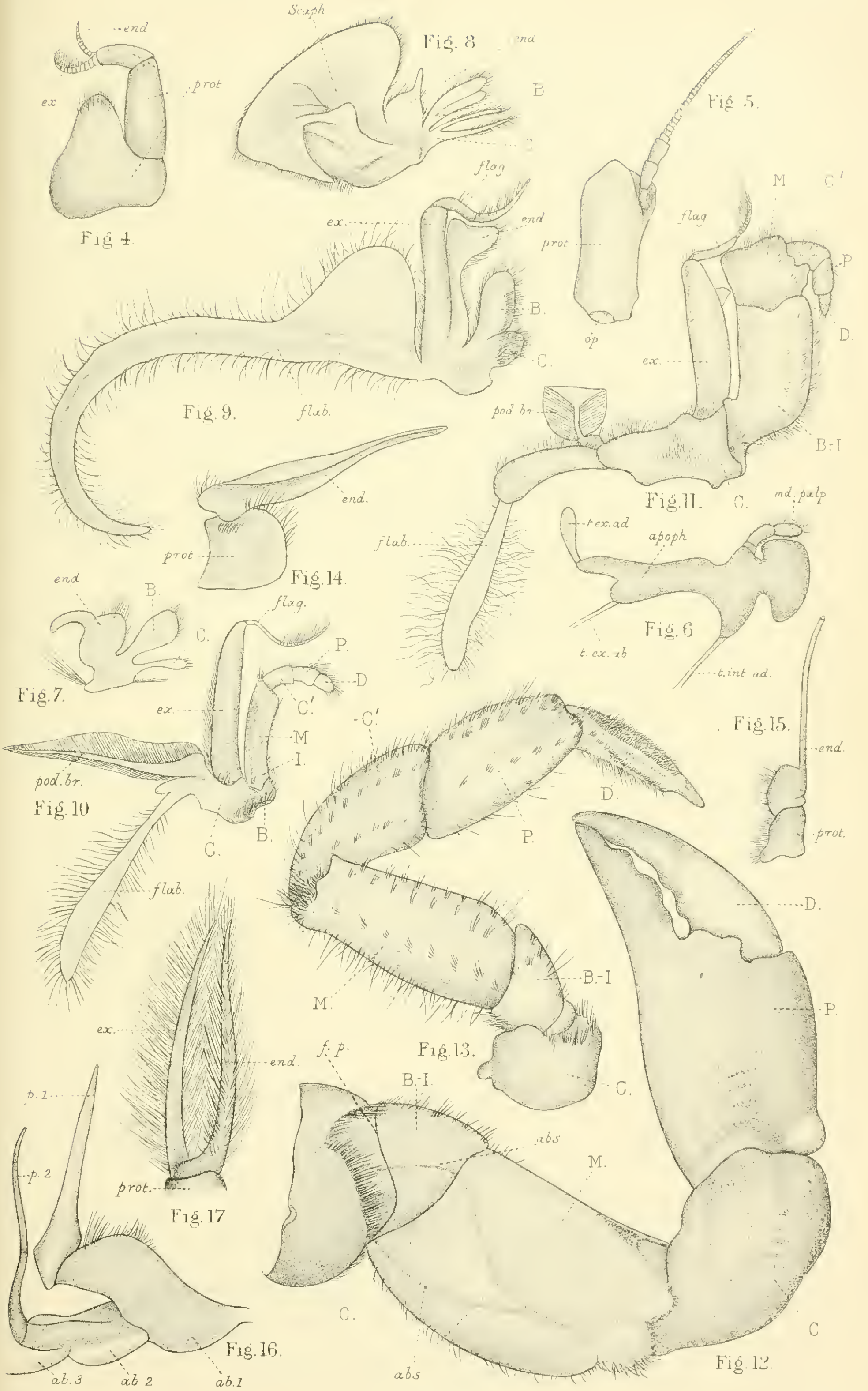


Fig. 1.

Fig. 2.

Fig. 3.

CANCER.



CANCER

M'Farlane & Erskine, Lith. Edinr

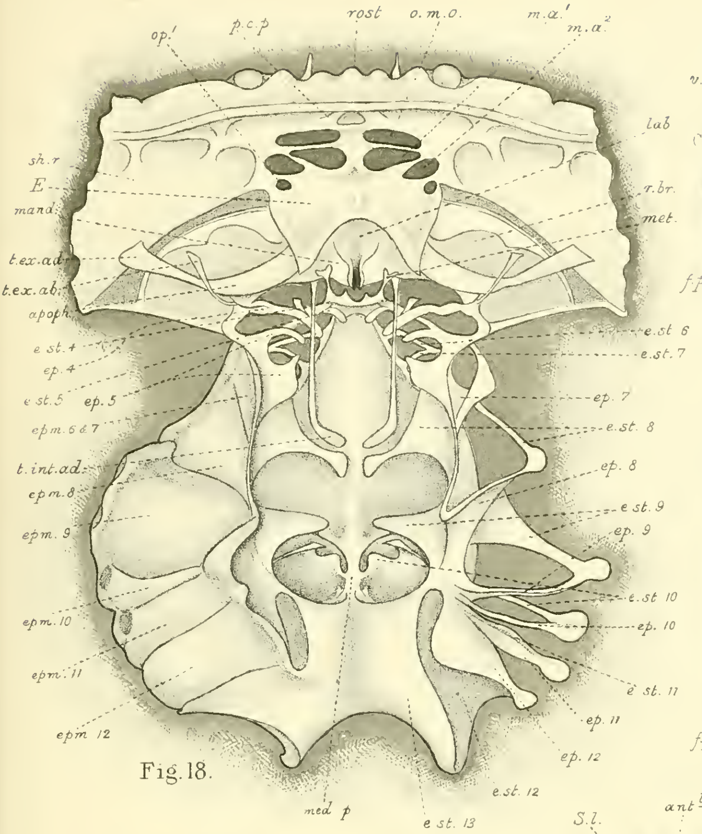


Fig. 18.

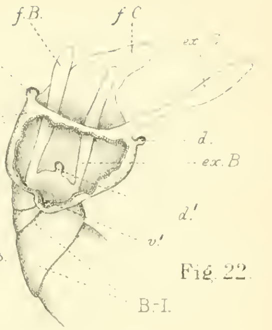


Fig. 22.

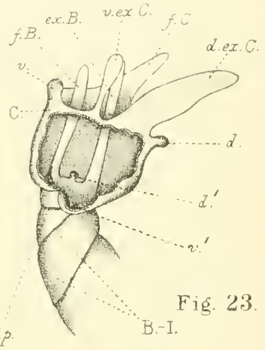


Fig. 23.

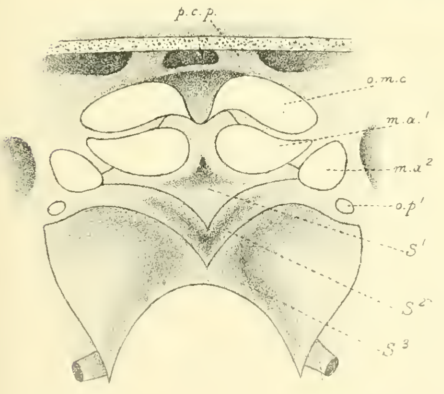


Fig. 19.

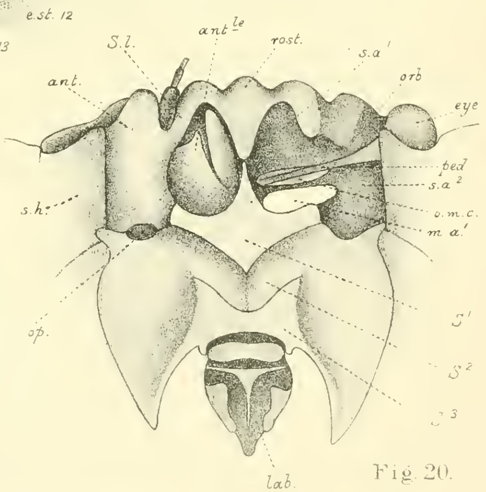


Fig. 20.

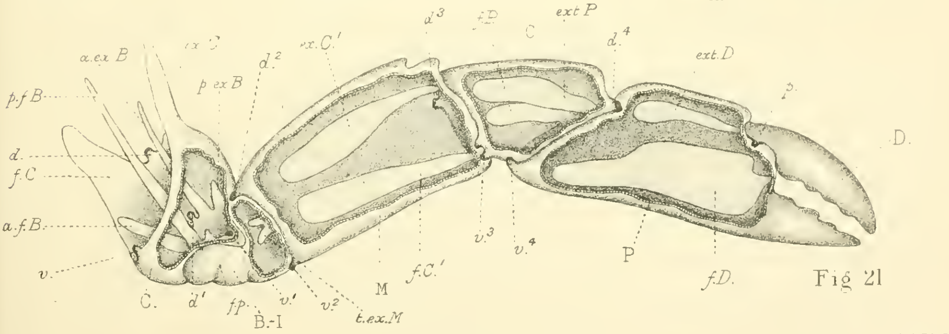


Fig 21.

J. P. del.

McFarlane & Erskine Lith. Edinr.

CANCER.

L M B. C. MEMOIR XVI PLATE IV.

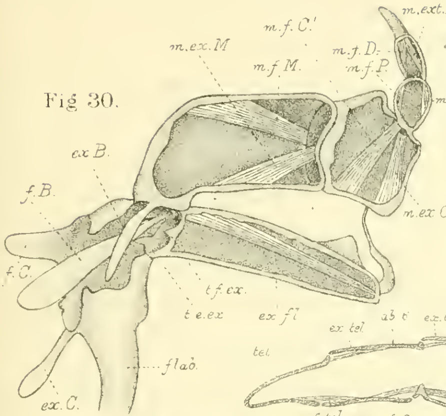


Fig 30.

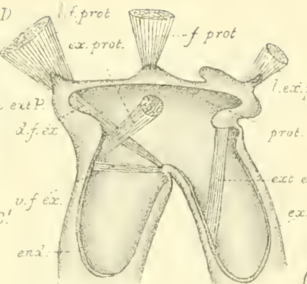


Fig. 25.

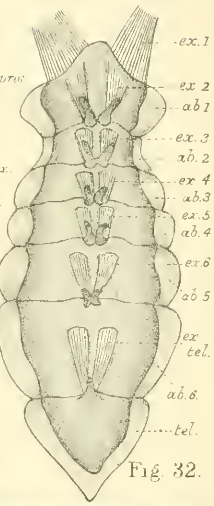


Fig. 32.

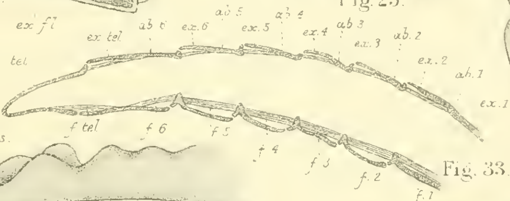


Fig. 33.

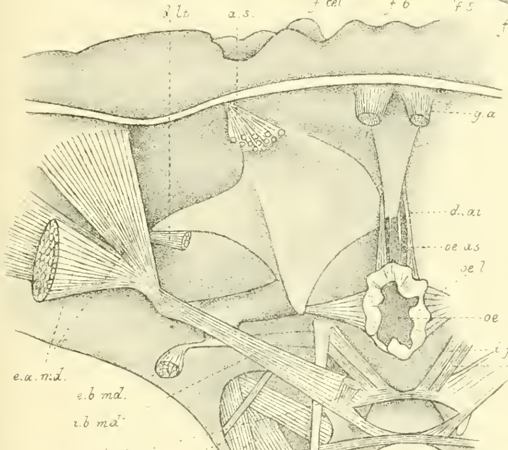


Fig. 31.

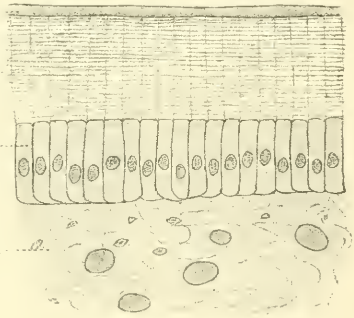


Fig. 24.

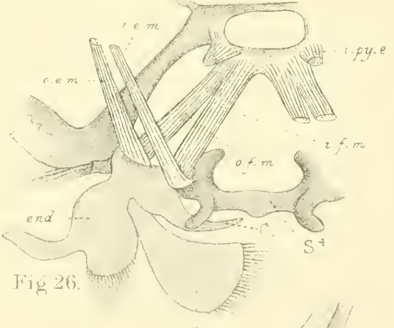


Fig 26.

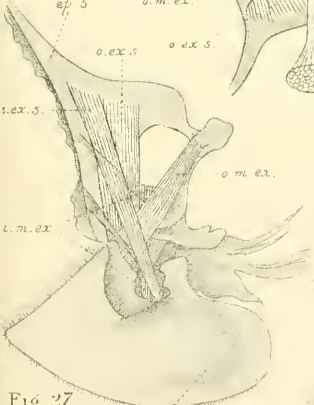


Fig 27.

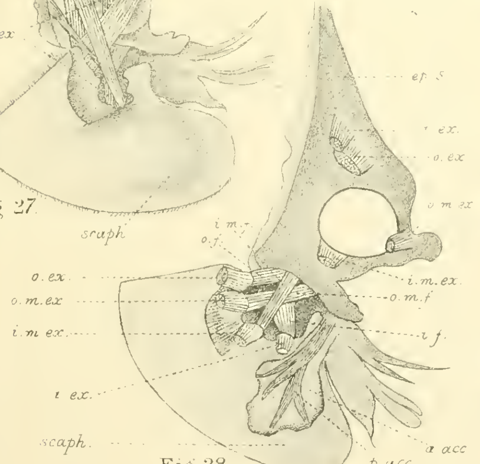


Fig 28

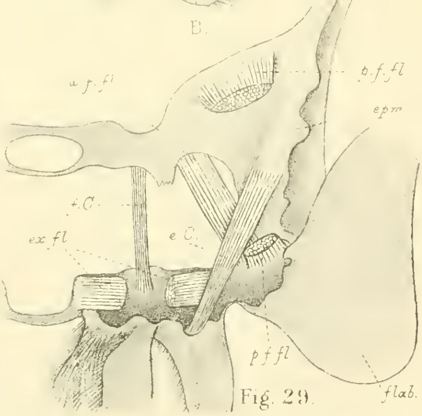


Fig. 29.

J P. del.

CANCER.

McFarlane & Erskine Lith Edinr

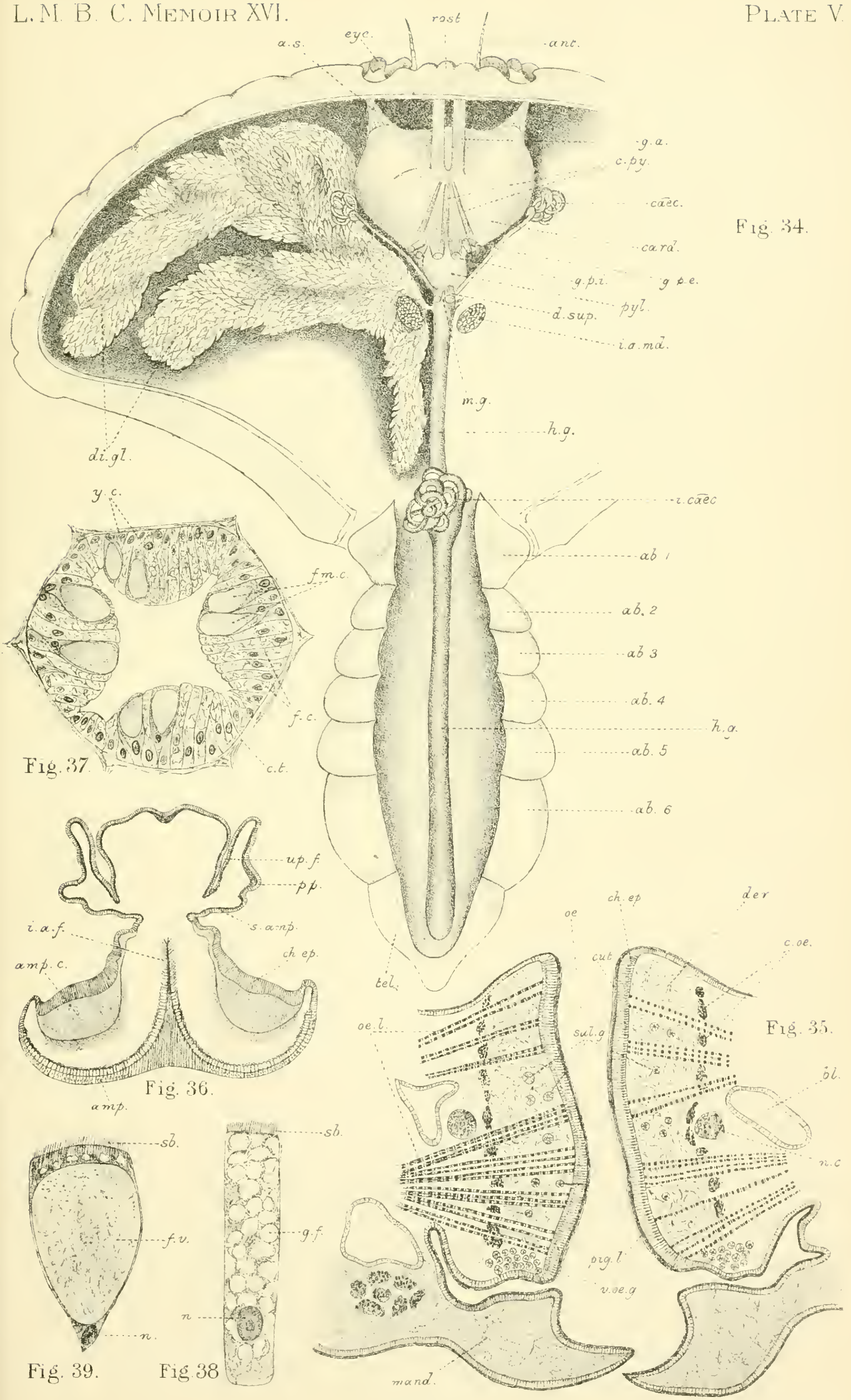


Fig. 34.

Fig. 35.

Fig. 36.

Fig. 37.

Fig. 38

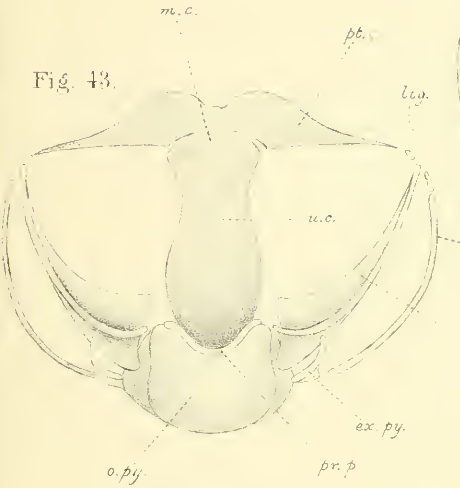
Fig. 39.

J. P. del.

CANCER.

McFarlane & Erskine Lith Edinr

Fig. 43.



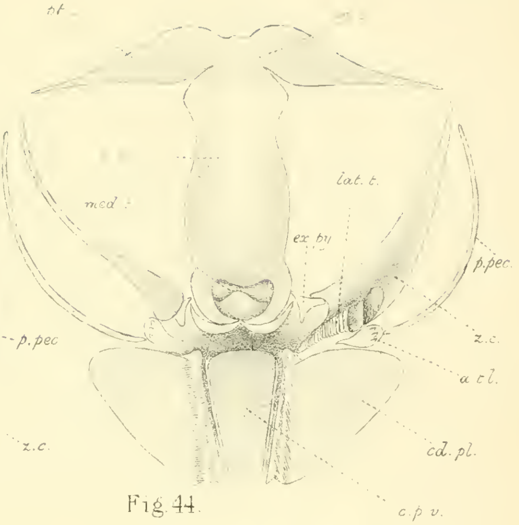


Fig. 44.

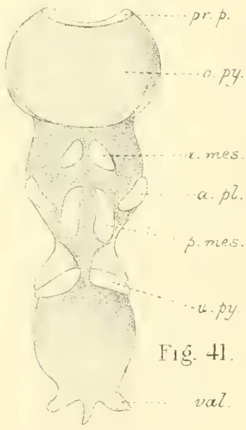


Fig. 41.

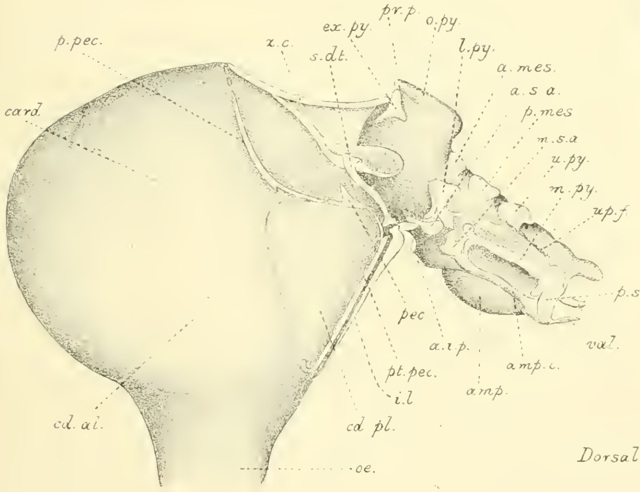
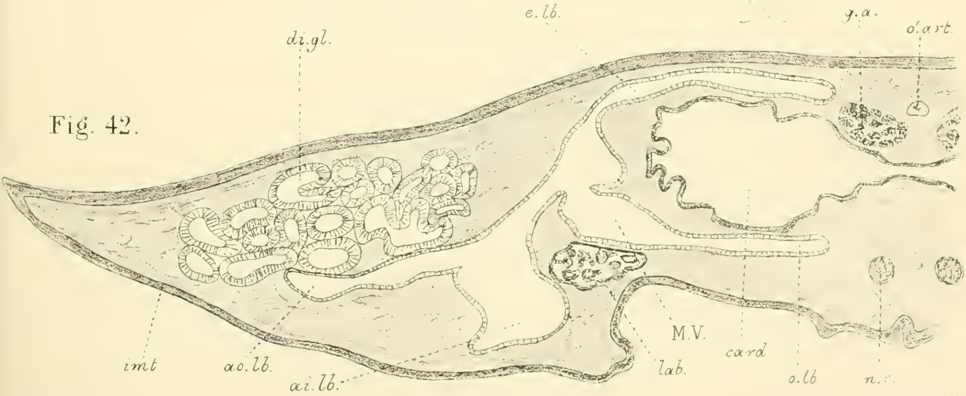


Fig. 40.

Fig. 41a.

Fig. 42.



J P del

CANCER.

McFarlane & Erskine Lith Edin

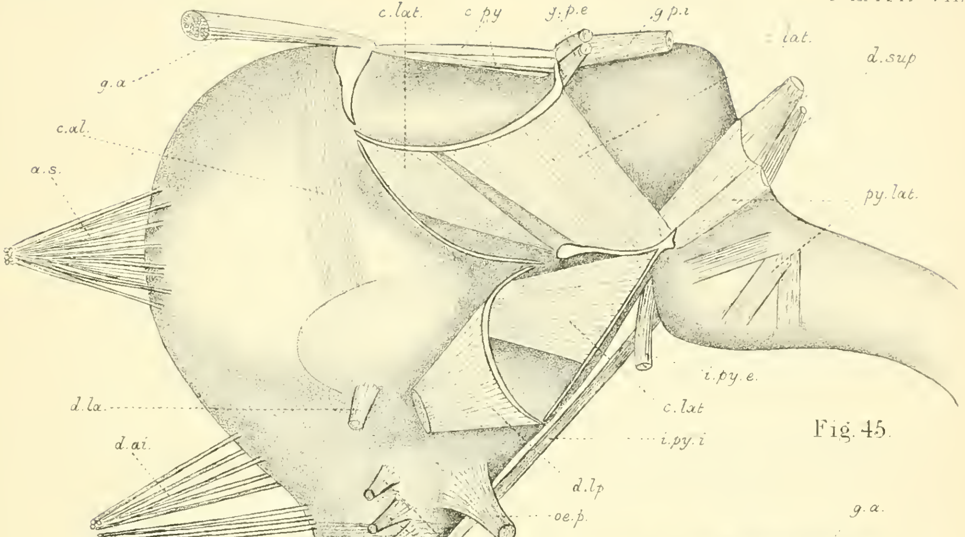


Fig. 45.

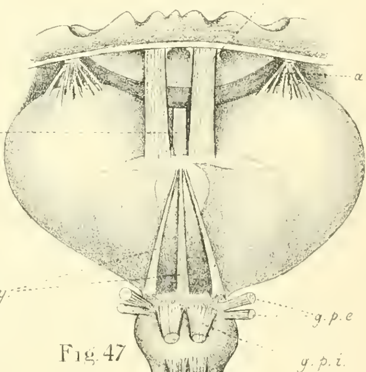


Fig. 47

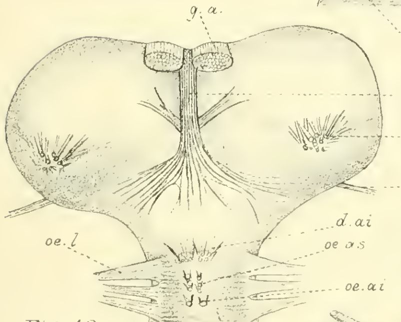


Fig. 46.

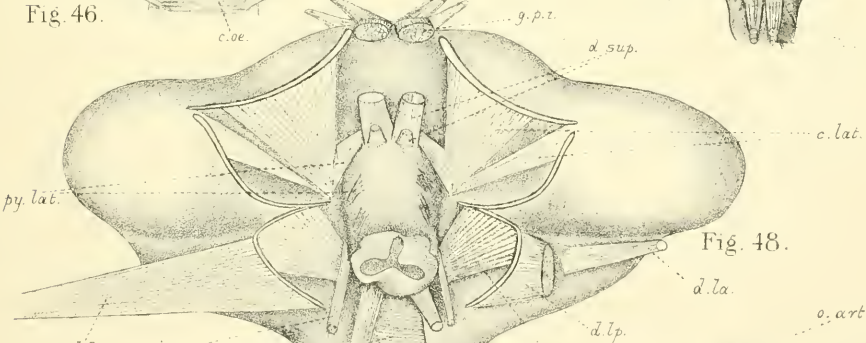


Fig. 48.

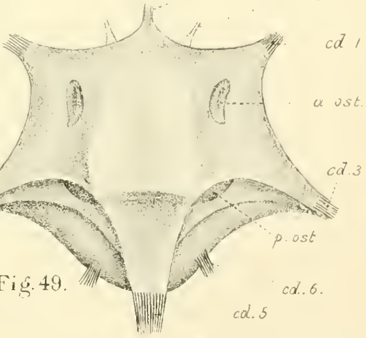


Fig. 49.

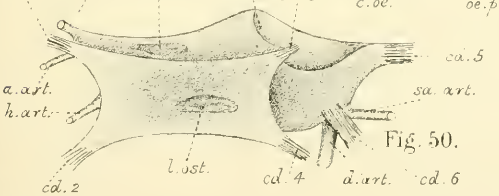


Fig. 50.

J. P. del.

CANCER.

McFarlane & Erskine Lith. Edinr

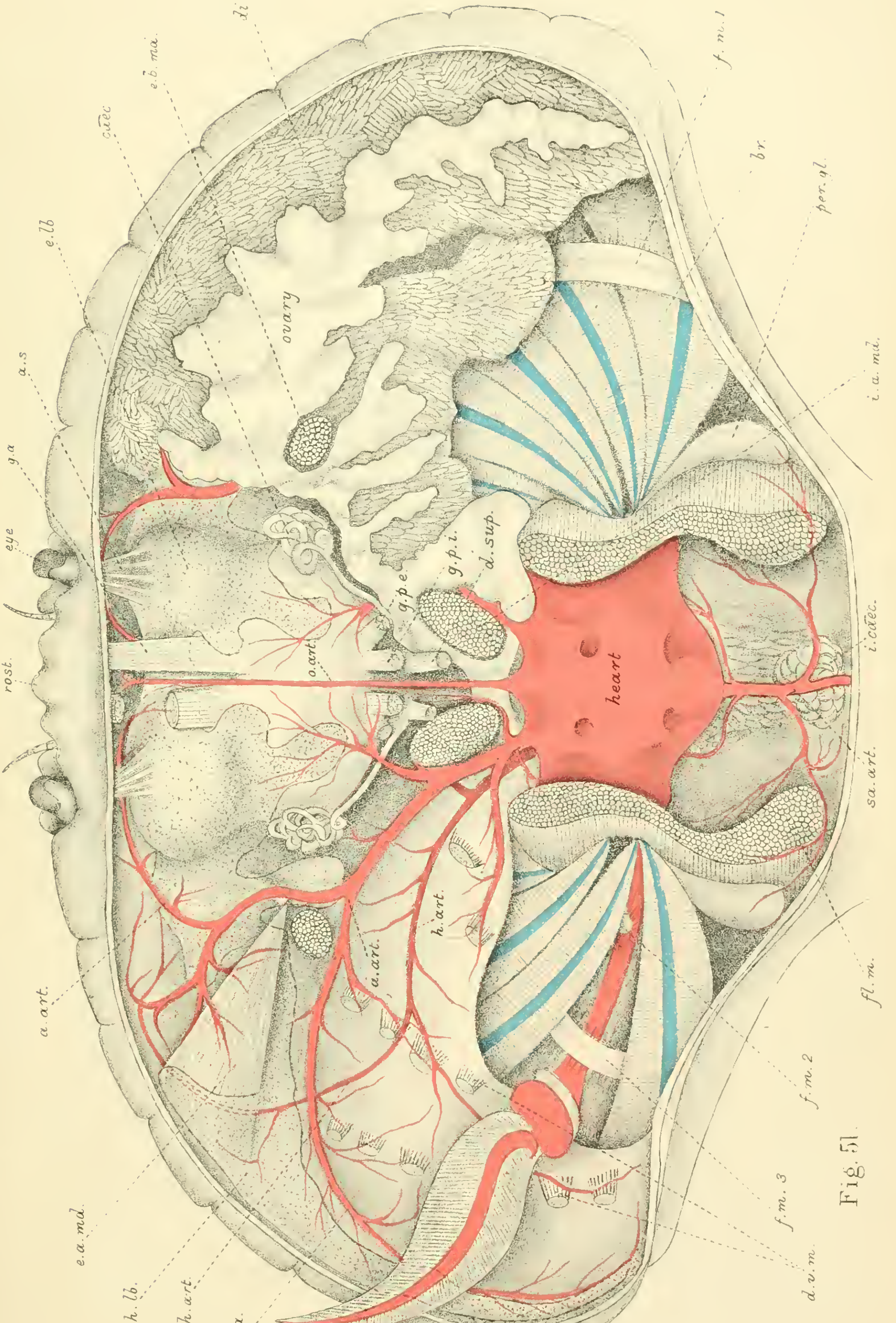


Fig. 51.

J. P. del.

McFarlane & Erskine Lith Edin'

CANCER.

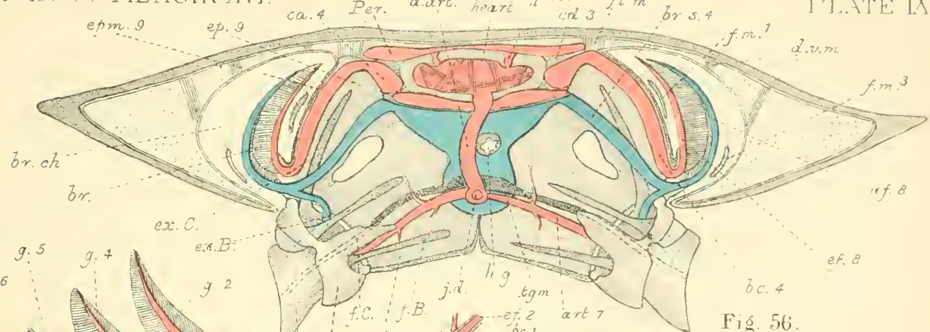


Fig. 56.

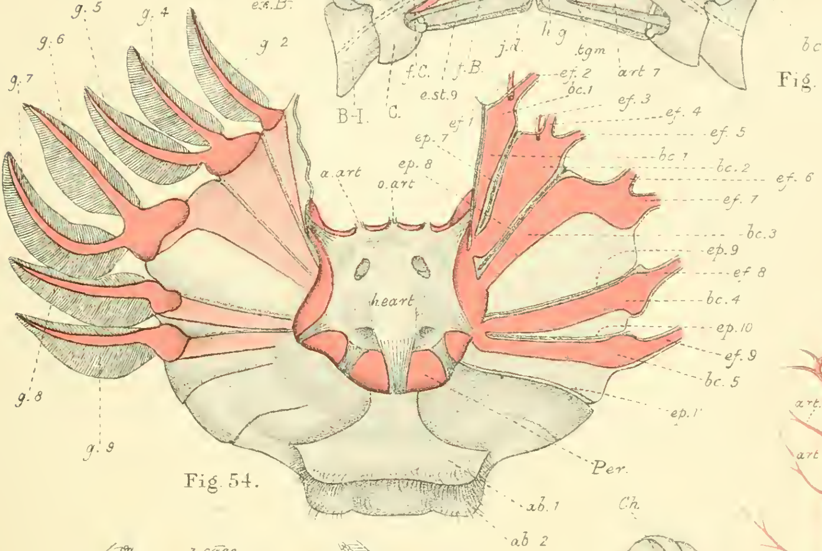


Fig. 54.

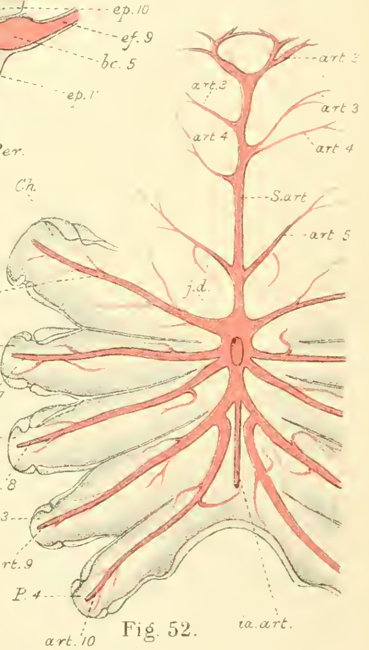


Fig. 52.

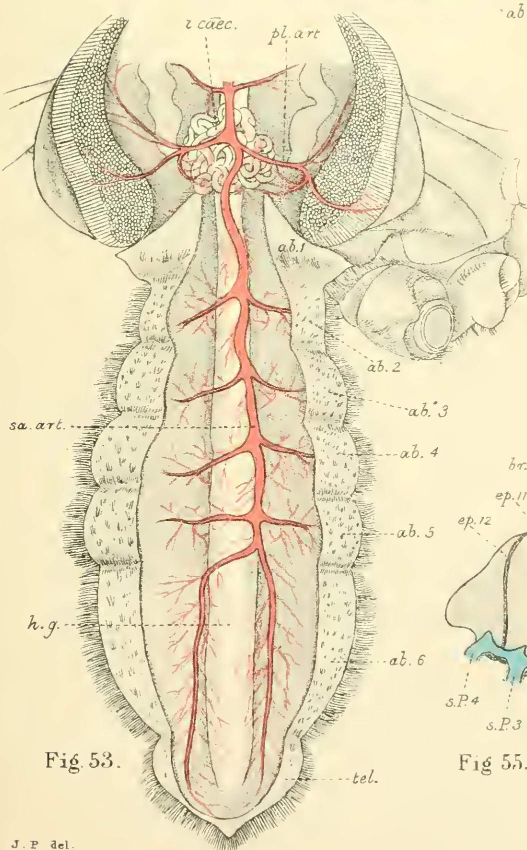


Fig. 53.

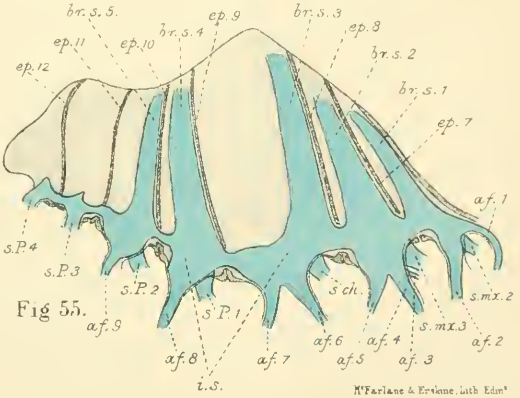


Fig 55.

J. P del.

McFarlane & Erskine, Lith Edin^r

CANCER.

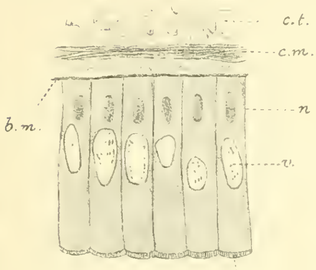


Fig. 61.

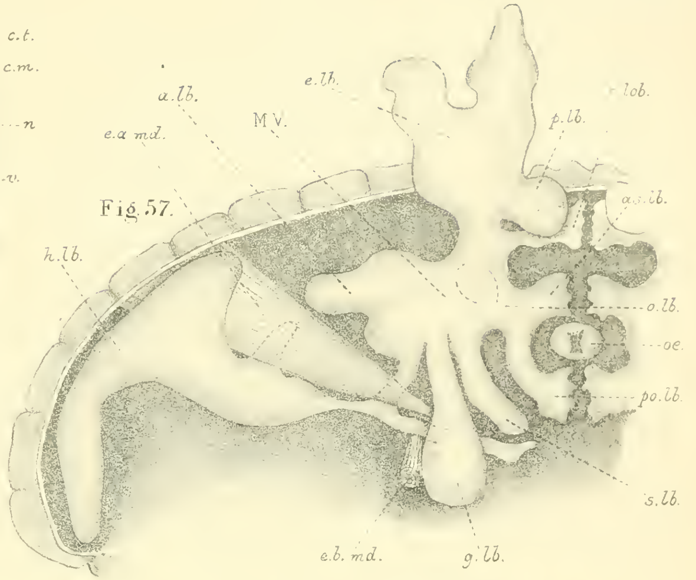


Fig. 57.

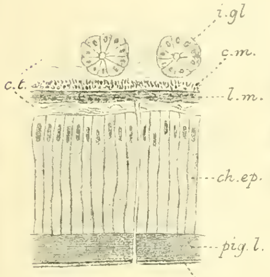


Fig. 62.

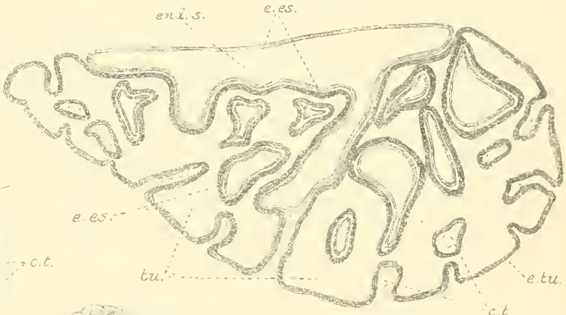


Fig. 58.

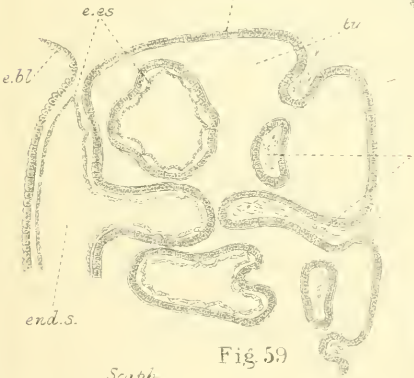


Fig. 59

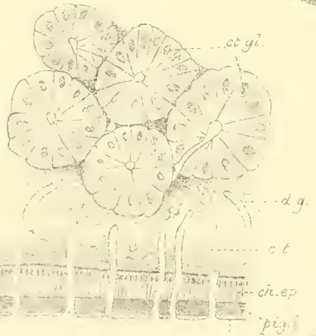


Fig. 60.

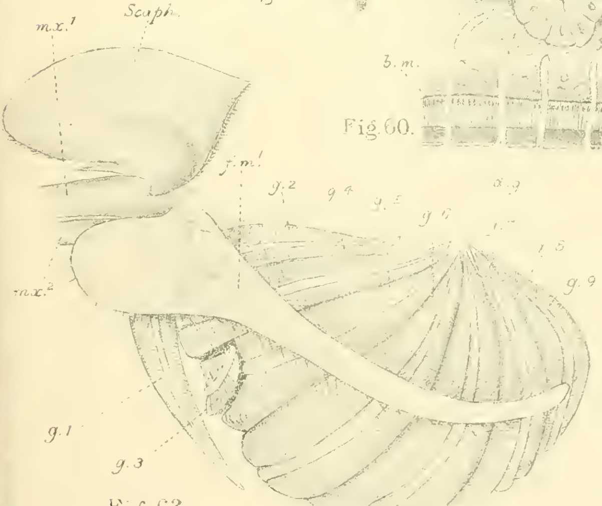


Fig. 63.

Fig. 64.

J. P. del.

McFarlane & Erskine Lith Edin

CANCER.

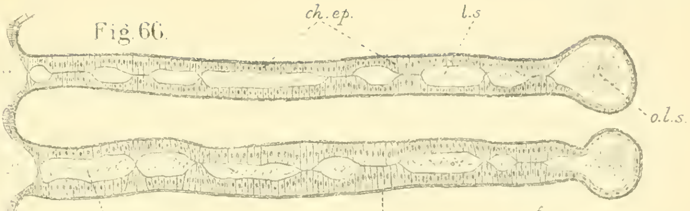


Fig. 66.

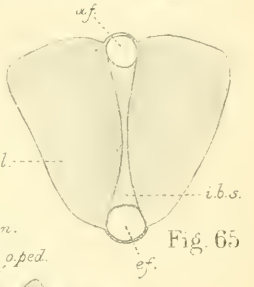


Fig. 65

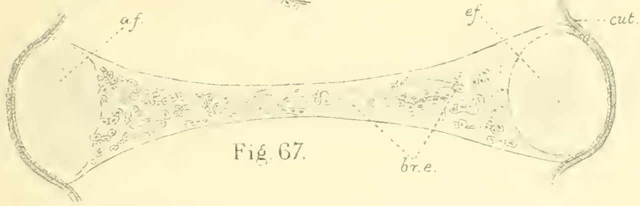


Fig. 67.

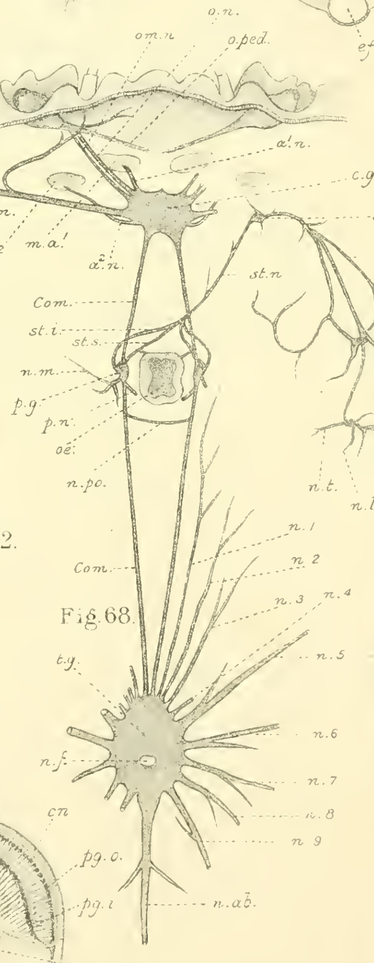


Fig. 68.


Fig. 70.


Fig. 71.


Fig. 72.


Fig. 73.


Fig. 74.

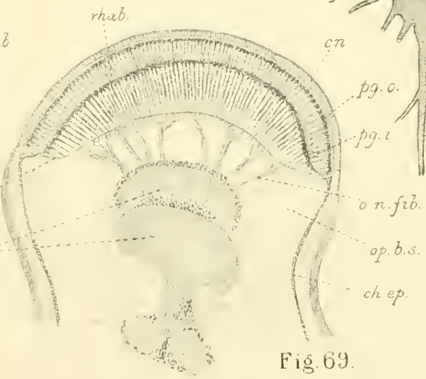


Fig. 69.


Fig. 75.


Fig. 76.

J. P. del. McFarlane & Erskine, Lith. Edin^r

CANCER.

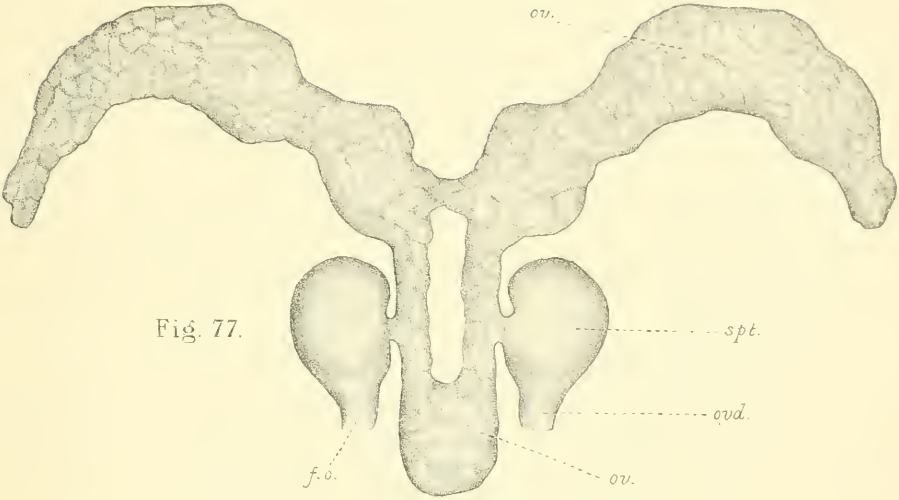


Fig. 77.

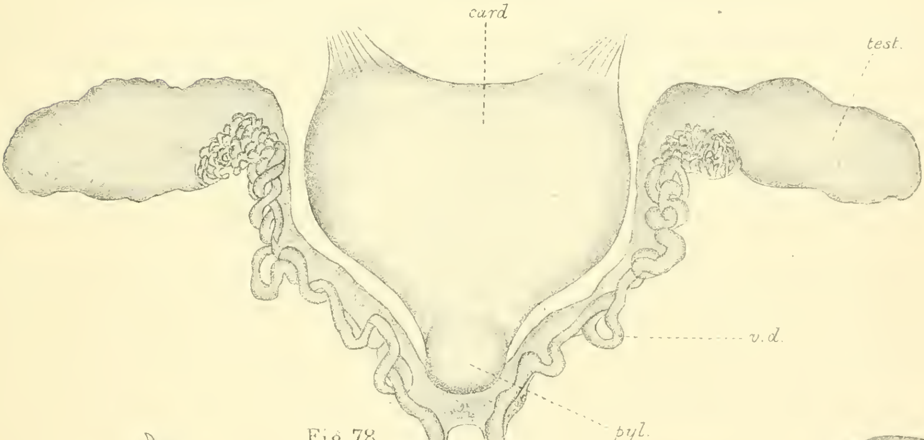


Fig 78.

Fig. 81.

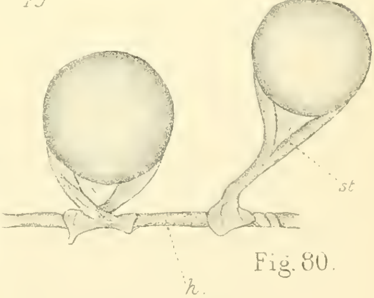


Fig. 80.

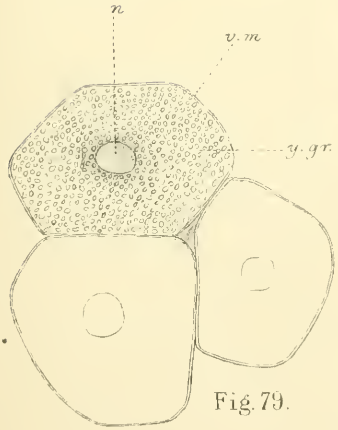


Fig. 79.

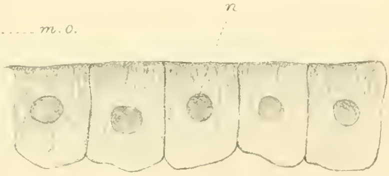


Fig. 82.

J F del
McFarlane & Erskine, Lith Edinr

CANCER.

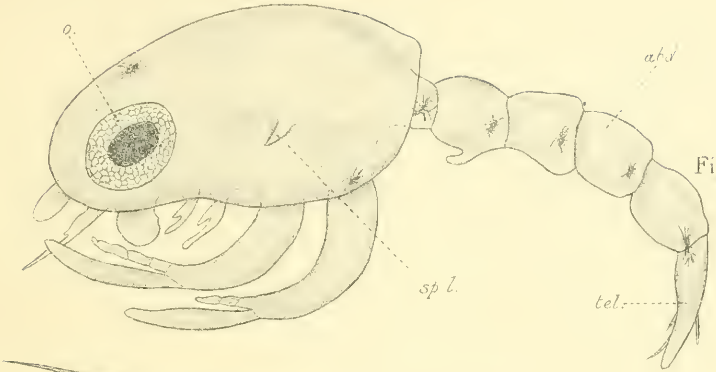


Fig. 83.

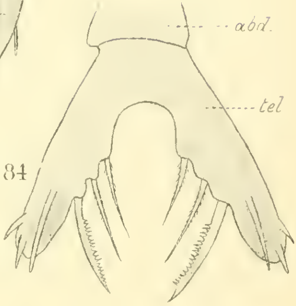


Fig. 84

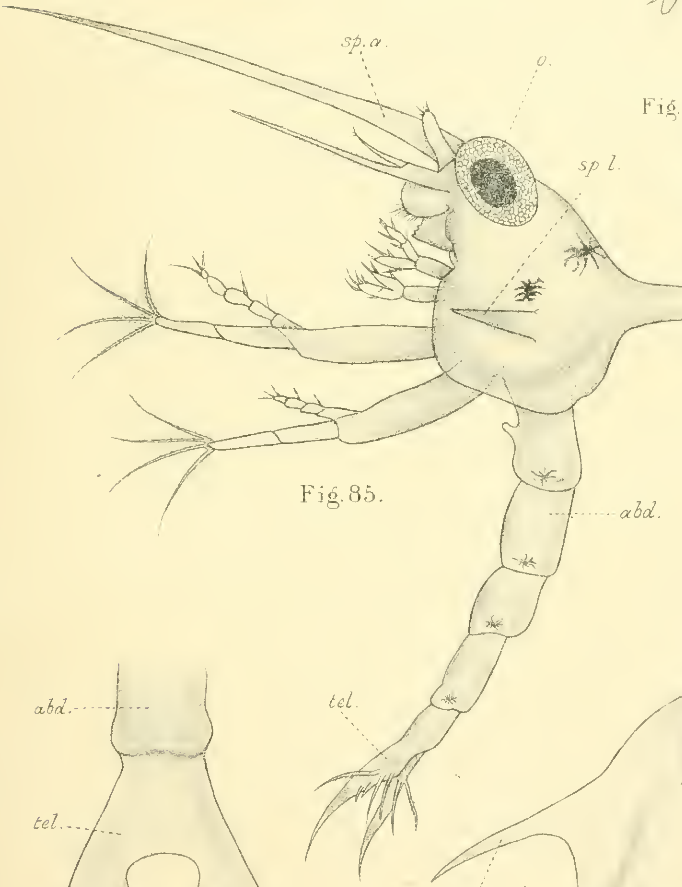


Fig. 85.

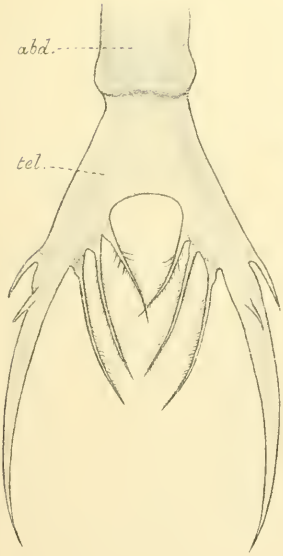


Fig. 87.

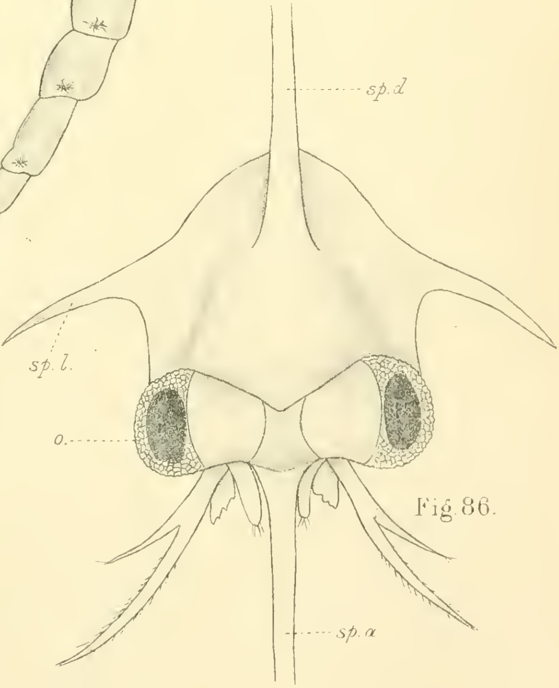


Fig. 86.

J. P del

McFarlane & Erskine Lith Edinr

CANCER.