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THE ANATOMY OF THE CAPE ROCK LOBSTER, *JASUS LALANDII* (H. Milne Edwards)

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By

NELLIE F. PATERSON

South African Museum, Cape Town

(With 81 figures)

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INTRODUCTION

The common European and American fresh-water crayfishes, *Astacus* and *Cambarus*, have long been accepted as classical examples of decapod Crustacea, and the anatomy of the former in particular has been described and illustrated in most text-books of elementary zoology. In the absence of fresh-water crayfishes from South Africa, the marine species, *Jasus lalandii* (H. Milne Edwards), is an excellent substitute for practical instruction, not only on account of its large size, but also because supplies are plentiful.

Popularly called the spiny crayfish, spiny lobster, Cape crawfish, kreef, or Cape rock lobster, this species and closely related forms abound along the rocky shores of countries in the southern hemisphere and, as a result of important fisheries established for their collection, canning, and marketing, a number of interesting articles dealing with their applied biology and economic significance have appeared from time to time. Reports by the pioneers of systematic investigations based in Cape Town have been cited by Barnard (1950), and flourishing industries have been surveyed more recently by Matthews (1962) and Soares-Rebelo (1964), while further intensive research is currently in progress under the direction of Dr. A. E. F. Heydorn, of the Division of Sea Fisheries, Cape Town.* In addition, the observations of Hickman (1945), Chace & Dumont (1949), Sheard (1949), Bradstock (1950), Angot (1951), and Grua (1960) may be mentioned as examples of the aims and achievements of various research stations in other countries. Most of the published information summarizes the results of comprehensive investigations concerning essential commercial and ecological problems, including the distribution of and fluctuation in populations of the species in divers breeding grounds and the legal measures adopted in different countries for the protection of rock lobster 'sanctuaries'. Regarding their general distribution, Hickman (1945) has stated that they occur off the coasts of Tasmania, New Zealand, South Africa, Tristan da Cunha, and Juan Fernandez, Chile. To these areas Gruvel (1911), Chace & Dumont (1949), Barnard (1950), Angot (1951), and Grua (1960) have added the islands of St. Paul and New Amsterdam in the southern Indian Ocean, while Sheard (1949: 8) has specified 'a circumpolar distribution range from 32° to 45° S latitude', and has also given particulars of fishing grounds in Australian waters, including those off Tasmania.

For many years it has been assumed that the animals which have been commercially exploited in the aforementioned geographical areas were widely

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* Appointed Deputy Director, Oceanographic Research Institute, Durban, as from July 1967.

dispersed *Jasus lalandii*, but Holthuis (1963) has determined that six separate species are represented in these localities, and that they are distinguishable mainly by variations in the spines on the carapace and the squamous patterns on the abdominal terga. The species recognized by Holthuis and their respective regional distribution are: *Jasus lalandii* (H. Milne Edwards), South Africa; *J. paulensis* (Heller), St. Paul and New Amsterdam Islands; *J. edwardsii* (Hutton), New Zealand; *J. frontalis* (H. Milne Edwards), Juan Fernandez; and two new species, *J. novaehollandiae* from south-east Australia, and *J. tristani* from Tristan da Cunha. One of the distinctive features of *J. lalandii* indicated by Holthuis is that it has a number of squamae immediately in front of the transverse groove on the first abdominal tergum (figs 1, 9, 43), whereas in the other five species the whole of the anterior half of the first abdominal tergum is non-squamous and smooth.

According to Gilchrist (1913*a*, 1918) and Von Bonde & Marchand (1935), *J. lalandii* shows a preference for the cooler waters of the Atlantic coast, along which productive fishing grounds range from Cape Point in the south to Cape Cross 60 miles north of Walvis Bay, those north of the Orange River being now controlled by the Administration of South West Africa. In these localities the rock lobsters are stated to have a vertical distribution from low-water mark down to 20 or 25 fathoms. The choice of cooler waters has also been confirmed by Sheard (1949), but apparently the Australian specimens are fished at greater depths, special pots having been devised for their capture at approximately 40 to 45 fathoms. From Angot's (1951) and Grua's (1960, 1964) analyses of fishing operations off the islands of St. Paul and New Amsterdam, it also emerges that growth takes place when the water temperature is low and that the reproductive period does not coincide with the austral summer.

While most of the research projects have been designed with the object of compiling data and statistics immediately concerned with the promotion of the rock lobster industry, the more academic studies of *Jasus lalandii* have not entirely been neglected. Preliminary observations of early embryonic development and descriptions of the main larval stages by Gilchrist (1913*b*, 1916, 1918, 1920) have been supplemented by Von Bonde's (1936) fuller account of both the embryonic and the post-embryonic development. Jointly in 1922 these two investigators and also Von Bonde & Marchand (1935) have been responsible for what little published information there is concerning the general anatomy of both sexes of this species. Thus, for the past forty years the article by Gilchrist & Von Bonde (1922) has been relied upon as a guide to practical studies in a number of South African zoology departments. While this has proved adequate for elementary courses, most of the systems of organs have been treated rather superficially and, in view of the universal upsurge of interest in the physiology of Crustacea, the need for a more profound understanding of its anatomy has arisen. In connexion with the taxonomy of the order, the external features of the majority of Decapoda have been examined carefully but, although a number, including certain palinurids, have been widely used as experimental animals, there are few comprehensive accounts of the internal organs. The foundation laid by Huxley (1881) in his excellent monograph on *Astacus astacus* (L.) has been amplified by the painstaking studies of Keim (1915), Schmidt (1915), Baumann (1921), Panning (1924), and Stoll (1925) on different systems of the same species. Apart from these publications and Herrick's (1911) account of the American lobster, information relating to the internal organization of Macrura Reptantia is somewhat scattered and often fragmentary, but much of it has been collated by Balss and his associates in the classical treatise on Decapoda in *Bronns Klassen und Ordnungen des Tierreichs* (1940–1961), and in two volumes entitled, *The physiology of Crustacea*, edited by T. H. Waterman (1960, 1961). Such details as seem essential to a comparison of the anatomy of the Cape rock lobster with that of other decapods have been drawn from these and other sources, and are discussed wherever pertinent.

The following account of the various systems of organs in *J. lalandii* is intended to convey elementary facts for the information of students attending a course in general zoology, but it also includes some finer details that may serve as a basis for any future physiological investigations. It has been concluded that its overall organization resembles that of the better-known fresh-water crayfish, *Astacus astacus* (L.), and that some of the structural differences between the two species may be ascribed to idiosyncrasies of habits and habitat.

MATERIAL AND METHODS

The specimens on which most of the present observations are based were taken from the stock maintained for practical classes in the Zoology Department, University of Cape Town: they comprised small to medium-sized mature males and females, averaging 21 to 22 cm in total length and having a cephalothoracic length of approximately 7·5 cm. Such specimens were usually obtained alive from a local fisherman operating off Robben Island in Table Bay; they were then killed and preserved in 5% formalin. Occasionally, to check certain details, freshly killed specimens were used. Observations were also made of living animals at the Sea Point Aquarium, and on a few kept alive in the constant temperature rooms of the Zoology Department, in which the water temperature was about 13° C. A number of juvenile males and females, kindly collected at Lüderitz Bay, South West Africa, by Mr. M. J. and Dr. Mary-Louise Penrith of the South African Museum, were also a source of useful and interesting information.

Most of the dissections were prepared by making lateral incisions along the cephalothorax and abdomen and, after removal of the dorsal part of the exoskeleton, the various systems of organs were traced in succession from the most superficial dorsal to the deeper ventral structures. A complete impression of each system was thus gradually built up as the dissections proceeded. A good overall picture of a median or parasagittal view of the general anatomy (fig. 31) may also be obtained by making a mid-dorsal incision followed by careful excision of the organs, especially the muscles, of one side, and final clearance of the exoskeleton of that side. In this way, all the organs of the other side and also median structures are left intact, resulting in a proper perspective of the anatomy with the essential organs *in situ*.

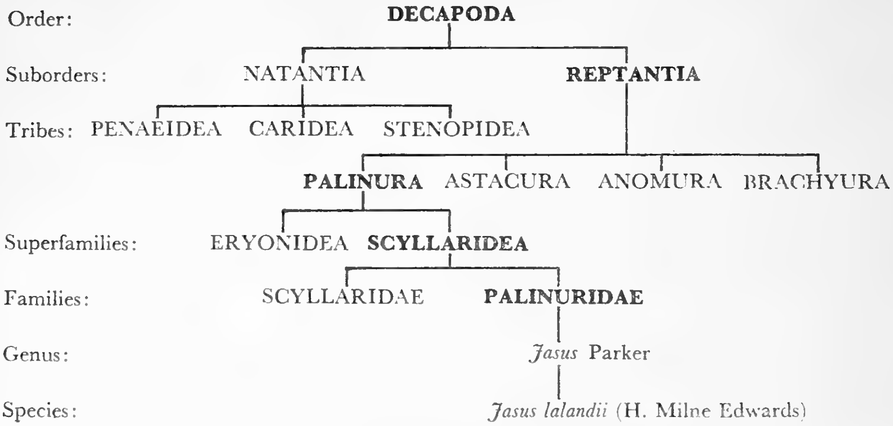
To check some of the details observed in gross dissections of adult specimens, transverse serial sections, cut at 10 μ thick, were made of the young planktonic puerulus stage (fig. 81) which had been fixed in Bouin's aqueous fluid when collected by Dr. Heydorn. Some difficulty was experienced in softening the rather thick, transparent exoskeleton. Treatment of specimens for two or three days with 3% nitric acid in 70% alcohol and then placing them for three or four days in a 10% solution of soft soap in 70% alcohol gave poor results. When diaphanol, followed by tetra-hydro-naphthalene (tetralin) as a clearing agent, proved almost as unsatisfactory, mushroom extract, as recommended by Carlisle (1960), was tried. It was found advisable to subject the specimens to the action of a 1 : 10 dilution of the extract at 37° C. for two to four days, transferring them to fresh mushroom extract daily. After washing the specimens thoroughly in distilled water for 15 minutes or longer, they were then dehydrated in three changes of triethyl phosphate, cleared in methyl benzoate celloidin, and embedded in paraffin wax in a vacuum oven. The various stains employed to differentiate the tissues were: Mallory's triple stain, Hansen's haematoxylin or Heidenhain's iron haematoxylin with eosin Y or eosin B as counterstains, and Weigert's iron haematoxylin followed by Biebrich scarlet and methyl blue, but pleasing results were also obtained by using Mayer's haemalum and counterstaining in eosin B.

Subsequent to fixation in Zenker's fluid, serial sections were also made of the eyes, the excised sinus gland, the gills, and the antennal gland of the adult. The sections of the eyes and sinus gland were stained in Heidenhain's iron haematoxylin and phloxine, while the histology of the gills and the antennal gland was clearly defined by employing Heidenhain's iron haematoxylin and eosin B. Following the procedure elaborated by Steedman (1960), some specimens were sectioned and stained after infiltration with Tropical Ester Wax and, although the sections were inclined to overstretch a little even at room temperature, on the whole the preparations were good and stained well.

It should also be indicated here that additional notes on simple techniques used in preparations of the endophragmal skeleton (p. 42), the blood vascular system (p. 133), and parts of the nervous system (p. 167) have been included, and that, while the illustrations are drawn to scale, certain liberties have been taken in displacing some of the organs to clarify the position of the parts relative to one another. This is particularly evident in the figures of the musculature of the appendages, in which the individual muscles are diagrammatically represented and some of the superficial elements have been slightly reflected to expose the more deeply seated ones.

CLASSIFICATION

The classification of decapod Crustacea proposed by Borradaile (1907) has been broadly adhered to by other taxonomists, including Calman (1909), Barnard (1950), and Balss (1957), and, using it as a basis, the systematic position of *Jasus lalandii* relative to other members of the order may be tabulated as follows:



The suborder Natantia and the tribes Palinura and Astacura are frequently distinguished from the remaining Reptantia as the MACRURA or forms with a large, straight abdomen and a broad, strong tail-fan. Of the MACRURA REPTANTIA, Von Bonde & Marchand (1935) have listed 14 South African species, and Barnard (1950) has accounted for at least another 17 species, including some from Mauritius. In both publications two species of *Jasus* are recorded: *J. lalandii* (M. Edw.) and *J. parkeri* Stebb. The latter occurs off the coast of East London and, among other characteristics, is distinguished from *J. lalandii* by the absence of squamae, by the submedian and lateral rows of strong spines on the carapace, the indistinct cervical groove, and the mid-dorsal keel on the first five abdominal segments. The distinctive features of *J. parkeri* Stebb. have been considered by George & Grindley (1964) to be sufficient justification for its removal to a new genus, designated *Projasus*.

As some of the characters mentioned in Borradaile's (1907) keys are relevant to a description of the external features of *J. lalandii*, it seems pertinent to review them briefly, although they have been abstracted elsewhere by Pearson (1908), Barnard (1950) and other authorities.

The REPTANTIA are differentiated from the Natantia by the following characters: the body is usually depressed; in the abdomen the first segment is generally the smallest; the rostrum is small or absent; the basal segment of the antennulary peduncle is not enlarged into a stylocerite; the exopodite of the antenna is reduced or wanting; the pereiopods lack exopodites and each appears to be composed of six segments owing to the coalescence of the basipodite and the ischiopodite; the pleopods are not natatory and may be reduced or absent.

Some of the distinctive features of the PALINURA are: the macrurous abdomen and the broad tail-fan; the small or absent rostrum; the lateral fusion of the epistoma with the carapace; the numerous gills; and the presence, at least in the female, of an appendix interna on some of the pleopods.

The SCYLLARIDEA are distinguished by the carapace being secured between an inner knob on the last thoracic segment and an outer flange on the first abdominal segment; the antenna is uniramous and the proximal segment of its peduncle is fused with the epistoma; with the exception of the last pair in the female, none of the pereiopods is normally chelate; in both sexes the first abdominal segment has no pleopods; the telson is more or less truncate.

In the family PALINURIDAE the cephalothorax is subcylindrical; the eyes are not lodged in separate sockets; and each antenna has a three-segmented peduncle which supports a long whip-like flagellum.

Barnard (1950) has shown that species of at least five genera belonging to this family, namely, *Jasus* Parker, *Palinurus* Fabr., *Palinustus* M. Edw., *Linuparus* Gray, and *Panulirus* (Gray) White, are represented in the South African fauna, while the genus *Palinurellus* Von Martens has been collected off the coast of Mauritius and, according to Balss (1941), is exceptional among Scyllaridea, in having vestiges of pleopods on the first abdominal segment of both sexes. Barnard (1950) has also indicated that in 1946 Holthuis created the genus *Justitia* for the species *Palinurus longimanus* M. Edw., the relatively long and sturdy first pereiopods of which are unusual in being subchelate.

Based on certain marked structural differences, Parker (1883, 1884) rearranged the species which had originally been included in the genus *Palinurus* Fabr. into three subgenera, namely, *Jasus*, *Palinurus*, and *Panulirus*, and these were later arbitrarily accepted as valid genera. It was not until 1961, however, that an application by Holthuis (1960) was approved by the International Commission on Zoological Nomenclature (Opinion 612, *Bull. zool. Nom.*, 1961, **18**: 312–315), and the generic name *Jasus* Parker, 1883, was placed on the Official List of Generic Names in Zoology. The generic features of *Jasus* Parker recognized by various taxonomists are: its small pointed rostrum which is clasped by a pair of pedate processes; the presence of procephalic processes; the short antennulary flagella; the approximation of the bases of the antennae; and the absence of stridulating organs. (With the exception of *Jasus* and *Palinurellus*, both sexes of Palinuridae produce harsh noises when the antennae are raised and, because of this, Parker (1884) separated the family into two natural groups, the *Silentes*, or non-stridulating forms, and the *Stridentes*, or stridulating species. In the *Stridentes* the dorso-medial articulation of the basal segment of the antennal peduncle with the head is modified into a projecting, ventrally ridged process which slides over the lateral, keeled, frontal region of the exoskeleton and makes an audible creaking sound.)

Although probably first popularly called 'langouste de Lalande' by Lamarck, the original systematic description of the spiny rock lobster as *Palinurus* *lalandii* is generally ascribed to H. Milne Edwards (1837). Its subsequent removal to the genus *Jasus* by Parker in 1883 has, of course, not affected the account of the specific characters which were expressed as follows by H. Milne Edwards (1837: 293–294):

> 'LANGOUSTE DE LALANDE.—*P. lalandii.*
>
> *Cornes latérales du front lisses en dessus et en dessous,* et beaucoup moins avancées que la petite corne médiane, au-dessous de la base de laquelle on voit deux petites épines. Carapace armée d'épines et couverte de gros tubercules ovalaires déprimés et séparés à leur base par des poils courts et serrés. *Abdomen entièrement couvert de tubercules aplatis, squammiformes,* et garnis sur leur bord postérieur d'une rangée de poils très-courts; une seule dent sur le bord postérieur des cornes latérales de l'abdomen. Antennes internes courtes. Pates antérieures très-grosses, courtes et armées en-dessous de deux dents coniques très-fortes, dont une placée sur le deuxième article, et l'autre sur le bord inférieur du bras ou troisième article; pates suivantes, granuleuses en-dessus. Couleur brun-rouge, irrégulièrement tacheté de jaune. Longueur (du corps), environ 15 pouces.
>
> Habite les côtes du cap de Bonne-Espérance. (C. M.)'

Some confusion regarding the orthography of the specific name has been evident, for it has appeared in print either as *J. lalandii* or as *J. lalandei,* but in 1960 Holthuis proposed that the latter spelling receive official recognition. This emendation was later abandoned, however (Opinion 612, *Bull. zool. Nom.* 1961, **18**: 312–315), and the specific name *lalandii* was ratified.

The obvious transverse furrow on each abdominal tergum, produced by the prominence of the penultimate row of squamae, is another noteworthy characteristic referred to by Stebbing (1902) and Barnard (1950). To the specific features supplied by Milne Edwards, Barnard has also added the presence of a distinct cervical groove, while details concerning the mandibular palps and the exopodites of the three pairs of maxillipeds have been specified by Gruvel (1911).

As indicated by Milne Edwards (1837), the general coloration of the body is brownish red, but it is also frequently tinged with an iridescent purplish hue which is particularly noticeable on the tail-fan. One of the sexual differences noted by Gilchrist (1913*a*), Von Bonde & Marchand (1935), and Von Bonde (1936) is that the females are usually rather darker than the males, while among animals collected in the vicinity of St. Paul and New Amsterdam Islands, Angot (1951) has observed an appreciable colour range, varying from light red in shallow coastal waters to dark red in specimens captured at greater depths. Size variations are also apparent, a total length of up to 460 mm (18 inches) for South African specimens and up to 510 mm (20 inches) for Australian forms having been recorded by Barnard (1950). Moreover, reports by Gilchrist (1913*a*), Von Bonde & Marchand (1935), Von Bonde (1936), Hickman (1945), Bradstock (1950), and Grua (1960) show that certain size differences may be correlated with sexual dimorphism, mature males being invariably larger than the females; but a possible explanation of this, offered by Von Bonde (1936), is that the females attain sexual maturity earlier than the males, the estimated ages being approximately 2½ years in females as against 5 to 6 years in males.

EXTERNAL FEATURES

A. Exoskeleton and Ecdysis

The whole surface of the body is covered by a thick, epidermal *exoskeleton*, the constituents and structure of which have been minutely examined in Brachyura by Drach (1939), and discussed relative to Crustacea in general by Dennell (1960). Briefly, it is composed of a chitin-protein complex impregnated with calcium carbonate, and is structurally differentiated into a thin, non-chitinous epicuticle and a thicker, chitinous endocuticle, with the latter subdivided into three strata, viz. a pigmented layer, a thick calcified layer, and an uncalcified layer adjacent to the epidermis. Calcium salts are reported to be deposited heavily in the epicuticle and the pigmented layer, as well as in the calcified layer proper, but the latter is distinguished from the other three zones of the exoskeleton by its poor protein content. To allow of movement, the exoskeleton remains thin and flexible between the segments of the body and also between the parts of the appendages, where the softer areas consist mainly of epicuticle and uncalcified endocuticle and are termed *arthrodial membranes* (figs 1, 5, 8, 16, 25, 31).

In the taxonomic notes it has been indicated that the dorsal surface of the exoskeleton of *J. lalandii* is furnished with pointed spines and a mosaic of closely-set, flattened scales or *squamae* (fig. 1) which are bordered by reddish, plumose setae. Similar setae also fringe the free edges of the carapace and the posterior margins of the abdominal segments and, as a rule, the setae at the bases of the cephalothoracic squamae project forward, while those on the abdomen are backwardly directed. The spines are arranged in regular longitudinal rows on the dorsal part of the cephalothorax; they generally point forward and become progressively smaller behind the conspicuous, acutely-pointed postocular processes. The more lateral regions of the cephalothorax lack spines, but are covered with small contiguous squamae and are smoother in appearance and lighter in colour than the dorsal surface of the cephalothorax.

As the body is encased in a calcified exoskeleton, growth is discontinuous and can only be effected during relatively short periods when the animal sheds its exoskeleton and endoskeleton and also the cuticular lining of the gut. The process of exuviation or *ecdysis* is characteristic of all Arthropoda, and in Crustacea it has been most fully investigated in brachyuran Decapoda. It has been shown by Drach (1939) and Passano (1960) that, although it only recurs from time to time during the life-span of the animal, each ecdysis is really the culmination of a number of phases which affect the animal's behaviour and metabolism throughout the comparatively long intermoult periods between successive ecdyses. The secretion of the epicuticle and the pigmented layer of the endocuticle of the new exoskeleton precedes ecdysis, while the expansion of the thoracic region of the body and the resultant rupture of the old exoskeleton along a resorptive or ecdysial suture are implemented by a marked absorption of water. From studies of ecdysis in *Panulirus argus* (Latreille), Travis (1954) has concluded that uptake of water probably takes place through the gills and the intersegmental membranes, and that the accumulation of an unknown gas between the old and the new linings of the stomach is also of material assistance in the enlargement of the body. Carlisle & Knowles (1959) have accepted the theory of integumentary and branchial uptake of water, but Passano (1960) has favoured the opposite view, expounded by Drach (1939), that in aquatic decapods pre-ecdysial water is absorbed through the lining of the gut.

During the present observations of *J. lalandii* the resorptive suture became evident along the branchiostegite some time before ecdysis, and a relatively broad vertical resorptive band was also noticed at the junction of the prebranchial and the branchial chambers. Ecdysis of captive *J. lalandii* was observed on several occasions between sunset and midnight, and an examination of the cast shells indicates that the carapace becomes detached from the epimera and the inner lining of the branchiostegite along the cervical and the branchiocardiac grooves. Furthermore, it is apparent that ecdysis also involves the endoskeleton, parts of which, especially the mesophragms, are markedly resorbed, so that sufficiently wide gaps are formed for the extrication of the new endoskeleton. In most of the exuviae examined the branchiostegites were intact, and it would appear that, as in *Panulirus argus* (Travis, 1954), calcium resorption along the ecdysial suture helps to loosen the branchiostegite from the articular condyle on the last epimeron, and that during ecdysis slight flexure of the branchiostegite takes place along its weakened suture. Although the branchiostegites do not necessarily fracture, there is an important transverse hinge between the epistoma and the supralabral ridge. On this the old carapace is tilted upward and forward at an angle of about 90° after rupture of the thoraco-abdominal intertergal arthrodial membrane by pressure from the underlying soft-bodied animal. This results in a wide dorsal opening between the thorax and the abdomen of the old exoskeleton through which the animal gradually emerges, withdrawing its appendages, gills and abdomen and eventually jerking itself free from the old exoskeleton and endoskeleton. The whole process takes about five minutes, and in a normal ecdysis the old skeletal framework of the animal is shed completely and within the exuviae the old cuticular linings of the fore-gut and the hind-gut remain attached anteriorly and posteriorly.

It is also evident from the deliberations of Drach (1939) and Passano (1960) that the intermoult cycle is characterized by a number of events which contribute to the general reorganization of the tissues and the preparatory stages of the next ecdysis. Shortly after exuviation, there is a gradual hardening of the new exoskeleton combined with the formation of the calcified layer of the endocuticle; and, subsequent to the completion of tissue growth and the secretion of the uncalcified layer of the endocuticle, organic reserves (lipids, glycogen, and proteins) and mineral reserves (Ca and Mg phosphates) are stored in the digestive gland or hepatopancreas against a period of fasting and the elaboration of a new exoskeleton prior to the next ecdysis.

According to Passano (1960), there is experimental proof that these activities are influenced by such environmental factors as light and temperature, and that they are regulated by the interaction of certain hormones and neurosecretions. The incidents leading up to ecdysis are initiated by the release of a moulting hormone into the blood from a small, paired Y-organ, which in crabs is located towards the anterior limit of the branchial chamber near the mandibular external (posterior) adductor muscle. It is believed, however, that one of the neurosecretions produced by the X-organ and periodically released from the sinus gland in each eyestalk has a moult-inhibiting effect and suppresses synthesis by the Y-organ of the moult-promoting hormone.

Observations by Von Bonde & Marchand (1935) have revealed that in *J. lalandii* ecdysis takes place twice a year until a cephalothoracic length of 3½ to 4 inches is reached, after which there is probably a regular annual moult; sexual maturity may, however, be attained when the cephalothoracic length is 2 to 3 inches or even less. These investigators also noted that the moulting season varied in different localities and that, whereas in males it usually took place from September to February, the time of annual ecdysis of females was not determined, but was thought by them and by Gilchrist (1913*a*) to occur during the winter months. Some corroboration of the latter supposition is implied in Matthews's (1962) statement that ecdysis in female South West African rock lobsters coincides with the peak spawning period from August to November, but from operations off the South African west coast, in which soft-shelled specimens were collected at quarterly intervals from June 1962 to March 1963, Heydorn (1965) has concluded that in the two areas investigated neither sex appeared to have a definite moulting season; nevertheless peak moulting periods for males occurred during September at Port Nolloth and during December at St. Helena Bay, and a slight increase in the percentage of moulting females was observed during March at Port Nolloth.

The moulting cycle and growth rate of captive Australian spiny lobsters have recently been studied by Fielder (1964*a*), who found that experimental animals with a cephalothoracic length of from 5 to 7·9 cm moulted three times a year, while those in the 8 to 8·9 cm category underwent two annual moults, and the frequency of moulting seemed to be influenced by increases in the temperature of the water. Hickman (1945) has also mentioned that immature Tasmanian *Jasus* moult several times a year, and his findings confirm reports by Gilchrist (1918) and Von Bonde & Marchand (1935) that ecdysis of the female is a precursor of mating and egg-laying, the latter usually taking place a few days after the female has moulted. Hickman's further observation that oviposition occurs mainly from April to June is more or less in accordance with Grua's (1964) account of events in *J. paulensis*, but is hardly compatible with records for South African rock lobsters which, although variable and somewhat confusing, nevertheless indicate that egg-production tends to be later in *J. lalandii* than in *J. novaehollandiae* and *J. paulensis*. Thus, Gilchrist (1918) noted that in 1916 spawning occurred from October to about the middle of December, while in the following year it started in June. Females 'in berry' were found by Von Bonde & Marchand (1935) from July to February, but the times varied at different stations, and it was estimated that the average ovigerous period lasted approximately two to three months. More recently, Matthews (1962) has reported that South West African female rock lobsters reach maximum fertility from August to November and are practically barren during the period from February to April or May. Analyses of egg-carrying females collected by Heydorn (1965) in two areas off the South African west coast in June, September, and December 1962, indicated that the highest percentages were in September, but the general impression is that June to August probably represents the period of maximum productivity, especially in larger females, and this more or less corresponds with Fielder's (1964*b*) remarks on fishing surveys in South Australia. The reason for these variations is not apparent, but may be associated with environmental factors, particularly with differences in the temperature of the water. In this connexion, Sheard (1949) has mentioned that Australian forms of *Jasus* prefer waters of less than 18° C., especially during ecdysis, mating, and oviposition, while Grua (1960, 1964) has established that spawning takes place off the islands of St. Paul and New Amsterdam in autumn when the water temperature is approximately 14° or 16° C. In his treatise on the crayfish industry in Western Australia, Sheard (1962) has given some significant information regarding the correlation between the monthly water temperatures and ecdysis in *Panulirus cygnus* George [*Panulirus longipes* (H. Milne Edwards)]. In this species he has ascertained that the following four moulting cycles prevail: when the water temperatures are falling in June, maturing females moult prior to the mating season in July and early August; coinciding with periods of rising temperatures, moulting takes place in January and early February in females after the larvae have emerged from the eggs; males and some females were observed to moult in January to March; and the immature crayfish moulted in November. From this it is evident that the moulting period for males of *P. cygnus* is from January to March and that, as in *J. lalandii*, the main moult of the females is the one preceding mating. It is also notable that ovigerous females of *P. cygnus* were collected from late August to February, a period which roughly corresponds with that in records for *J. lalandii* published by Von Bonde & Marchand (1935), Matthews (1962), and Heydorn (1965), and it seems likely that in most palinurids spawning takes place once a year. There seems to be some uncertainty regarding the number of annual ecdyses that occur in mature females of *Jasus*, and it could be assumed that, because the female strips the empty egg-capsules from the pleopods, another moult is not required after the larvae have hatched. Grua (1964), however, has remarked that, in addition to the pre-mating ecdysis in *J. paulensis*, a summer ecdysis may be necessary for the renewal of the ovigerous setae which are damaged when the female cleans the pleopods. Some confirmation of Grua's statement was obtained while making recent observations of captive *J. lalandii* at the Sea Point Aquarium. During the summer months, when some mature males and both sexes of juvenile rock lobsters were moulting, a number of mature females, including several that had been 'in berry' and had cleared the ovigerous setae, underwent a second annual moult. It is rather significant that after this ecdysis the pleopods were devoid of ovigerous setae, and it has been concluded that they are only developed at the moult which precedes mating. It is therefore probable that, as in species of *Panulirus* (Crawford & De Smidt, 1922; Lindberg, 1955; Sheard, 1962), a post-ovigerous ecdysis also occurs in *Jasus*.

B. Parts of the Body

Fundamentally the body may be divided into three regions or tagmata, the *head* or cephalon, the *thorax*, and the *abdomen* but, in common with other Decapoda, secondary fusion of the first two parts has resulted in the formation of a *cephalothorax*.

In the Malacostraca the number of body segments is limited to twenty-one, some of which are indistinctly marked, but most of which are indicated externally by the presence of paired, jointed appendages. The estimation of the total number of segments, however, is contingent upon the interpretation of the components of the head region, and recently the problem of head segmentation in the Arthropoda has been reviewed in articles by Butt (1960) and Manton (1960). The former author has attempted to identify four head segments, while Manton has substantiated her previous convictions (1928, 1934, 1949) that there are six head somites.

The main differences of opinion relate to the preantennulary and the antennulary segments: on the one hand, Butt doubts their existence while, on the other hand, from studies of the ontogeny of various arthropods, Manton has provided evidence which justifies their recognition. Basing his conclusions mainly on insect embryology, Butt has introduced another version of the concept of arthropod head segmentation in which the intercalary segment, with the labral lobes representing its appendages, is regarded as the first segment: accordingly, in his opinion the arthropod head is composed of an unsegmented acron plus the intercalary (second antennal of Crustacea), the mandibular, the first maxillary, and the second maxillary segments. Arguments in favour of regarding the second antennal segment as the first true body segment have previously been presented by Snodgrass (1938, 1951, 1952), who compared the arthropod acron to the annelid prostomium. He stated that in the arthropod embryo this region bears the eyes, the labrum, the preantennae occasionally, and the first antennae (antennules of Crustacea), and concluded that in the majority of Eumalacostraca the head is composed of the unsegmented acron and one segment, that of the tritocerebral or second antennal somite. Snodgrass therefore discounted the preantennulary and the antennulary segments and assigned the mandibles and the first and second maxillae to the thorax, but Manton (1949, 1965) has found that many of his views concerning some of the cephalic appendages and arthropod head segmentation are fallacious.

Paired mesodermal somites, neuromeres, and limb-rudiments, which are accepted as reliable criteria of segmentation, have been reported in the anterior region of the head of various arthropods by a number of embryologists, whose conclusions are reviewed by Manton (1960). Moreover, in studies of the ontogeny of certain Crustacea, Manton (1928, 1934) has clearly demonstrated that, as in Myriapoda and Insecta, three preoral segments, the preantennulary, the antennulary, and the antennal, are present. The labral rudiment originates in anterior unsegmented ectoderm and forms a median transverse bridge between the anterior ends of the U-shaped germinal band level with the preantennulary somites. As development proceeds and the preoral somites become more marked on the germinal band, the labral rudiment derives most of its mesoderm from the preantennulary somites and gradually shifts back until it lies behind the antennal somites at the anterior margin of the mouth. As Manton (1960) has pointed out, there is proof that in insect embryos the paired labral lobes represent the transitory appendages of the preantennal somite and not those of the premandibular or intercalary segment. In Crustacea, although preantennulary limb-rudiments are not developed, other valid criteria of metamerism have been demonstrated in the preantennulary region. The preantennulary somites were first discovered by Manton (1928) in *Hemimysis*, in which definite and partly persistent coelomic cavities are formed. Nair (1949) has also described preantennulary coelomic cavities in *Caridina*, and preantennulary somites also occur in *Nebalia* (Manton, 1934) and in several other Crustacea which have been cited by Nair (1949) and Manton (1960). The denial of segmental status to the antennules is another obvious misconception, for they develop as the appendages of distinct somites which have a pair of ganglia.

On this premise it is considered that the first head segment is purely embryonic, but that the other five head segments are distinguished externally in the adults by a series of paired appendages, the antennules, the antennae, the mandibles, the first maxillae, and the second maxillae. Eight segments, bearing in succession three pairs of maxillipeds and five pairs of pereiopods, are present in the *thorax*. The *abdomen* consists of six apparent segments, each of which, except the first in *Jasus*, has a pair of appendages. The appendages of the sixth abdominal segment, the *uropods*, are large and when spread out they form the so-called *tail-fan*. The abdomen ends in a median, somewhat rectangular structure, the *telson*, which lies above and between the uropods and has membranous connexions and lateral articulations with the sixth abdominal segment, beneath which it can be flexed simultaneously with the uropods. It should be noted that studies of malacostracan embryos (Manton, 1928, 1934) have proved that the telson arises from the unsegmented posterior end of the embryo. It therefore has no segmental value and merely represents a dorsal extension of the last abdominal segment. Moreover, the latter segment has been shown by Manton to be formed by the fusion of two embryonic segments, and a similar conclusion is implied in Stoll's (1925) suggestion that the large ganglion in the last abdominal segment of *Astacus* may represent the ganglia of two fused segments.

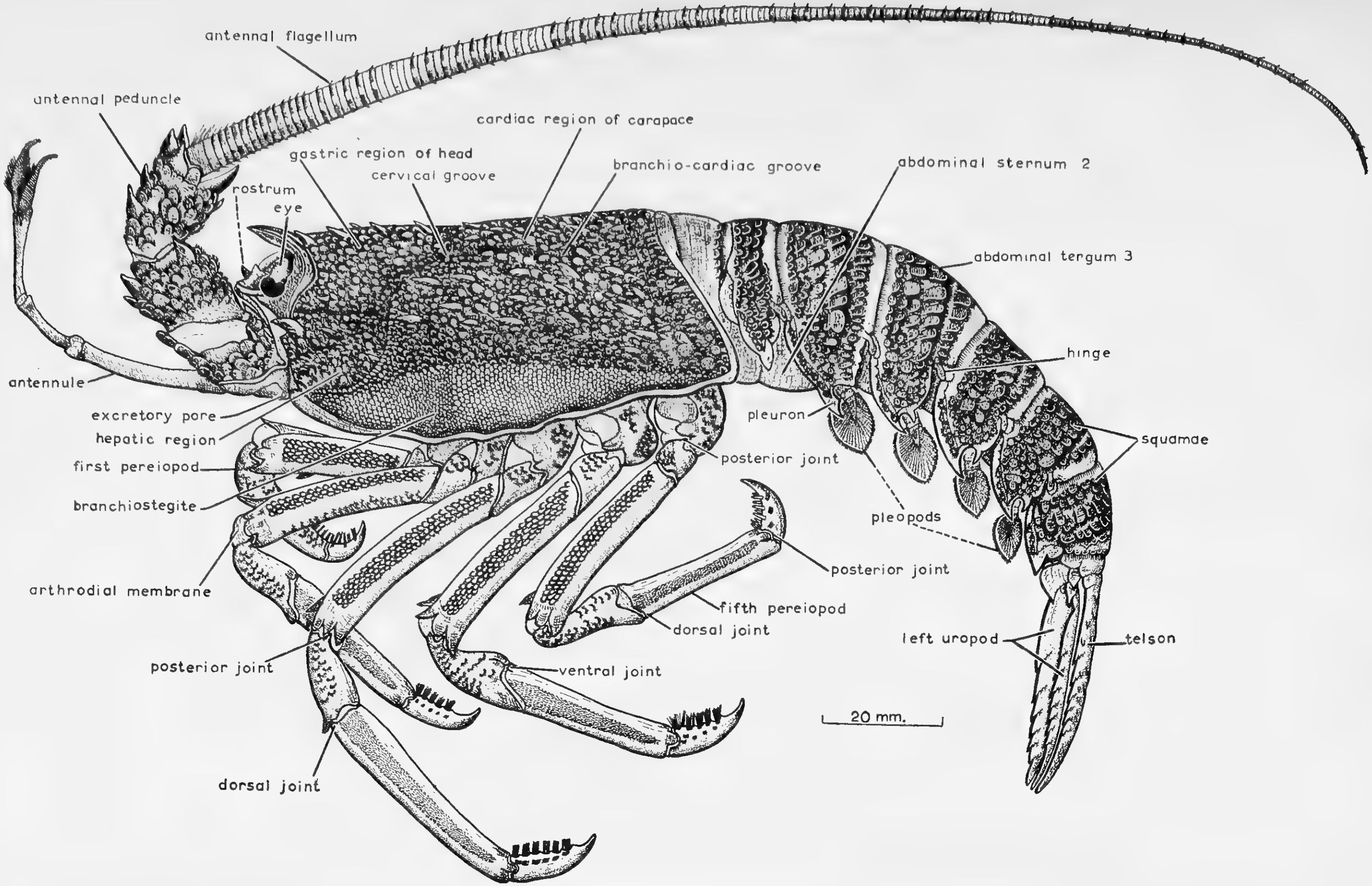


FIG. 1. *Jasus lalandii* (H. Milne Edwards), left lateral view of small male.

1. CEPHALOTHORAX

Dorsally and laterally the cephalothorax is covered by a thick exoskeleton on which a number of areas are defined by certain grooves. Following Huxley's (1881) account of the anatomy of *Astacus*, it has generally been supposed that the possible boundary between the head and thoracic regions is marked by a fairly deep *cervical groove* (fig. 1) which runs transversely across the middle of the exoskeleton and is continued forward and downward on each side as an oblique, slightly curved depression. The cephalic area of the exoskeleton is somewhat indistinctly demarcated by a faint dorso-lateral furrow into a median *gastric* and two lateral, yellowish *hepatic regions* (fig. 1), respectively so called because the former lies above the fore-gut while the latter cover the anterior mandibular apodemes and their contained lateral extensions of the digestive gland. Anteriorly between the paired stalked eyes, the gastric region is produced into a short median spine, the *rostrum* (figs 1, 3, 10, 60, 77), which is characteristically embraced by a pair of structures (figs 3, 10, 60, 77), termed the clasping or *pedate processes* by Parker (1883, 1884, 1889).

Behind the cervical groove the thoracic region is enveloped by a dorsal shield, called the *carapace*, a term which is also frequently used by carcinologists to describe the whole of the dorsal cephalothoracic exoskeleton. Two shallow, longitudinal *branchio-cardiac grooves* divide the carapace into a mid-dorsal *cardiac region* overlying the pericardial cavity and a pair of lateral folds, the gill-covers or *branchiostegites* (figs 1, 2, 10, 53, 77). Each branchiostegite forms the outer wall of the branchial chamber and may represent the conjoined thoracic pleura. In *J. lalandii* the carapace is typically broader in the mature male than in the female, a feature which has been cited by Gilchrist (1913*a*), Von Bonde & Marchand (1935), and Von Bonde (1936) as one of the reliable means of distinguishing the sexes.

The development of the carapace results not only in the rigidity of the cephalothorax, but also obscures all traces of metamerism on the dorsal surface. Ventrally, however, there is a series of firmly-united, calcified plates, the *sterna* (figs 2, 7, 80), separating the bases of the eight pairs of thoracic appendages. Between the first three pairs of appendages the sternum is a narrow, median ridge, but behind this it gradually widens into a large, triangular shield which reaches its maximum breadth between the penultimate pair of limbs and narrows appreciably in the last thoracic segment. The last five thoracic segments are clearly defined by transverse, setose grooves on the sternum, the lateral margins of which are notched for the ventral articulations of the appendages.

The thoracic segmentation is also evident laterally where vertical plates, considered by Snodgrass (1952) to be thoracic pleura but herein designated *epimera* (figs 2, 3, 7), form the inner wall of the branchial chamber. They extend upward from the arthrodial membranes of the appendages and are confluent dorsally with the inner lining of the branchiostegite. Resulting from the invagination of the endopleurites of the endophragmal skeleton, the proxi-

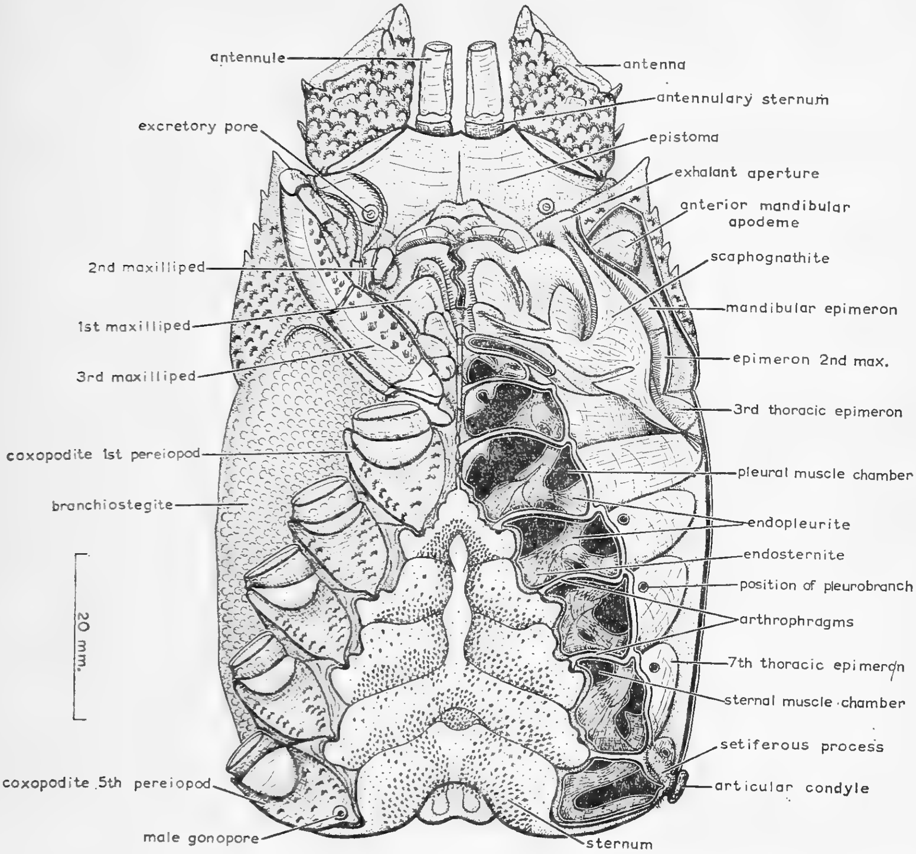


FIG. 2. Ventral view of cephalothorax of male, showing position of right appendages and left half of endophragmal skeleton after removal of left thoracic appendages and left branchiostegite.

mal regions of successive epimera are demarcated segmentally by external indentations, and their contiguous margins are folded and loosely connected above the dorsal articulations of the coxopodites of the appendages. These areas form the convex outer walls of the pleural muscle chambers of the limbs, and those of the last four segments support the pleurobranch gills. The first two thoracic epimera are small, triangular plates applied to the anterior margin of the third and largest epimeron, behind which there is a gradual decrease in the extent of the outlines of the pleural muscle chambers in the fourth to the eighth thoracic segments. The last thoracic epimeron is produced into a knob or *articular condyle* (figs 2, 3, 7, 9, 43) which fits closely like a 'press stud' into a depression on the inner surface of the branchiostegite, so that the postero-ventral angle of the latter is firmly secured to the side wall of the body. A conspicuous, triangular setiferous process (figs 2, 7) and a posterior ridge, likewise covered with setae, occur ventral to the condyle and surround the dorsal articulation of the fifth pereiopod. Although distinct from the coxopodite of the fifth pereiopod, the setiferous process is comparable to similar plates on the coxopodites of other pereiopods, and it and the posterior ridge probably prevent ingress of water to the branchial chamber between the branchiostegite and the last leg.

2. ABDOMEN

In the abdominal region, which is broader in the female than in the male, the six segments are distinct and the exoskeleton of each is divisible into several well-marked areas (fig. 1). Dorsally there is a wide, convex *tergum* which is continuous on each side with a pointed, downwardly-directed *pleuron.* The ventral surface is occupied by the *sternum* which is usually thinner and more flexible than the tergum, but is strengthened posteriorly in front of the abdominal appendages by a narrow, calcified bar for the insertion of some of the abdominal muscles. The first abdominal sternum, however, consists largely of a relatively wide plate, but in front of this there is a pair of oval medial sclerites. The separation of the latter probably allows of greater flexibility of the thoraco-abdominal junction, while the division of the posterior bar of the sixth sternum into two fairly broad sclerites which do not meet in the middle may represent a similar slight modification associated with movements of the posterior part of the abdomen. Each abdominal appendage is attached by flexible membranes to the postero-lateral edge of the sternum, and the small ventro-lateral area between the appendage and the lateral margin of the pleuron is sometimes referred to as the *epimeron*; that of the sixth segment has a rounded protuberance against which the protopodite of the uropod abuts when the tail-fan is flexed.

The successive abdominal segments are connected with one another by intertergal and intersternal arthrodial membranes (figs 8, 31) which, by alternate folding and stretching, permit of movements between the segments. As, however, adjacent segments are hinged together laterally by a process from the posterior edge of one segment fitting into an anterior depression in the next segment behind, movement is limited to the vertical plane in which the whole abdomen is capable of strong extension and flexion. For such movements the abdominal terga are structurally adapted, each having a smooth anterior surface (fig. 9) which is exposed during flexure of the abdomen, but slides beneath and is overlapped by the tergum in front when the abdomen is extended. When fully flexed, the abdomen is bent under the cephalothorax and, correlated with this, the broad tail-fan may spread out laterally and curve ventrally forward, enabling the animal to make escape movements by darting rapidly backward through the water.

The cephalothorax and the abdomen are also connected by thin arthrodial membranes, the intertergal one and the smooth anterior half of the first abdominal segment being overlapped by the inturned posterior margin of the carapace. In addition, when the abdomen is extended, a forwardly-directed, lateral flange (fig. 9) on the first abdominal segment fits over the posterior edge of the carapace, and the two regions of the body are thus practically interlocked.

3. CEPHALIC SCLERITES

It is apparent from the foregoing remarks concerning the external features of the body that the full complement of plates or sclerites of a typical crustacean segment comprises the dorsal tergum, the ventral sternum, and the lateral pleura and epimera. The head is considered to consist initially of six segments, but fusion or *cephalization* of the parts has taken place, and in the adult, apart from the paired appendages, there is little evidence of metamerism in the head. Most of the head appendages, however, articulate with lateral and ventral sclerites which have been interpreted as analogues of the epimera and the sterna of thoracic and abdominal segments. Some published opinions concerning similar structures in other species are discussed, and a characteristic dorsal lobe located in front of the rostrum has been termed the frontal tubercle.

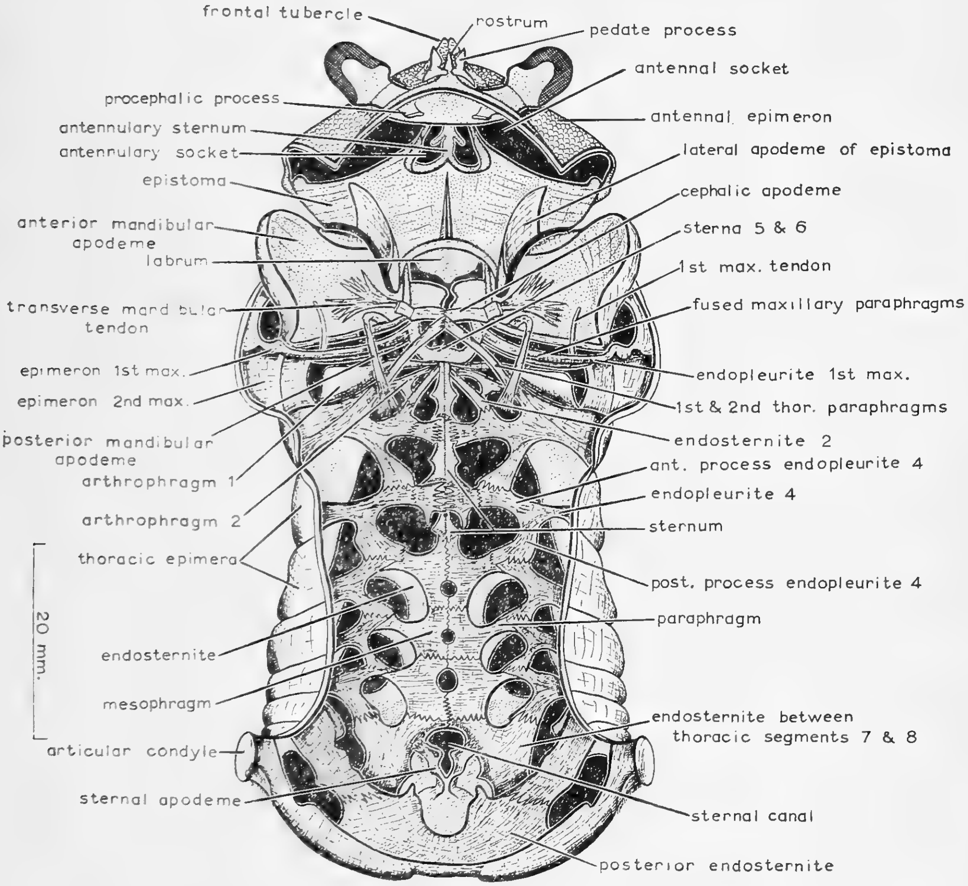


FIG. 3. Dorsal view of endophragmal skeleton and adjacent parts of cephalothoracic exoskeleton.

(a) *Frontal tubercle*

At the anterior end of the head there is a small, blunt, orange-coloured projection which is marked by a median suture. It is situated mid-dorsally antero-ventral to the rostrum and, as Parker (1883, 1884, 1889) has shown, it corresponds to the region which in other palinurids is enlarged and modified into the fixed part of the stridulating organ. Parker (1883, 1884) originally identified it as the antennulary sternum, but later (1889) emended the term to inter-antennulary bar. Surmounting it and clasping the rostrum is a pair of forked pedate processes (figs 3, 10, 60, 77), considered by Parker firstly (1883) as belonging to the antennulary sternum, secondly (1884) as probable outgrowths of the antennulary epimeral plates, and finally (1889) as projections of the prostomial plate, and this vacillation of opinion serves to emphasize the difficulties of interpreting the parts of the head, particularly in the Palinuridae. The frontal lobe of *J. lalandii* is situated in the region comparable to that which Huxley (1881) considered to be the ophthalmic sternum in *Astacus*, while Balss (1940) has referred to it as the frontal sclerite of the ocular segment in Palinuridae. The presence of an ophthalmic segment is questionable and, while this sclerite lies above the antennules, it is also significant that the basal segment of the antennal peduncle articulates with it. It has been called the frontal tubercle (figs 3, 10, 77), but it seems to be merely an anterior projection of the antennal epimeron.

(b) *Cephalic sterna*

The antennulary sternum (figs 2, 3, 17) is probably formed by the fusion of a pair of adjacent narrow sclerites, to which the antennules are attached ventrally by arthrodial membranes. When viewed from within (fig. 3), it is obvious that these plates are continuous with marked ridges which curve round the lateral margins of the antennulary sockets, arch dorsally to the frontal tubercle, and may represent arthrophragms between the antennules and the antennae. In addition, there is a median ridge which is shaped like a spearhead and passes vertically upward to join the presumed antennulary epimeron: this part is similar to the antennulary sternum described by Huxley (1881) and separates the antennulary sockets medially, its lateral barbs serving as struts for the articulation on each side of a strong, dorsal, hinge-like spur (fig. 60) which passes inward from the base of the first segment of the antennulary peduncle.

The most conspicuous structure on the ventral surface of the head is a broad smooth plate, the *epistoma* (figs 2, 3, 4, 17, 18, 31), the lateral margins of which are fused with the head exoskeleton. The antennae are joined ventrally to the anterior border of the epistoma and articulate with it ventro-laterally, and projecting from the middle of its posterior margin there is a transverse *supralabral ridge* (fig. 4) to which the labrum and a spinous process from each mandible are attached. A slight postero-median groove marks the position of an internal *median apodeme* (fig. 8), and arising on each side of the supralabral ridge there is a conspicuous *lateral apodeme* (fig. 3) for the attachment of some of the antennal muscles.

Huxley (1881), Pearson (1908) and others have interpreted the epistoma as a fusion of the antennal and mandibular sterna. Snodgrass (1951, 1952), however, has asserted that, being a preoral structure, it represents neither of these sterna, and has suggested that the mandibular sternum has either disappeared or that its vestige is to be found in the postoral metastomal plate. The whole issue is complicated by embryological events accompanying the backward displacement of the mouth (Manton, 1928, 1934, 1949). During this process, the labrum and the stomodaeum shift from a position just in front of the developing antennae to one in the mandibular segment, so that the antennae become secondarily preoral. The homologies of the epistoma are therefore somewhat vague, but it has been concluded that the ventral articulations of the antennae and the attachment of the antennal muscles to the epistomal apodemes in *J. lalandii* probably indicate that the epistoma is a ventral sclerite of the antennal segment. There is no certainty as to whether or not the mandibular sternum is bound up with this region, but Balss (1940), who regarded the epistoma as the antennal sternum, identified the supralabral ridge of Scyllaridea as the mandibular sternum, and this supposition appears to be substantiated when it is recalled that the lower articulation of an appendage is with the sternum of its segment.

It has further been suggested by Borradaile (1907), Calman (1909), and Balss (1940) that in the Scyllaridea the segment corresponding to the coxopodite of the antenna of other Decapoda has been incorporated into the epistoma. In this connexion, it is significant that, in describing the external features of the genus *Puerulus*, Ramadan (1938) rejected previous convictions concerning the homology of its broad inter-antennal sclerite with the epistoma of other groups, and suggested that it simply represents the concrescence of the proximal segments of the antennal peduncles, the median suture marking their line of fusion. In view of the position of the excretory apertures in Palinuridae, Parker (1884, 1889) and Snodgrass (1951) have expressed a similar opinion, contending that in this family the fused antennal coxopodites have displaced the epistoma, which is thus reduced to a small, median, transverse sclerite supporting the labrum. Nevertheless, a comparison of available South African species of Astacura and Palinuridae suggests that there is no appreciable difference between the large epistoma of the Astacura and the conspicuous, triangular plate which separates the antennal bases in the Palinuridae. In both groups the anterior margin of the plate is indented medially behind the antennules and, furthermore, the reduced epistoma of Palinuridae, as interpreted by Parker and Snodgrass, bears a resemblance to the supralabral ridge of the epistoma of Astacura. In all the palinurids examined, the region in question is somewhat furrowed medial to each excretory pore, and in *Palinustus mossambicus* Brnrd this depression is accentuated into a distinct groove, which may be an external indication of a possible fusion of the lateral antennal coxopodite with a median epistoma. Bearing in mind that the excretory apertures of Astacura are located more or less medially on the antennal coxopodites, it seems likely that the processes herein identified as lateral apodemes of the epistoma in *Jasus* may also partly represent the lines of fusion of the antennal coxopodites with the epistoma. Some support for this assumption appears to be given by the resemblance between the attachments of certain of the basal antennal muscles on these apodemes and the origins of the corresponding muscles in *Astacus* (Schmidt, 1915) on the proximal borders of the antennal coxopodites. Moreover, in both *Astacus* and *Jasus* the two ventral cephalic muscles are also inserted on the lateral apodemes of the epistoma, and have no connexions with the supralabral bar identified by Parker and by Snodgrass as a reduced epistoma in palinurids; it is assumed that such connexions would probably be established if the transverse bar in the Palinuridae were a real epistoma. For these reasons, the definition of the palinurid epistoma given by Borradaile and by Calman has been retained in describing the parts of *J. lalandii*, but it is conceded that further comparative studies may be required before the problem can be resolved satisfactorily.

Apparently there has been less dispute concerning the last two cephalic sterna (figs 3, 19) which are generally regarded as having coalesced to form a small, transverse, ventral plate between the bases of the maxillae. In some Reptantia, however, Snodgrass (1951) has interpreted this as a probable remnant of the mandibular sternum, termed by him the metastomal plate, and in his opinion compression of the maxilliped segments has resulted in the fusion of the maxillary sternum with the maxilliped sternum. While the metastoma and its paragnaths are attached to the anterior margin of this cephalic sternal element and are considered by some authorities as likely derivatives of the mandibular segment, it is also noticeable that the transverse maxillary paraphragms are associated with this ventral plate and it is thus conceivable that it belongs mainly to the maxillary region. It is nevertheless possible that part of the mandibular sternum has also merged with it, for paired processes (figs 3, 19), which are thought to be comparable to the transverse mandibular tendons described by Manton (1928, 1934, 1964) in a variety of arthropods, occur anterior to it and the maxillary paraphragms and seem to indicate the presence of mandibular skeletal elements at this level.

(c) *Cephalic epimera*

Some of the lateral plates in the head region are more elusive than the sterna, but all the segments have certain sclerites which may be described as epimeral. A slightly tuberculated plate, which extends vertically downward from the overhanging edge of the frontal tubercle to the wide arthrodial membranes of the antennules, has been suggested as the possible epimeron of the antennulary segment (figs 17, 60). It forms part of the frontal area of the head between the bases of the antennae, and corresponds to the region determined as the antennulary sternum in *Astacus* by Huxley (1881) and in palinurids by Parker (1884) and Balss (1940). The later author distinguished it as the proepistoma, while Snodgrass (1951) defined it as the head plate in *Panulirus argus*.

Underlying the eyestalk and the pedate process and curving forward to meet the frontal tubercle, there is a broad transverse plate to which the basal segment of the antennal peduncle is attached dorsally by an arthrodial membrane. While Huxley (1881) regarded it as the antennulary epimeron in *Astacus*, it seems as though it may be interpreted equally well as the epimeron of the antennal segment (fig. 3) and, as previously suggested, it probably forms the frontal tubercle with which the dorso-medial articulation of the antenna takes place.

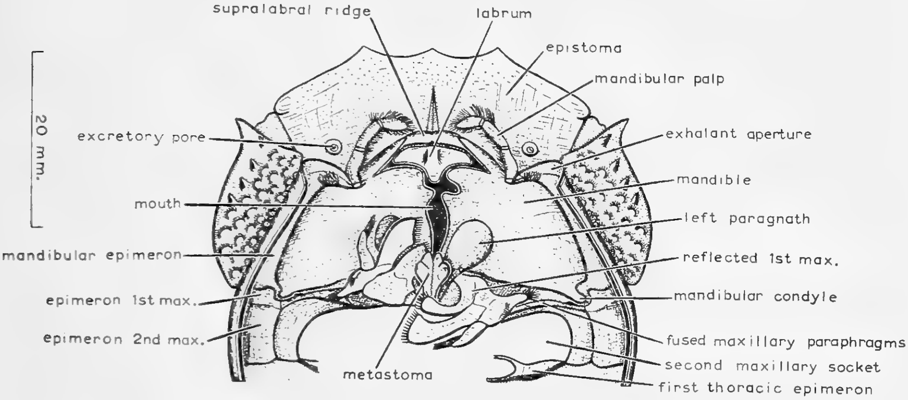


Fig. 4. Ventral view of mouth region; the left first maxilla has been reflected to show the metastoma and the paragnath, and the branchiostegite on each side has been removed to expose the roof of the prebranchial chamber.

On each side of the mandibular segment, the epimeron (figs 2, 4) is represented by the anterior two-thirds of the thin, arched roof of the prebranchial chamber. Towards its posterior limit the condyle of the mandible articulates with it, while anteriorly it lies beneath the anterior mandibular apodeme and unites with a transverse extension of the epistoma which forms the upper boundary of the exhalant aperture of the respiratory system and has been called the wing of the epistoma by Snodgrass (1951, 1952).

The first and second maxillary epimera are indistinctly demarcated from each other, but the former (figs 3, 4) may be manifest in a narrow ridge which separates the mandibular epimeron from the second maxillary epimeron. The latter (figs 2–4) is a fairly broad plate occupying the posterior third of the roof of the prebranchial chamber, and is comparable with the maxillary pleural bridge described by Snodgrass (1951) in Astacura and Palinura.

C. Appendages (Fig. 5)

The paired appendages occur on most of the body segments, to which they are attached by arthrodial membranes and are usually articulated by two joints located more or less opposite each other on the epimera and the sterna of their respective segments. The complete series of appendages and their corresponding segments may be summarized as follows:

CEPHALON: Segment 1 – Embryonic and transitory, without appendages
,, 2 – Antennules
,, 3 – Antennae
,, 4 – Mandibles
,, 5 – First maxillae
,, 6 – Second maxillae

THORAX: Segment 7 – First maxillipeds
,, 8 – Second maxillipeds
,, 9 – Third maxillipeds
,, 10 – First pereiopods
,, 11 – Second pereiopods
,, 12 – Third pereiopods
,, 13 – Fourth pereiopods
,, 14 – Fifth pereiopods

ABDOMEN: Segment 15 – Appendages absent in both sexes
,, 16 – First pleopods
,, 17 – Second pleopods
,, 18 – Third pleopods
,, 19 – Fourth pleopods
,, 20 – Uropods

Most of the limbs are biramous and distinctly jointed and thus conform to the *stenopodium* type of crustacean appendage, but in the arrangement of their lamellate parts the first and the second maxillae are suggestive of *phyllopodia.* Like the stenopodia, the phyllopodia are biramous, the stem carrying medial lobes or *endites* and lateral lobes or *exites.* The parts, however, are broader and less cylindrical than those of a stenopodium and are interconnected by thin flexible membranes; joints are absent and turgor is maintained chiefly by internal pressure.

A typical stenopodium, as exemplified by the third maxilliped (fig. 5 *H*), consists of a basal *protopodite* which supports two rami, an inner *endopodite* and an outer *exopodite.* The *protopodite* (fig. 16) usually has two segments, the *coxopodite* and the *basipodite,* while the *endopodite* is divisible into five segments, namely (fig. 16), the *ischiopodite,* the *meropodite,* the *carpopodite,* the *propodite,* and the *dactylopodite.* In each maxilliped an *exopodite,* featuring a peduncle and a tapering flagellum, is attached to the basipodite, while arising from the coxopodite there is a setiferous process which commonly supports a thin respiratory lamella, the *epipodite,* and a podobranch gill. Nowadays it is customary to shorten the above terms by omitting the terminal 'ite' but, as the longer versions have been used in naming the appendicular muscles, they have been retained here. Thus the parts of the endopodite (endopod) may be abbreviated

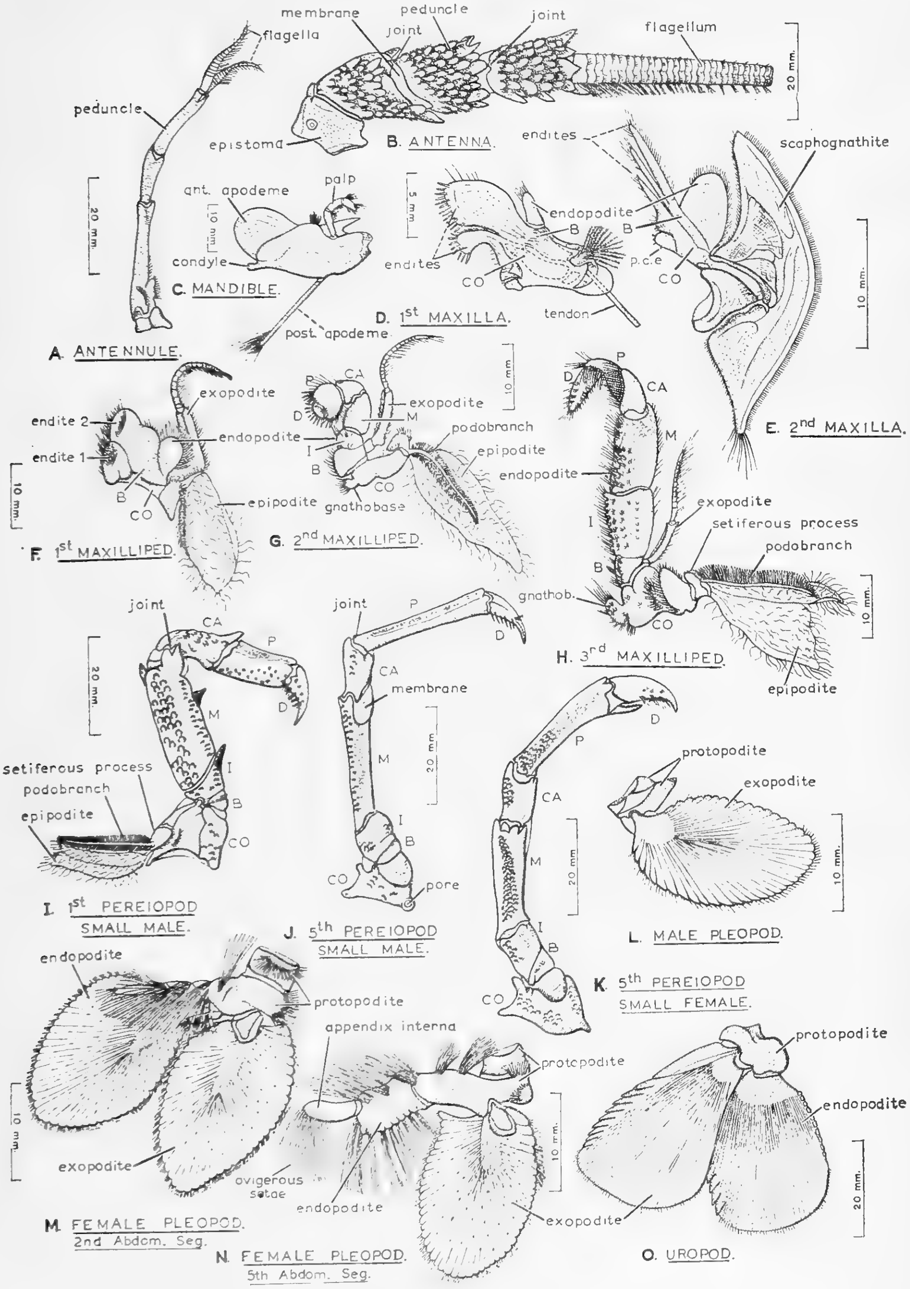


FIG. 5. Appendages of right side, drawn from various aspects to illustrate some of their respective structural features. Ventral views are given of the antenna, the mandible, the male pleopod, and the uropod; caudal views of the pereiopods; and dorsal views of the other appendages. *B*, basipodite; *CA*, carpopodite; *CO*, coxopodite; *D*, dactylopodite; *I*, ischiopodite; *M*, meropodite; *P*, propodite; *p.c.e.*, precoxal endite of second maxilla.

to ischium, merus, carpus, propodus, and dactyl, and the two segments of the protopodite (protopod) may be referred to as the coxa and the basis.

Various modifications of the generalized type which are apparent in several of the appendages are: the flat, unsegmented endopodite of both pairs of maxillae and the first maxilliped, the fusion of such parts as the basipodite with the ischiopodite in limbs behind the first maxilliped, and the absence of exopodites in the anterior cephalic appendages and all the pereiopods. Exopodites are present, however, on the pereiopods of the phyllosoma larva, but become reduced in the puerulus stage to small, vestigial protuberances which, according to Gilchrist (1920), are suppressed during transformation into the post-puerulus stage.

1. ANTENNULE (Fig. 5 *A*)

The antennule, which is connected by wide arthrodial membranes to the head exoskeleton, projects forward from the middle of the frontal region, its base being somewhat concealed dorsally by the large antenna. As in other Decapoda, it consists of a long, slender, three-segmented *peduncle* which bears two short distal *flagella*. The first segment of the peduncle is the longest and is about equal in length to the combined measurements of the other two segments. Located in its somewhat swollen base is a balancing organ or statocyst, the position of which is indicated by a lighter dorsal area which is bordered by ridges and setae (fig. 67). Antero-medially between the ridges is the small aperture through which the statocyst communicates with the exterior (fig. 60).

The homologies of the parts of the antennule with those of other appendages are doubtful, but it is apparent from Gilchrist's (1913*b*, 1916) descriptions of the naupliosoma larva of *J. lalandii* that the antennules are primarily uniramous and that the two terminal flagella appear in the 24 mm phyllosoma larval stage. In the nauplius larva of other Crustacea and in adult non-malacostracans the antennules are also uniramous, and the suggestion that the antennulary flagella of adult Malacostraca represent the exopodite and the endopodite of a generalized appendage is not universally accepted. Assuming that the antennule was biramous, Huxley (1881) and Pearson (1908) naturally concluded that the whole of the peduncle was the protopodite, but Gilchrist & Von Bonde (1922) have identified the first peduncular segment of the antennule of *J. lalandii* as the protopodite and the other two segments as the endopodite. To some extent, this latter view appears to be substantiated by the musculature, from which there is evidence that the proximal segment may be double and may represent the fused coxopodite and basipodite. It would therefore seem that the antennules of *J. lalandii* are not strictly biramous and that they are more accurately described as biflagellar appendages.

Both flagella have membranous connexions with the distal margin of the third peduncular segment, and each is multisegmented, relatively broad near its base, and produced distally into a curved pointed tip. The widest part of each flagellum is furnished with setae which are arranged in regular rows on each annulus. Those on the slightly longer and narrower *inner flagellum* comprise rather stiff feathered hairs along the dorsal margin and softer plumose setae, edged by stiff bristles, along the ventral rim (fig. 65). Most of the surface of the *outer flagellum* is beset with long, delicate, colourless, partly annulated setae, the *aesthetascs* (fig. 66), which are bordered laterally by conspicuous bristles. The outer flagellum, which fits basally into a relatively deep lateral cleft on the distal margin of the third peduncular segment, vibrates constantly against the slightly concave lateral surface of the rather more porrect inner flagellum. The setae of the two flagella thus impinge on one another, and the different types are doubtless correlated with the several functions attributed to the antennules. While handling experimental animals, it was observed that the outer flagellum was the last external structure to show signs of movement in moribund specimens and, on cessation of its activity, death could be presumed.

2. ANTENNA (Fig. 5 *B*)

As in other Scyllaridea, the antenna is uniramous in the adult, the exopodite being lacking, but Gilchrist (1913*b*, 1916) has shown that in the nappliosoma larva it is a biramous, locomotory appendage, the exopodite of which gradually diminishes during the various phases of the phyllosoma larva until it atrophies in the 24 mm stage. The adult appendage thus consists of a stout, three-segmented *peduncle* and a very long, tapering *flagellum*. Calman's (1909) statement that the decapod antennal peduncle is primarily five-segmented, the two proximal segments representing the protopodite and the other three segments the first three parts of the endopodite, seems to imply that either the dactylopodite is absent or that it has fused with the propodite to form the flagellum. The reduction of the peduncle of Scyllaridea to three segments is assumed to have been effected by concrescence of the basal segment (coxopodite) with the epistoma and the fusion of the second and third segments (basipodite and ischiopodite) which are commonly united in other appendages of Reptantia. A comparison of the antennal muscles of *J. lalandii* with Schmidt's (1915) description of the system in *Astacus* apparently confirms these conclusions regarding the modification of the base of the scyllarid antenna. A resemblance between the musculature of the more distal segments of both forms is also indicated but, in view of Balss's (1940) criticism of Schmidt's interpretation of the parts of the peduncle of *Astacus*, it seems likely that the second and third segments in *J. lalandii* correspond to the meropodite and the carpopodite of other forms; whether or not the flagellum is a combination of the propodite and the dactylopodite is still uncertain.

The segments of the peduncle are spinous and covered with squamae; they are strongly jointed together and the action of their powerful muscles produces the sudden elevation and lashing movements of the whip-like flagellum. Although the latter is multisegmented, it is rather rigid and easily broken. It is usually as long as or even longer than the body, has incomplete rings of stiff setae, and is generally dark coloured, but several pale bands are normally present.

As a result of the supposed fusion of the antennal coxopodite with the epistoma, the paired excretory organ, instead of discharging on the proximal segment of the antenna as in most Decapoda, opens ventro-laterally on the epistoma (figs 2, 4, 38); in certain other South African palinurids examined, the apertures tend to be more posterior and occur nearer the outer angles of the triangular epistoma.

3. MANDIBLE (Fig. 5 *C*)

The mandible has no exopodite and bears little resemblance to a typical stenopodium. Following Borradaile's (1917) deliberations, however, it seems likely that its strongly-calcified body and broad gnathal lobe (fig. 19) represent the fused coxopodite and gnathobase (precoxa) of a generalized appendage, while the three segments of the short palp correspond to the basipodite and two parts of the endopodite. The two palps curve inward towards the mid-line between the labrum and the anterior margins of the gnathal lobes, assisting in the manipulation of food and preventing any loss from the anterior border of the mouth. Whereas in many Caridea the gnathal lobe is characterized by pronounced incisor and molar processes and is a powerful chewing organ, in *Jasus* and other Reptantia these processes are not clearly differentiated and the appendage is less effectual in shredding the food. A blunt, tooth-like projection, which perhaps replaces the incisor process of the mandible of other decapods, is demarcated by an antero-medial indentation, and that of the left mandible is consistently the more protuberant. With the exception of *Palinustus mossambicus* Brnrd and *Linuparus trigonus* (Von Siebold), the mandibles of other South African Palinuridae in the South African Museum collection have similar asymmetrical anterior processes; but these are distinguished from the whitish process of *Jasus lalandii* and *J. tristani* Holthuis in that either both of them, as in *Projasus parkeri* (George & Grindley) and *Palinurus gilchristi* Stebb., or only the right one, as in *Panulirus homarus* (L.) [*Panulirus bürgeri* (De Haan)], *Panulirus ornatus* (Fabr.), and *Panulirus versicolor* Latr., has a reddish-brown cap. Behind this process, the broad gnathal surface has a fairly sharp ventro-medial edge and a few blunt tubercles and shallow depressions. The edge of the right mandible underlies and is usually finer than that of the left side and, as the marginal contours of the pair fit together precisely, the food is grasped tightly and compressed when the mandibles are in apposition. Laterally the body of the mandible is produced into a hollow, rather thin-walled, dome-shaped *anterior apodeme* (figs 2, 3, 5, 19) which lies below the hepatic region of the head exoskeleton and provides attachment for some of the mandibular muscles, while its concavity is almost filled by a portion of the digestive gland. Near the base of the palp there is a tuft of finely-feathered setae which may have some functional significance, for it is located behind the excretory pore at the ventral border of the exhalant aperture (figs 2, 4) through which the current of spent respiratory water flows from the prebranchial chamber.

Although the mandible has powerful muscles, its movement is restricted to the transverse plane because it articulates dorsally by a postero-lateral condyle (figs 4, 5, 19) with the mandibular epimeron in the roof of the prebranchial passage, and close to the base of the palp it has a long spinous process which is projected medially and is firmly attached to the margin of the supralabral ridge. Snodgrass (1950, 1952) identified the latter as the epistoma in Palinura and, accordingly, he considered the spinous process to have a marginal epistomal hinge and an apical epistomal articulation. The slender but strong *posterior apodeme* (figs 3, 5, 19) for the insertion of the posterior adductor muscle of the mandible is attached to the hinder margin of the body of the mandible; it passes vertically into the head and forms an obvious landmark at the side of the fore-gut.

4. FIRST MAXILLA (Fig. 5 *D*)

Characteristically, the first maxilla is a small flattened appendage which is closely applied to the lower surface of the ipsilateral paragnath. The exopodite is lacking and the *endopodite* is a short fairly flexible process with relatively long terminal setae. The *protopodite* is strengthened by a number of ventral sclerites and is produced into two stout median *endites*. The latter are often referred to as the coxopodite and the basipodite, but they have been defined as the inner and the outer laciniae by Borradaile (1917, 1922), who concluded that they probably represent the first and the third endites of a generalized crustacean limb. Thus, the proximal endite would correspond to a gnathobase, while the area lateral to it is the true coxopodite and the outer endite is a process of the basipodite. At the same time, at the base of the proximal endite in *J. lalandii* there is an additional, small, median lobe which resembles a reduced precoxal endite. In his description of the first maxilla of *Jasus edwardsii*, Parker (1889) also used the term laciniae for the endites, but he subscribed to the belief that the inner process is supported by the basipodite and the outer process by the ischiopodite, and considered that they are, therefore, not strictly homologues of the endites and the laciniae of other appendages. The two endites probably work independently, and their medial margins are furnished with strong spines which meet those of the endites of the contralateral first maxilla in the mid-line and assist in the retention and comminution of the food. The inner and smaller endite has an indented posterior margin, and its sclerotized base is concave dorsally where it abuts on the base of the paragnath. This endite curves medially towards the mouth between the metastoma and the paragnath, and appears to function mainly in thrusting food into position between the mandibles. Two other noticeable features are the long tendon for the insertion of the abductor muscle and the tuft of long plumose setae located on a lateral sclerotized area which may be likened to a setiferous process of the coxopodite.

5. SECOND MAXILLA (Fig. 5 *E*)

The second maxilla is considerably larger than the first maxilla and is remarkable for its modification into a flattened, thin-walled organ which is an essential part of the respiratory system. It consists of three main regions, namely, the *protopodite*, prolonged medially into three slender *endites*; a flat, subtriangular, rather more heavily sclerotized *endopodite*; and its most striking feature, a broad curved plate, the *scaphognathite* or 'baler', which has variously been interpreted as representing an enlarged exopodite, an epipodite, or a combination of both of these elements. In many decapods the second maxilla is provided with four endites, and Borradaile (1917, 1922) has suggested that the first belongs to the precoxa, the second to the coxopodite, and the third and fourth to the basipodite. From this it would seem that the two outer lobes in *J. lalandii* are basipodite endites and the inner one a coxopodite endite. Near the base of the latter is an inconspicuous lobe which may be comparable with the more obvious precoxal endite of other forms. The margins of most of the parts are fringed with finely plumose setae, and the endites seem to be too delicate to be effective in feeding. In any case, the second maxilla is located in the prebranchial chamber some distance lateral to the mouth: it lies almost horizontally, with the anterior tip of the scaphognathite reaching the exhalant aperture and the posterior end, with its rather stiff setae, curving into the anterodorsal part of the branchial chamber. The whole appendage is attached by a soft arthrodial membrane and moves freely. The action of the scaphognathite was not fully investigated in living animals but, as its movements are more or less dorso-ventral and sinuous, it is assumed that water is scooped up from the anterior part of the branchial chamber and propelled into the prebranchial chamber by the upturned posterior half of the lamella. It is then driven forward and expelled through the exhalant aperture by the undulation of the anterior half of the scaphognathite. In resting animals the anterior tips of the scaphognathites were observed to beat rhythmically up and down at the exhalant apertures at the rate of about 110 to 120 times a minute. The action of the two scaphognathites was not always synchronized, and in restive animals the frequency is probably higher.

One of the salient features of the Decapoda is that the first three pairs of thoracic appendages, the *maxillipeds*, are directed forward and serve as accessory mouth-parts.

6. FIRST MAXILLIPED (Fig. 5 *F*)

The first maxilliped, although fundamentally a stenopodium, is largely a flattened lamellar appendage, situated to the side of the mid-ventral line behind the first maxilla. As in the latter appendage, the *protopodite* bears two *endites* which are interconnected along their adjacent margins by a very narrow membrane, and each has rows of strong setae on its somewhat obtuse medial margin. The *endopodite* is a small, flat, unsegmented lobe, the medial margin of which is joined to endite 2, while the lateral margin, with its fringe of long setae, rests against the inner wall of the *exopodite*. The latter is conspicuous and typical of stenopodia in having a stout *peduncle* and a curved, flexible and active *flagellum* which usually consists of 16 segments. The exopodite underlies the second maxilla; its peduncle is flattened laterally to form the floor of the prebranchial chamber and projects in front of a broad thin-walled *epipodite*, the surface of which bears long thread-like setae. The epipodite is attached to a small setiferous process and arches dorsally behind the scaphognathite of the second maxilla, forming a vertical partition between the prebranchial and branchial chambers and having its lateral margin firm and thickened where it comes into contact with the branchiostegite.

7. SECOND MAXILLIPED (Fig. 5 *G*)

The second maxilliped is distinguished from the first maxilliped by its more pediform appearance. The two parts of the *protopodite*, the coxopodite and the basipodite, are aligned with the five segments of the *endopodite*, the whole forming a strong forwardly-directed shaft in which all the segments, except the united basipodite and ischiopodite, are movable on one another by joints that are essentially similar in position to those of the pereiopods (fig. 16). The *endopodite* is applied to the mouth region and its parts are somewhat flattened. The meropodite is the longest segment and the three terminal segments are short and broad. The anterior margin of the propodite is curved and fringed with stiff setae, in addition to which there are four or five strong lateral spines. The small dactylopodite is almost semicircular in shape and is usually furnished with nine terminal spines. Flexure between the short carpopodite and the meropodite carries the two distal segments towards the mid-line so that their spines meet those of the contralateral second maxilliped. The basipodite is longer than the ischiopodite and, as in other appendages, attached to it is the *exopodite*. The latter resembles that of the first maxilliped in having a 16-segmented flagellum, but its peduncle is more cylindrical. On the medial margin of the broad coxopodite is a rounded, setose lobe which probably acts as a gnathobase, and articulating laterally with the coxopodite is a setiferous process which supports a conspicuous, thin-walled *epipodite* and a *podobranch*.

8. THIRD MAXILLIPED (Fig. 5 *H*)

The third maxillipeds are longer and stronger than the second maxillipeds and project forward covering the other mouth-parts ventrally. The *endopodite* has the same number of segments as that of the second maxilliped, but differences in the lengths of the parts are apparent. The basipodite is rather short, while the ischiopodite and the meropodite are subequal in length and their flattened medial surfaces are covered with tufts of strong setae which tend to obscure a row of small blunt teeth arranged along the dorso-medial edge of the whole of the ischiopodite and the proximal half of the meropodite. As in the second maxilliped, marked flexure occurs between the meropodite and the short carpopodite, and the two terminal segments are turned somewhat obliquely towards the mid-line and reflexed on the medial border of the meropodite. The dorsal surface of the propodite is furnished with long setae and the whole surface of the dactylopodite has tufts of shorter setae. When the carpopodite flexes, the conical dactylopodite approximates the mouth and the spinous anterior margin of the second maxilliped of the same side. The coxopodite has a medial protuberance resembling a gnathobase, and laterally there is a setiferous process bearing an *epipodite* and a *podobranch*. The *exopodite*, which is attached to the basipodite, is proportionally shorter than that of the first two maxillipeds, and its flagellum commonly has 12 segments. In describing the specific features of *Jasus lalandii*, Gruvel (1911) commented on the dissimilarities of the exopodites of the three pairs of maxillipeds and concluded that there were 16 or 17 flagellar segments in the first two pairs and 11 segments in the third maxillipeds. The numbers, however, are by no means constant, and 13 or even 15 segments have been counted in the exopodite flagella of the third maxillipeds of several specimens selected at random.

9. PEREIOPODS (Fig. 5 *I–K*)

Apart from a few minor points, the five pairs of pereiopods are structurally alike. Moreover, the only significant differences between them and the third maxillipeds are the suppression of the exopodites and the elongation and strengthening of the endopodites, which are thus adapted to support the body and act as walking legs. The longest segments are the meropodite and the propodite which are slender and generally subequal in length. As in the third maxilliped, the basipodite and ischiopodite are fused and the limb can be flexed acutely between the meropodite and the carpopodite.

The orientation of the segments is largely determined by the position of the articulating *joints* (figs 1, 16, 25) on which the several segments swing in different planes and so effect the movement of the appendage as a whole. The coxopodite has dorsal and ventral joints which articulate respectively (fig. 7) with the epimeral and sternal plates of the skeleton and permit the limb to be moved forward and inward and pulled backward and outward in the horizontal plane. The conjoined basipodite and ischiopodite articulate with the coxopodite by antero-ventral and postero-dorsal joints and the movement is upward and downward in a vertical direction. The elongate meropodite has ill-defined dorsal and ventral joints and is nearly rigid, being capable of only slight independent to-and-fro movements, but its orientation is largely influenced by the action of the preceding segments. The joints of both the carpopodite and the dactylopodite are anterior and posterior in position and the segments swing vertically, while the propodite, which has dorsal and ventral joints, moves transversely on the carpopodite. The successive limb segments are interconnected by arthrodial membranes and, while the carpopodite shows the greatest freedom of movement, the propodite is almost as mobile even though its joints differ from those of the carpopodite.

Different types of locomotion and modern ideas concerning the mechanisms involved in the movements of the limbs of Crustacea have been discussed by Lockhead (1961) and Wiersma (1961), and the results of intensive research on locomotion in a great variety of arthropods have been presented by Manton

(1958, 1964, 1965, and earlier articles). Three main types of joints have been distinguished by Manton (1958, 1965) in the legs of Diplopoda and Chilopoda. These are the joint between the coxa and the body and two functionally distinct kinds of intersegmental leg articulations which Manton has called pivot joints and hinge joints. *Pivot joints* are located on the anterior and posterior surfaces of the leg, and 'the axis of movement passes horizontally through the middle of the overlapping leg segments' (1958: 504). *Hinge joints*, which occur at the dorsal junctions of leg segments, are operated mainly by flexor muscles. Precise structural and functional details of the joints of diplopod and chilopod legs and the properties of the cuticle have been given by Manton, but these aspects have yet to be investigated in *Jasus*. In position and function, the anterior and posterior joints of the basipodite, the carpopodite, and the dactylopodite of a *Jasus* pereiopod are comparable to the pivot joints of diplopod legs, while the dorsal and ventral joints of the meropodite and the propodite are analogous to hinge joints. Whereas the meropodite has only reductor muscles and its movements are limited, the propodite is provided with antagonistic reductor and productor muscles and its range of movement is probably equivalent to that of the diplopod leg segments which have dorsal hinge joints and flexor muscles.

In addition to differences in the position of the gonopores (figs 2, 80), sexual dimorphism is apparent in a few structural peculiarities of certain of the limbs. In both sexes the first pair of pereiopods is shorter than the others, and not chelate as in many Reptantia, but they are furnished with the sharp spines described by Milne Edwards (1837) in his original account of the species. They are also usually directed forward, and the medial surfaces of the dactylopodites and the distal half of the propodites of the right and left limbs can be approximated and are markedly setose in both sexes. In the male the first legs (fig. 5 *I*) are robust and strongly flexed between the meropodite and the carpopodite, while in the female (fig. 16) they tend to be slightly straighter and more slender. In all the pereiopods the dactylopodite forms a strong pointed claw, the tip of which may be used for scraping and cleaning parts of the exoskeleton or for clinging to rock surfaces, while the dactylopodites of the last three pairs of legs normally act as a support for the body when the animal is resting or walking on the substratum. The dactylopodite of the fourth pereiopod of both sexes and also that of the fifth leg of the male (fig. 5 *J*) has five or six pairs of strong ventral spines, more or less replacing the tufts of setae present on the other dactylopodites. In the female the fifth pereiopod (fig. 5 *K*) is chelate, the pincer being formed by the dactylopodite working against a relatively short, pointed, slightly movable projection of the lower distal edge of the propodite. Paired, stiff spines are also present on the under surface of the dactylopodite of the fifth pereiopod of young females, but seem to become reduced in number in mature forms and obscured by a horseshoe-shaped brush of short, fairly stout setae, into the midst of which the tip of the propodite process fits when the dactylopodite is flexed. The main function of the chela only becomes apparent during the breeding season when it is used by females 'in berry' to arrange and clean the eggs and to remove the empty egg-capsules from the ovigerous setae of the pleopods. These events have been reported by Gilchrist (1913*a*), Von Bonde & Marchand (1935), Fielder (1964*b*), and Grua (1964), and have also been observed in captive females during the present study.

An *epipodite* and an accompanying podobranch, similar to those of the third maxilliped, are attached to the setiferous process of the coxopodite of all except the last pereiopod, opposite which the only gill is a *pleurobranch*.

10. PLEOPODS (Fig. 5 *L–N*)

On the second to the fifth abdominal segments in both sexes there are paired appendages or pleopods which are sexually dimorphic. They all agree in having a short protopodite which is distinctly divisible into a narrow, ventrally incomplete coxopodite and a somewhat larger basipodite, but they differ in that the female pleopods are biramous, while those of the male are uniramous. The *female pleopods* are larger than those of the male, the pair on the second abdominal segment (fig. 5 *M*) having subequal, flexible, foliaceous exopodite and endopodite which, with the exopodites of other pleopods enfold the eggs in the ovigerous females. The pleopods on the third, fourth, and fifth abdominal segments (fig. 5 *N*) are distinguished by the reduction of the endopodite to a somewhat cylindrical rod which in mature females is furnished with long non-plumose setae to which the eggs are attached during the breeding season. The proximal segment of these endopodites bears a remnant of the lamella observed in the first pair of pleopods, and in each of the female pleopods the endopodite has a distal conical projection, the *appendix interna*. The latter is particularly well marked in the biramous pleopods of the puerulus stage (fig. 6), where it is about equal in length to the relatively long setae fringing both the endopodite and the exopodite, and bears a subterminal seta and a group of six or seven terminal coupling hooks for connecting the pleopods in

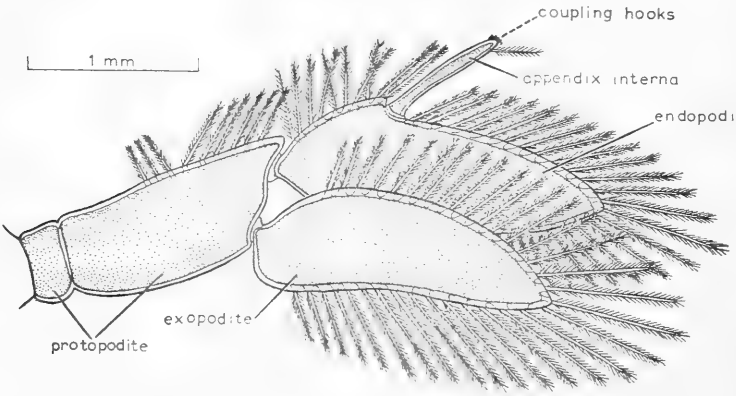


FIG. 6. Ventral view of right pleopod on second abdominal segment of a 22 mm long puerulus stage.

pairs when they are used in swimming. Gilchrist (1920) has indicated that the change from the puerulus to the post-puerulus condition is accompanied by the disappearance of the seta and the coupling hooks on the appendix interna, and also that sexual dimorphism becomes manifest for the first time in the progressive differentiation of secondary sexual characters in the pleopods of the developing males and females.

The basipodite of the *male pleopod* (fig. 5 *L*) only supports a relatively small, oval, lamellar exopodite, the endopodite having practically disappeared and being represented at most by a minute, pointed, medial process on the basipodite. In small specimens of the closely-related *Jasus tristani* Holthuis and in *Projasus parkeri* (George & Grindley), however, traces of a biramous condition are still evident in the male pleopods, each having a vestigial but recognizable endopodite, which in the first pair of pleopods of both species is distinctly lobular and setose. This may indicate that the pleopods of the males of these two species are structurally closer to the possible ancestral type than are those of *J. lalandii* and other Palinuridae in which the remnant of the endopodite is hardly discernible on the male appendages.

11. UROPODS (Fig. 5 *O*)

The uropods are alike in both sexes, being larger than the pleopods and heavily sclerotized. The two segments of the protopodite are inseparably fused and the exopodite and endopodite are broad lamellae, equal in length to the telson, with which they form the tail-fan. The lateral margins of the telson and the exopodites and endopodites of the uropods are markedly serrated, and the dorsal surfaces have rows of backwardly-directed spines, each fringed with setae.

D. AUTOTOMY AND REGENERATION OF APPENDAGES

Autotomy, or reflex amputation of an injured appendage, is a phenomenon characteristic of a number of Arthropoda and, among decapod Crustacea, it is said to occur in all Brachyura, most Anomura, and some Macrura. Having regard to the recent critique of autotomy and various aspects of regeneration in Crustacea by Bliss (1960), only two other publications need be cited, namely, Pearson's (1908) description of the process in *Cancer pagurus* and the more comprehensive account by Wood & Wood (1932) of the mechanism in a wide range of Crustacea.

According to the latter authors, *autotomy* is strictly a reflex response to external stimulation that induces an injured pereiopod to break off cleanly along the suture which demarcates the basipodite from the ischiopodite. Of the various designations given to the line of detachment, Pearson's (1908) '*fracture plane*' (fig. 16) is concise and apposite, and seems preferable to other terms mentioned by Bliss (1960).

Two additional closely related phenomena, which have been distinguished from autotomy by Wood & Wood (1932), are *autospasy* and *autotilly*. The former term describes the rupture of a limb at the fracture plane when it is seized and pulled by an outside agent; autotilly is the removal of a limb along the fracture plane by the action of other appendages of an injured animal.

A significant feature of the mechanism involved is that no muscles pass across the fracture plane from the basipodite into the ischiopodite, and Wood & Wood (1932) and Bliss (1960) have demonstrated that the main levator (levator *a*, fig. 26) or 'automizer' muscle, which is inserted by a long tendon rostro-laterally on the proximal margin of the basipodite, is responsible for the breakage of the limb. Normal contraction of this muscle elevates the fused basipodite and ischiopodite, but undue contraction of the muscle causes these segments to be pressed so strongly against the distal margin of the coxopodite that they separate along their weakest point, the fracture plane.

When the distal part of the limb has been discarded by autotomy or autospasy or autotilly, the stump is covered by a thin diaphragm to which, according to Wood & Wood (1932), the pedal artery and nerve are so attached by connective tissue that they are also severed at a fixed point. Excessive bleeding is prevented by a valvular structure, and the small quantity of blood that exudes forms a scab, beneath which a small limb bud is soon formed for the *regeneration* of the limb segments. The time required for the complete regeneration of a limb seems to vary in different Decapoda and several successive moults may take place before the limb attains its normal proportions.

Apart from occasional fracture of the pereiopods and antennal flagella while handling live specimens and indications of rather thin regenerated limbs and the presence of a dark brown scab on an amputated leg in some captive animals, no attempt was made to analyse these events in the course of the present study. Bradstock (1950), however, has reported autotomy and autospasy of the pereiopods and autospasy of the antennae in *Jasus* collected off Wellington, New Zealand; in these animals autotomy of the pereiopods was more frequent in females than in males, and a period of a year was required for the complete regeneration of an antennal flagellum lost by autospasy.

E. External Apertures

The *mouth* (figs 4, 31) is a mid-ventral opening between the mandibles, and is obscured by the forwardly-directed maxillipeds. In addition to soft lateral lips, it is bounded anteriorly by an upper lip, the *labrum*, and posteriorly by a lower lip, the *metastoma*. Both of these are cushion-like, fleshy structures, the exposed surfaces of which are strengthened by sclerites. The hood-like *labrum* (figs 3, 4, 8, 31) is attached to the posterior edge of the supralabral ridge and is continued postero-medially into a soft process which extends between the mandibles and overhangs the mouth. The *metastoma* (fig. 4) has a deep mid-ventral groove and is produced basally into a pair of conspicuous lobes, the *paragnaths*. Each forwardly-directed paragnath (fig. 4) is intercalated between the mandible and the first maxilla and is closely applied to the ventral surface of the former, as well as being confluent with the lateral lips.

The *anus* (fig. 31), situated ventrally on the telson, is an elongate aperture flanked by a pair of strong semilunar lobes. At the base of each lobe there is a longitudinal depression for the insertion of the dilatator muscle of the anus, while antero-laterally another groove marks the insertion of the anal compressor muscle.

The *excretory apertures* (figs 1, 2, 4, 38, 39, 43) are crescentic slits on the surface of an obvious pair of tubercles which are located laterally on the epistoma and seem to be slightly more anterior in position than those of some other South African palinurids examined.

The *exhalant apertures* (figs 2, 4, 43), through which the spent respiratory water is expelled, are situated ventro-laterally behind the excretory apertures.

The *male gonopores* (fig. 2) occur ventrally on the coxopodites of the last pair of pereiopods; each is a semicircular opening partly overlapped by a cuticular flap.

The *female gonopores* (fig. 80) are two crescentic apertures on the ventral surface of the coxopodites of the third pair of pereiopods.

F. Food and Feeding Mechanism

Chace & Dumont (1949) have remarked that palinurids in general are omnivorous and, in so far as experimental animals are known to select fresh rather than decomposing food, they are not altogether scavengers. From observations of the feeding habits of captive and free-living animals, Lindberg (1955) has concluded that *Panulirus interruptus* is primarily a scavenger, and the composition of the stomach contents suggests that it is an omnivore, while Sheard (1962) has also expressed the opinion that *Panulirus cygnus* is omnivorous.

Although a number of investigators have reported that the fore-gut of *Jasus* is either empty or contains only portions of the bait used in trapping the animals, some idea of its natural food is gradually emerging. Gilchrist (1913*a*) styled *J. lalandii* as a scavenger and stated that small specimens were occasionally cannibalistic on larger soft-shelled individuals, but he also noted the remains of mollusc shells in analyses of the stomach contents and observed that captive animals would eat live *Turbo* and the spines of living echinoids. It is obvious, however, that the diet depends on the food available in different localities. In the gut contents of Tasmanian specimens Hickman (1945) has identified the remains of other crayfish, crabs, echinoids, the small mollusc *Cantharidus eximus* Perry, *Mytilus planulatus* Lamarck, *Ischnochiton*, and seaweed, while Fielder (1964*a*) has kept other *Jasus novaehollandiae* in captivity on a supply of *Katelysia scalarina* (cockles) and *Modiolus* sp. (mussels), supplemented by pieces of sharks, bony fishes, and squids. The presence of fragmented molluscan shells, crustaceans, echinoids, Bryozoa, and algae in the stomach contents was subsequently reported by Fielder (1965), who concluded that, as dead and not living Crustacea were preferred by experimental animals, a predilection is shown for scavenging. He also established that they are normally nocturnal with a peak period of feeding and locomotion at dusk, and that olfaction is probably of greater significance than vision in detecting food. The majority of the Cape rock lobsters examined had been captured in baited traps, and the cardiac fore-gut was almost empty or contained unrecognizable particles. However, in young specimens collected in a rock pool at Lüderitz, South West Africa, and having a cephalothoracic length of from 30 to 40 mm, the cardiac fore-gut was fully distended by a mixture of sand grains and semi-digested food, comprising fragments of echinoid spines, sphaeromid isopods, amphipods, acephalous dipterous larvae measuring about 6 mm long, the hard head-capsules of other insect larvae, pieces of lamellibranch shells, and the intact shells of a minute gasteropod resembling *Eatoniella nigra* (Krauss).

Preliminary investigations as to the attractiveness of food offered to two medium-sized males kept in the laboratory were not very convincing. Although the animals had been starved for some time, they could not be induced to feed readily on portions of stockfish (*Merluccius capensis*). When, however, a variety of living marine molluscs, such as *Siphonaria capensis*, small *Patella granularis*, *Oxystele variegata*, small *Aulacomya magellanica* (Chemn.) = (*Mytilus crenatus* Lam.), and the seaweeds *Ecklonia* and *Ulva* were provided, more interest was displayed. One male showed an immediate preference for *Ecklonia* which was nibbled with apparent relish, a fact that suggests a partial retention of the vegetarian diet of the post-puerulus stage mentioned by Gilchrist (1920). Both specimens sought out and lifted individual *Patella* or *Aulacomya* to the mouth, using mainly the dactylopodites of the first pereiopods to insert the mollusc between the third maxillipeds. In all these observed attempts at feeding, the molluscs were dropped after a short period but, on leaving the tank in darkness overnight, it was apparent on the following morning that a substantial quantity of *Ecklonia* had been eaten, and scattered over the bottom of the tank were empty shells of *Patella* and *Aulacomya*; some of the latter had been broken up, but the *Siphonaria*, *Oxystele*, and *Ulva* were untouched. Subsequent observations of a number of experimental animals at the Sea Point Aquarium indicated that molluscs and *Ecklonia* were preferred to pieces of fish. On several occasions, some of the rock lobsters were seen feeding at night on small mussels which were grasped by the dactylopodites of the first pereiopods and so manipulated that the posterior end and dorsal surface of the mollusc shell were turned towards the rock lobster's mouth. While usually supported in this position by the third pereiopods, the dactylopodites of the first pereiopods were inserted between the lower edges of the shell valves of the mussel and the two valves were pulled apart, sometimes with the assistance of the dactylopodites of the second pereiopods. The latter were also used to loosen and remove parts of the posterior adductor muscle and the mantle of the prey and convey them to the third maxillipeds and the mouth.

These observations are by no means conclusive, but they seem to show that *J. lalandii* resorts to scavenging when there is insufficient live food. They also suggest that its principal food is seaweed, living molluscs, and perhaps other marine animals that will provide protein and some of the calcium required for impregnation of the exoskeleton. Drach's (1939) researches have proved, however, that this source of calcium is of minor importance. He has also determined that calcium reserves in the digestive gland are equally insufficient to meet all requirements, but absorption of calcium from the sea water, probably through the gills, is apparently essential to complete calcification of the exoskeleton.

At the Sea Point Aquarium, where rock lobsters are fed regularly each afternoon on pieces of fresh stockfish introduced into the large exhibition tank, the following observations were made before and during feeding. Some of the animals were ensconced in niches and crannies in the background of rocks, but the majority were resting or walking about on the bottom, usually supporting themselves on the last three pairs of pereiopods. Many were seen to be cleaning the antennulary flagella by drawing them through the apposed medial edges of the two third maxillipeds, and in some instances the dactylopodites of either the right or the left second pereiopod or frequently the dactylopodites of the fourth pereiopods were used to scrape the antennal peduncles, the eyes, and the dorsal and lateral surfaces of the head. Occasionally, the second to the fourth pereiopods were extended and their dactylopodites were drawn as far as possible along the ipsilateral antennal flagellum. In both sexes the dactylopodites of the fifth pereiopods were used to groom the surfaces of the abdomen, the tail-fan, and the pleopods.

The animals appeared to be on the alert and to anticipate the approach of feeding time for, immediately the pieces of fish were thrown into the tank from above, there was a general stampede in the direction of the descending lumps of food, the animals darting swiftly upward and seizing a portion between the dactylopodites of the paired first and second pereiopods. After having grasped the food, collision with other individuals was skilfully avoided by using the escape tail-fan mechanism to move rapidly backward and eventually settle either on the rocks or on the bottom to ingest the juicy morsels. The food was held in place against the mouth-parts usually by the dactylopodites of both pairs of first and second pereiopods, but sometimes only the first pereiopods and one or other of the second pair were used. While ingestion was in progress, many of the animals walked about on the bottom supported by the last three pairs of pereiopods and, as some approached the glass front of the tank, further observations were possible.

Gilchrist's (1913*a*) statement that the phyllosoma larvae employ the first and second pereiopods to capture floating food particles and convey them to the mouth is of interest, but in the adult the application of the anterior pereiopods and the third maxillipeds to the mouth during feeding tends to obscure the further sequence of events in the oral region. It is thus hardly possible to determine the part played by the first maxillipeds and the maxillae, but this difficulty has also been experienced by previous investigators who have attempted to discover the precise function of the mouth-parts in other Decapoda. From the present observations of the behaviour of adult specimens and the structure of their appendages it may be assumed, however, that the food is inserted between the mouth-parts by the dactylopodites of the first pereiopods and is held firmly in position by the mandibles. It was often noticed that, when a large piece of food had been seized and was gripped by the mandibles, the anterior pereiopods and the third maxillipeds would tug at it repeatedly, as though attempting to tear it apart. At the same time, the endopodites of the second maxillipeds were moved transversely across the outer surface of the portion of food in what seemed to be a kind of sawing action that would cut into the food. The spinous and setose medial margins of all the maxillipeds and the endites of the first maxillae seem able to retain the food and, perhaps by friction, may help to break it up. While this is taking place, the food will be forced gradually between the mandibles, no doubt assisted by the thrusting action of the inner endites of the first maxillae, but actual tearing of the food by the mandibles is doubtful. The labrum and the metastoma and its paragnaths are capable of various movements and appear to be complementary to the mouth-parts and the mandibular palps in holding the food between the bluntly-tuberculated mandibles while it is being crushed prior to its passage into the oesophagus. Dissections indicate that the labrum is furnished with a complicated musculature, comprising what appear to be constrictor, levator, abductor, and adductor muscles, while each paragnath has an abductor and an adductor muscle and the metastoma a pair of probable abductors. Moreover, examination of sections of the puerulus stage and dissections of the adult reveal that there is a pair of relatively large, compact glands between the bases of the first maxillae and the paragnaths; the parts bordering the mouth are also liberally supplied with glands, the secretion from which probably facilitates the process of ingestion.

Somewhat similar conclusions regarding the possible method of feeding in other decapod Crustacea were reached by Borradaile (1916, 1917, 1922) and by Yonge (1924), but in the animals examined by these authors actual seizure of the food is usually performed by the chelipeds. Borradaile (1916) has also remarked that in *Palaemon serratus* the second and not the third maxillipeds are the most important organs for grasping the food and directing it forward to the first maxillae and the mandibles and, if the piece of food is large, the incisor processes of the mandibles will bite into it and reduce it.

In captive *Jasus* the process of ingestion was completed in five minutes or longer, the time required depending on the size of the piece of food. It was then observed that the exopodites of the three pairs of maxillipeds became very active and were flicked to and fro across the mouth region, as if they were cleaning the surface. Simultaneously, vigorous movements of the scaphognathites seemed to take place, creating a strong forward current of water which apparently served to flush the parts.

INTERNAL ANATOMY

A. BODY CAVITY

One of the diagnostic features of the Arthropoda is the expansion of the primary body cavity or haemocoel to form the perivisceral cavity and the great reduction of the secondary body cavity or coelom. The arthropod *coelom* arises as cavities in some but not necessarily all of the mesodermal somites of the embryo, and variations in the number and the segmental position of the spaces have been reported in crustacean embryos. For instance, it has been established by Manton (1928) that coelomic spaces are developed in all the somites of *Hemimysis* except the antennulary, the mandibular, and the first maxillary somites, and that, although those originally formed in the preantennulary somites become obliterated, secondary preantennulary cavities persist in the adult. In *Nebalia* (Manton, 1934) there are no coelomic spaces in the anterior trunk somites, and the preantennulary spaces make a brief appearance in the late embryo. It has also been shown that in both these Crustacea the end sacs of the adult antennal glands are derived from the cavities in the antennal somites, and that the coelomic spaces in other somites disappear towards the end of embryonic development. Embryonic coelomic cavities have also been described by Nair (1949) in the preantennulary, the antennulary, the antennal, and the trunk somites of *Caridina*, while Waterman & Chace (1960) have mentioned that Shiino (1950) has ascertained that in *Panulirus japonicus* they are only evident in the antennal segment.

In conjunction with the suppression of the coelomic cavities in arthropod embryos, the blastocoelic spaces between the primary germ layers expand and become filled with haemolymph. The resultant cavity, termed the *haemocoel* by Lankester (1900), consists of irregular perivisceral venous sinuses which constitute an intrinsic part of the blood vascular system. The haemocoel is not merely a blood-filled cavity, but variations in its internal pressures may also assist in movements of the body and its appendages. In most Decapoda, however, the hard exoskeleton prevents marked changes in shape, but Manton (1965) has shown that hydrostatic pressures within the haemocoel can be demonstrated in some arthropods. By using weighted bridges and recording the maximum loads raised by certain burrowing annelids and the chilopod *Orya barbarica* (Gervais), she has noted significant differences in the pushing powers of the two types of animals, and has found that the pressure responses of the chilopod are greater than those of the annelids. She has concluded that, while hydraulic effects are still evident in some arthropods, the haemocoel as a hydrostatic mechanism has become less important in the larger and more advanced members of the phylum in which rapid movements result mainly from the action of sets of antagonistic muscles.

B. ENDOPHRAGMAL SKELETON (Figs 2, 3, 7)

A distinctive feature of many Reptantia is the presence in the thorax of an elaborate internal framework, the endophragmal skeleton (endoskeleton), which not only protects and supports the viscera, but also provides attachment for the thoracic muscles and greater structural stability for the movements of the appendages. The component parts of the arthropod endoskeleton have been carefully studied by Manton (1928, 1934, 1964), who has disclosed that it is a combination of cuticular apodemal invaginations and transverse segmental tendons; the latter are particularly evident in the head region, but also occur in the trunk of some species.

The parts of the endophragmal skeleton of the adult may be studied easily in preparations made as follows: after excising the abdomen, the carapace, and the appendages, the viscera and especially as many of the muscles as possible should be removed without damaging the endoskeleton; the specimen should then be boiled gently in a 10% solution of NaOH or KOH until clean and, after thorough washing in water, it may be preserved in 70% alcohol. Pilgrim & Wiersma (1963) also advocate the use of the stain, alizarin red S, as a means of determining calcified and uncalcified areas and the presence of certain epimeral hinges.

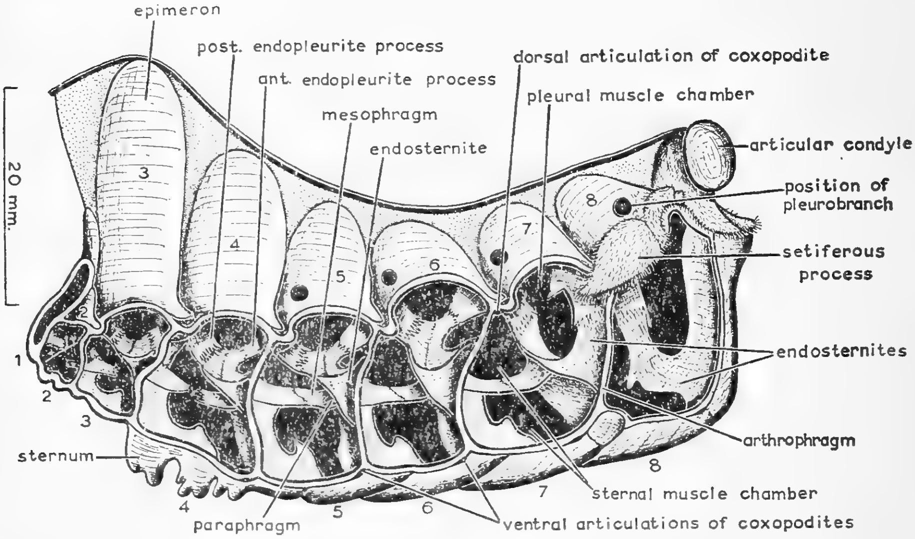


FIG. 7. Side view of thoracic epimera, sterna, and endophragmal skeleton.

As there are few available accounts of the adult endophragmal skeleton of other Decapoda, the terminology used for the structures observed in *J. lalandii* is based largely on the descriptions given by Huxley (1881) and Pearson (1908) for *Astacus* and *Cancer* respectively. Being associated with the broad sternal region, the endophragmal skeleton of *J. lalandii* is well developed and contributes to the general rigidity of the cephalothorax. Fundamentally, as in other Decapoda, it consists of a series of double sternal and epimeral infoldings from the walls of adjoining segments, termed respectively the *endosternites* and *endo-*

pleurites. These are inclined on each side of the body and combine to form the endoskeleton and, in addition, each endopleurite has a vertical process which unites with the corresponding endosternite to form an intersegmental partition or *arthrophragm* (figs 2, 7) between the bases of two successive appendages.

The *endosternites* (figs 2, 3, 7) are paired, flat, vertical plates jutting upward from the grooves between the sterna. The last of the series, projecting from the junction of the thorax and the abdomen, are more horizontal and partly resemble the 'sella turcica' of the brachyuran endoskeleton mentioned by Pearson (1908) and Drach (1939). In most segments the dorsal edge of each endosternite (fig. 3) is comparable to the *paraphragm* of *Astacus*, which Huxley (1881) described as a transverse projection of the head of a narrow, pillar-like endosternite. Beginning between the second and third segments, paired horizontal, somewhat cruciform pieces, the *mesophragms* (figs 3, 7) are differentiated at the dorso-medial ends of the endosternites; and, as the jagged borders of the two mesophragms of a pair usually interlock and are united by fibrous tissue not only with each other in the mid-line, but also anteriorly and posteriorly with the similar processes of adjacent segments, a more or less continuous series of flat, calcified plates results. These arch over the sterna and form part of the roof of a relatively shallow, mid-ventral *sternal canal* (figs 3, 31), through which pass the ventral nerve cord and the subneural artery. Typical mesophragms seem to be lacking in the first two thoracic segments, but it is possible that they may be represented by the fimbriated inner ends of the fused first and second thoracic paraphragms. The first obvious pair of mesophragms on the endosternites between the second and third segments are small and separated from each other and also from the stronger second pair, but the gaps between the two pairs are bridged by the superficial ventral thoracic muscles. Projecting upward from the middle of the eighth thoracic sternum and causing a marked external depression there is a pair of short, slightly divergent, independent *sternal apodemes* (fig. 3), which seem to have been developed for the attachment of the superficial ventral thoraco-abdominal muscles. The upper extremity of each sternal apodeme links up with the last mesophragm and the latter also has a slender ligamentous connexion with the broad posterior endosternite in the eighth segment.

Each *endopleurite* (figs 2, 3, 7) arises at the junction of two successive thoracic epimera and, projecting inward, it commonly bifurcates dorsally into wide, sloping anterior and posterior processes. The anterior process of any one endopleurite lies in the caudal half of a segment, while the posterior process of the endopleurite in front extends into the rostral part of the same segment, and both processes meet at the paraphragm and interlock with the endosternite. In each segment, as in *Cancer* (Pearson, 1908), the linkage of the endopleurite processes with the endosternite results in the separation of an upper *pleural muscle chamber* from a wider, lower *sternal muscle chamber* (figs 2, 7), in both of which the large muscles of the basal segments of the appendages are lodged and find attachment.

The endosternites and endopleurites of the first two thoracic segments are somewhat ill defined, but arthrophragms (fig. 3) are present for the attachment of the arthrodial membranes of the appendages. Behind the second arthrophragm there is a narrow process, presumably an endosternite from the second thoracic sternum (fig. 3), which meets the anterior process of the third endopleurite. The third endopleurite, which is a fairly prominent vertical strut behind the mandible approximately level with the anterior limit of the branchial chamber, apparently corresponds to the lamina in Pilgrim & Wiersma's (1963) description of this region in *Procambarus*. It divides into customary anterior and posterior processes, but the former passes medially to join the first obvious mesophragm and virtually serves as a paraphragm between the second and third segments. In addition, the endopleurite produces a conspicuous antero-dorsal process (fig. 3), which may be analogous to the so-called *fused first and second thoracic paraphragms* of other Decapoda. It passes obliquely forward and inward to meet its fellow of the other side in the mid-line at the anterior extremity of the endophragmal skeleton.

The latter, generally called the '*cephalic apodeme*' (figs 3, 8, 11, 13, 19), really consists of a pair of processes with interlocking medial margins, the conjoined pieces forming a raised, transverse bridge which supports the posterior region of the head and serves as a crutch for the hinder end of the fore-gut. It lies behind the mandibles and is slightly antero-dorsal to the fused sterna of the two last cephalic segments, of which, according to Huxley (1881), it represents the mesophragms. It is an important centre for the attachment of a number of anterior muscles and is itself firmly secured on each side to the base of the lateral apodeme of the epistoma by the short, strong ventral cephalic muscle (fig. 8).

The interpretation of structures bordering on the cephalic apodeme is rather uncertain and somewhat arbitrary, but some of them may be likened to the more typical parts of the endophragmal skeleton. The cephalic apodeme is elevated above the sternal region by short, lateral supports which may be considered as endosternites of the last two cephalic segments, and the arch so formed encloses the suboesophageal ganglion. Confluent with the side walls of the arch and extending to the epimera of the last two head segments, is a grooved, double bar, which has generally been thought to represent the *fused paraphragms* of these segments (figs 3, 4). To it, however, the posterior arthrodial membrane of the first maxilla and the anterior membrane of the second maxilla are attached, so that at least one arthrophragm also seems to be involved in this structure. Projecting antero-laterally beneath the cephalic apodeme and passing into the cavity of the mandible there is an obvious palmate process which carries the mandibular anterior adductor muscle. It has been shown by Manton (1928, 1934, 1964) and Snodgrass (1938, 1950) that in many arthropods the mandibular adductor muscles are attached to a transverse intermandibular tendon and that this resembles the endosternite which supports the ventral muscles of the prosomatic appendages of *Limulus*. The paired structure in *J. lalandii* appears to be analogous to the tendon of the mandibular adductor muscle of other arthropods, but the median bar connecting the two sides is no longer evident. Manton's (1964) term, *transverse mandibular tendon*, has, however, been applied to it (figs 3, 19), although there is no such tendon in *Astacus* (Schmidt, 1915; Manton, 1964).

The only other endoskeletal structures of importance in the head region are two *procephalic processes* (figs 3, 8) to which the anterior gastric muscles are attached. Each process is a small, backwardly-directed plate located postero-laterally on the dorsal surface of an infolding of the exoskeleton which passes from the base of the rostrum over the ocular peduncle and forms an internal shelf at the anterior extremity of the head.

C. Muscular System

The muscles of freshly killed specimens are too flaccid for satisfactory investigation, but in material treated with 5% formalin or in preparations fixed in Zenker's fluid and transferred to 70% alcohol, as recommended by Schmidt (1915), the individual components are more easily analysed.

The whole system, which is conveniently divisible into two parts, the trunk musculature and the muscles of the appendages, is broadly similar to that of *Astacus astacus* (L.) and *Pandalus danae* Stimpson, described respectively by Schmidt (1915) and Berkeley (1928). As might be expected, the complex abdominal muscles closely resemble those of *Jasus* (*Palinurus*) *edwardsii* (Hutton) investigated by Parker & Rich (1893), but they are also comparable with those of certain other Malacostraca studied by Daniel (1931, 1933) and with those of *Panulirus polyphagus* (Herbst) examined by George, Reuben & Muthe (1955). Some reference is made to Cochran's (1935) observations of the myology of the blue crab, *Callinectes sapidus* Rathbun, and to a new terminology proposed by Pilgrim & Wiersma (1963) for some of the muscles of *Procambarus clarkii* (Girard). For purposes of comparison between the different species, the nomenclature used in the following account has been based mainly on the observations of Schmidt and Daniel but, wherever possible, the names of the individual muscles have been simplified.

I. TRUNK MUSCULATURE

The body muscles form a complex system of dorsal, ventral, and lateral bundles, many of which are branched and intricately intertwined. They occupy the greater part of the body cavity, the large muscles of the cephalothorax showing few traces of segmentation and participating mainly in movements of the abdomen, while the abdominal muscles are proportionally more powerful and are arranged on a segmentally-repeated plan.

(a) *Cephalothoracic muscles*

Instead of dividing these into the different categories recognized by Schmidt (1915), they are described more or less in order as seen in progressive

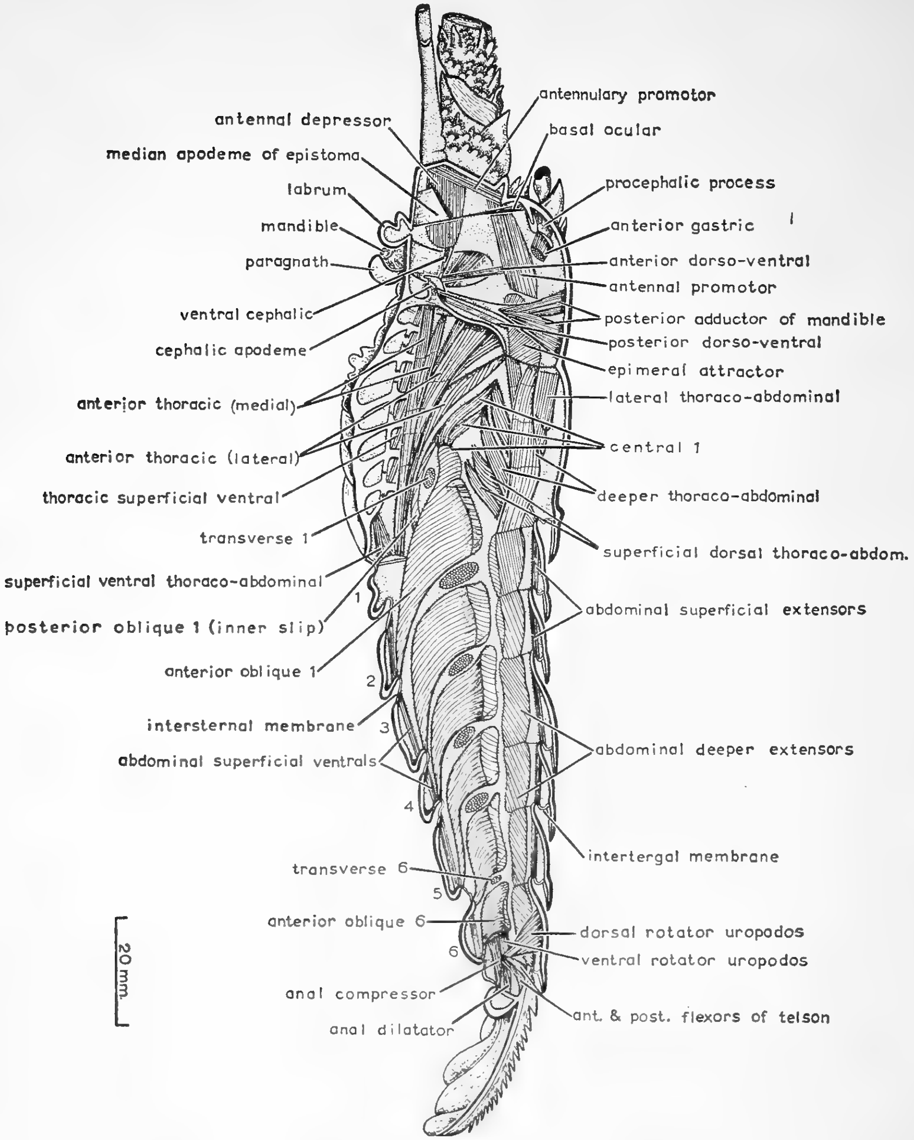


Fig. 8. Medial view of main muscles of right half of body.

dissections from the dorsal to the ventral surface in one half of the bilaterally symmetrical animal.

Epimeral attractor muscle (Figs 8–10, 13, 43, 53)

This name was used by Schmidt (1915) to define a band of short vertical fibres which connect the exoskeleton with the endoskeleton. The muscle band extends from the posterior limit of the branchio-cardiac groove to the antero-lateral end of the cervical groove, where it terminates approximately at the level of the anterior mandibular apodeme. All the fibres are attached to the carapace and are inserted on the inner, dorsal margin of the epimeral plates opposite the upper limit of the lining of the branchiostegite. The whole strip is clearly divisible into an outer or lateral series of short fibres and an inner row of somewhat longer, more medial fibres and, as the latter is interrupted at the level of the transverse part of the cervical groove, it is separable into an anterior portion coinciding with the lateral region of the cervical groove and a posterior part which is located beneath the branchio-cardiac groove.

These subdivisions are respectively comparable to the lateral, anterior, and dorsal heads of the epimeral attractor muscle of *Procambarus*, in which Pilgrim & Wiersma (1963) have also distinguished an antero-ventral, a posterior, and a receptor head. There can be little doubt that the latter is also present in *Jasus*, but no particular study was made of stretch receptors and their associated muscles. The antero-ventral head does not seem to be differentiated in *J. lalandii*, and there is some resemblance between the posterior head of the epimeral attractor muscle of *Procambarus* and one of the muscles, perhaps the transverse muscle, herein assigned to the wall of the pericardial pouch (p. 135).

It is also of interest to note that the short *musculus contractor epimeralis*, which Schmidt (1915) defined in *Astacus* and reported in *Homarus*, was not observed in *Jasus*. Alexandrowicz (1952) has also remarked that it is wanting in *Palinurus elephas* (Fabr.), and Pilgrim & Wiersma (1963) have attributed its non-existence in *Panulirus interruptus* to the absence of an uncalcified medial epimeral hinge that occurs in forms possessing this muscle.

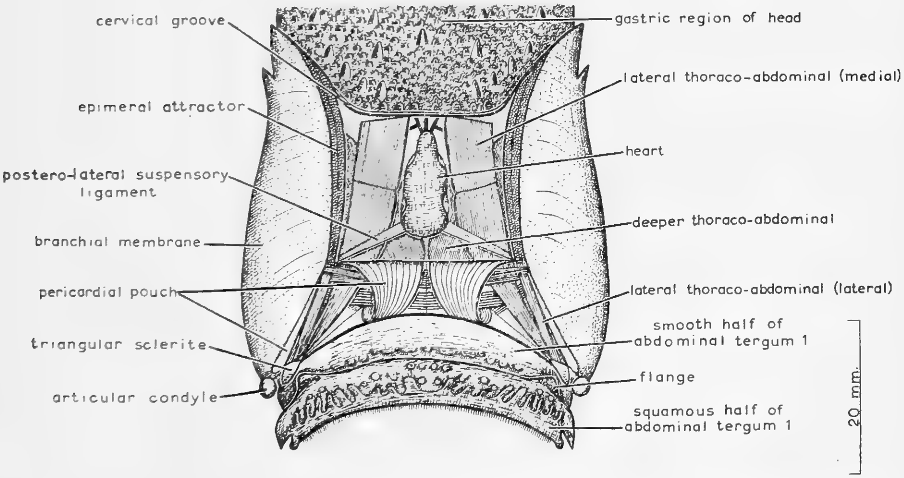


FIG. 9. Dorsal view of posterior half of cephalothorax after removal of branchiostegites and cardiac region of carapace.

Lateral thoraco-abdominal (Figs 8–10, 12, 45, 53)

Apparently so called by Schmidt (1915) because of its lateral insertion, this is the most superficial of the longitudinal muscles in the thorax and comprises medial and lateral portions. Its main purpose is probably to assist in straightening the abdomen, but independent unilateral contraction may also cause a sideways movement.

The *medial part* is the longer and stronger of the two and is a thick bundle with a marked transverse inscription; flanking the heart, it originates on the carapace behind the cervical groove. It tapers towards its insertion on a small, narrow sclerite antero-medial to a more conspicuous, triangular, calcified sclerite (figs 9, 45) that lies behind the pericardial pouch in line with the articular condyle for the carapace and fits into a dorso-lateral notch on the anterior margin of the first abdominal segment.

The *lateral part* is a flat, more or less vertical, fan-shaped muscle in the posterior region of the thorax. It is separable into two bundles, a narrower dorsal element and a broader ventral portion, both of which are attached one above the other on the epimeron of the penultimate segment behind the epimeral attractor muscle. The two bundles pass through the pericardial pouch below and lateral to the aforementioned medial part of the main muscle and have a broad insertion on the anterior margin of the triangular sclerite. By analogy with the insertions of the three heads of the similar muscle, the abdominal abductor, of *Procambarus*, the triangular sclerite is obviously comparable to one of the linking thoraco-abdominal sclerites, which collectively have been designated as the 'secula' by Pilgrim & Wiersma (1963).

Superficial dorsal thoraco-abdominal (Figs 8, 10, 12)

Connecting the posterior region of the thorax with the first abdominal segment is this flat, dorsal, double band, which resembles the first superficial dorsal muscle of *Astacus* (Schmidt, 1915) and the thoraco-abdominal superficial extensor muscle of *Procambarus* (Pilgrim & Wiersma, 1963). Its two parts arise one behind the other on the epimera at the posterior limits of the sixth and seventh thoracic segments, the posterior flap overlapping the anterior one as they both spread out beneath the medial section of the lateral thoraco-abdominal muscle and extend backward through the pericardial pouch to the proximal rim of the first abdominal segment, where they have a broad, superficial insertion.

Deeper thoraco-abdominal (Figs 8–10, 53)

Lying in the pericardial cavity and also uniting the thorax with the abdomen, this more extensive and more ventral muscle is identical with the medial and lateral musculi dorsales profundi thoraco-abdominales of *Astacus* (Schmidt, 1915) and the three heads of the thoraco-abdominal deep extensor muscle of *Procambarus* (Pilgrim & Wiersma, 1963). It shows possible traces of segmentation in that it consists of three compact bundles that arise in sequence on the epimera above the endopleurites at the posterior borders of the third,

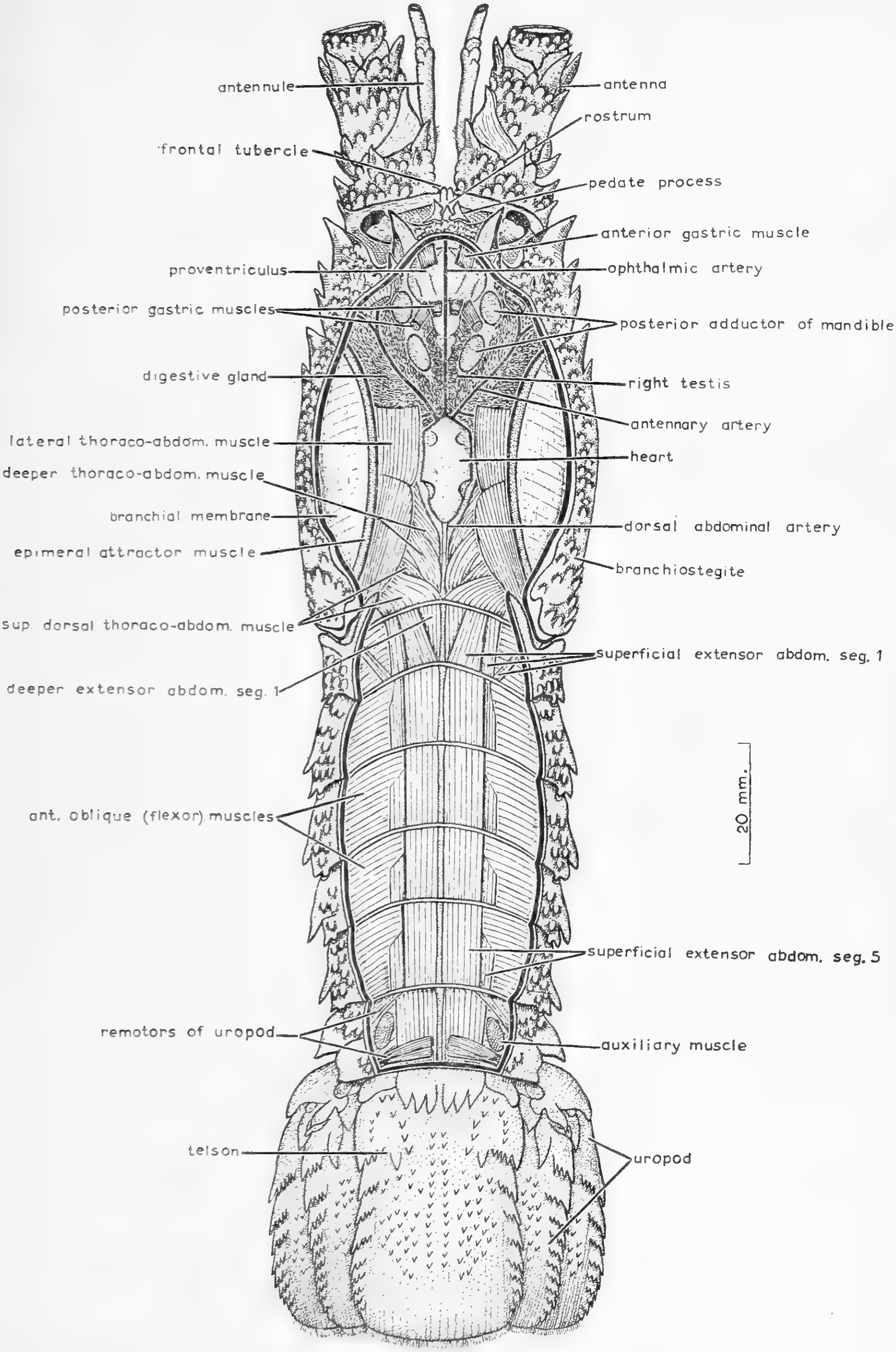


FIG. 10. Dorsal view of small male; part of the cephalo-thoracic exoskeleton and the abdominal terga have been removed.

fourth, and fifth segments in line with the origins of the previous muscle. Several inscriptions are evident on the first two bundles, each of which is bipartite and has dorsal and antero-ventral attachments. The small dorsal connexion of the anterior bundle is located near the anterior end of the branchio-cardiac groove and marks the subdivision of the medial vertical fibres of the epimeral attractor muscle into anterior and posterior sections. While the fibres of the first bundle are slightly twisted, those of the other two bundles are straighter, and it may also be noted that the branchio-pericardial orifices are apparent immediately behind the attachments of the three bundles. All three portions slant and expand towards the mid-line, the first and third underlying the second as they insert dorsally on the proximal margin of the first abdominal segment below the superficial dorsal thoraco-abdominal muscle. The latter and the present muscle are aligned with the two layers of the dorsal abdominal musculature to which they act as accessory extensors of the abdomen.

Anterior fascia

According to Berkeley (1928), this term may be applied to a tough coat of fibrous tissue, which surrounds the cephalic apodeme and may be equated with the two endophragmal compressor muscles distinguished in *Astacus* by Schmidt (1915). It also envelops the medial parts of the fused paraphragms of the fifth and sixth cephalic segments, particularly at their junction with the sternal region. In addition, it secures the inner ends of the fused paraphragms of the first and second thoracic segments to the upper surface of the cephalic apodeme. To it are attached the medial part of the paired anterior thoracic muscle, the posterior dorso-ventral muscle, and some of the muscles of the first and second maxillae.

Anterior thoracic muscle (Figs 8, 11, 13, 53)

This is one of the largest and strongest muscles of the thorax and occupies the ventral half of the body cavity between the deeper thoraco-abdominal muscle and the endophragmal skeleton. It consists of a number of interconnected parts, which serve as powerful flexors and are effectively thoraco-abdominal in nature. Unlike the similarly-termed system of *Astacus* (Schmidt, 1915) and the corresponding deep thoracic flexor muscles of *Procambarus* (Pilgrim & Wiersma, 1963), it does not join the bulky first anterior oblique muscle, but proceeds below this and the first (i.e. thoracic) transverse muscle to insert broadly on the proximal margin of the medial sclerite of the first abdominal sternum.

For convenience, the several components may be divided into narrower *medial* and more complex *lateral portions*. The former, like the medial part of the analogous muscle of *Astacus* and the first deep thoracic flexor muscle of *Procambarus*, consists of two slips, the inner of which arises ventrally on the anterior fascia below the cephalic apodeme, while the outer or more lateral head is attached to the paraphragm between the second and third segments.

The *lateral portion* comprises a series of four bundles, most of which are

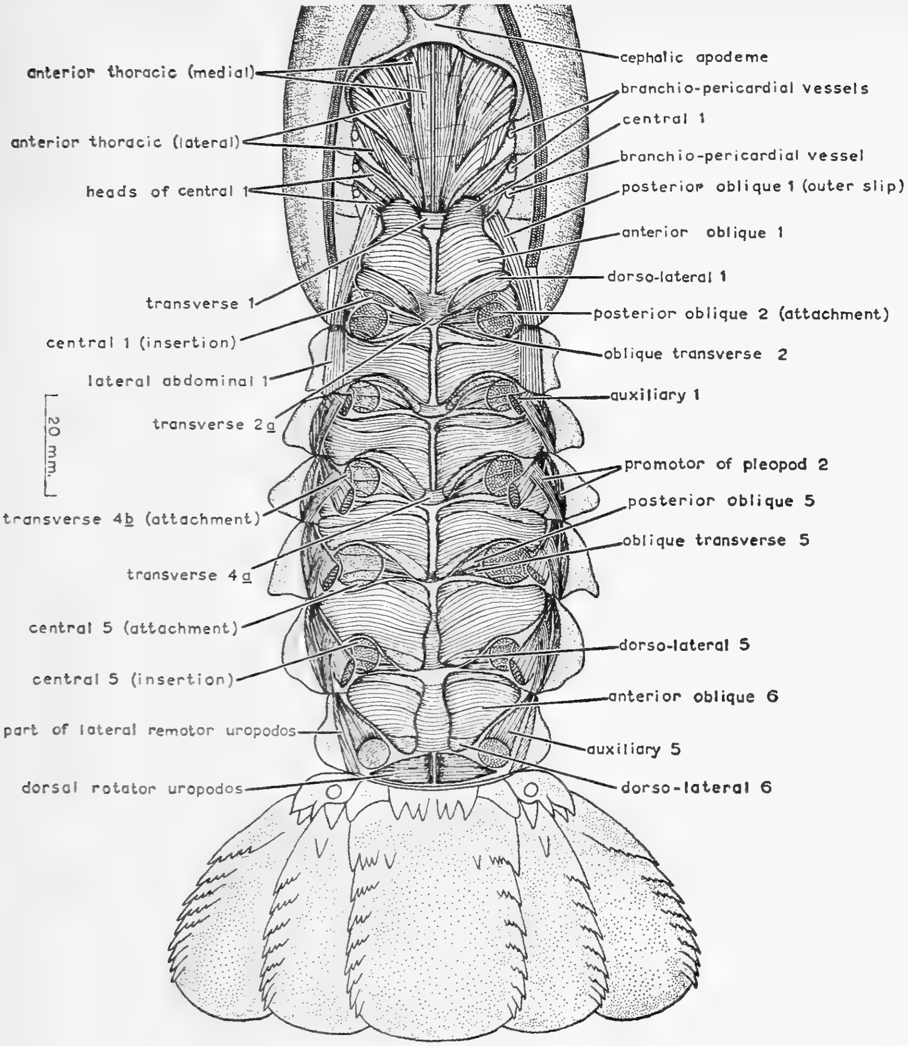


FIG. 11. Dorsal view of ventral trunk muscles.

marked by transverse inscriptions. The first bundle arises on the anterior process of the third endopleurite, while the next two have broad attachments on the frontal area of the epimeron of the third segment. The first bundle passes below the foregoing medial section of the muscle, which is joined by an antero-dorsal slip extending back from the second bundle. The fourth bundle differs from the others in that it consists of two overlapping parts: one arises antero-dorsally on the epimeron between the third and fourth segments, below the attachment of the anterior bundle of the deeper thoraco-abdominal muscle and in front of the upper end of the anterior branchio-pericardial vessel; the origin of the second part of the fourth bundle is more ventral and occurs on the endopleurite and the paraphragm between the third and fourth segments.

Posterior to the lateral constituents of the anterior thoracic muscle are two additional muscles, attaching respectively between the fourth and fifth and the fifth and sixth segments immediately below the middle and the posterior bundles of the deeper thoraco-abdominal muscle. Each has two heads, one originating dorsally on the epimeral ridge and the other on the endopleurite of the corresponding segment, and the dorsal heads occur at the anterior boundaries of the middle and the posterior branchio-pericardial vessels (fig. 11). These two elements seem to be lacking in *Astacus*, but Pilgrim & Wiersma (1963) have described an innominate muscle in *Procambarus* which appears to correspond with one of these. They converge towards the mid-line and crossing them posteriorly is a dorsal, transverse inscription, behind which they unite to form a cylindrical cord. The latter, by analogy with the arrangement of the abdominal musculature, may be assumed to represent the first central muscle, because it traverses and supports the first abdominal anterior oblique muscle; for this reason, the two muscles in question have been identified as the heads of *central muscle* 1 (figs 11, 13). A further complication in this region is that, attached to a ventral inscription on the anterior head of the first central muscle, there are two broad, flat slips which together may be regarded as forming the *first posterior oblique muscle*.

Anterior dorso-ventral muscle (Fig. 8)

Arising antero-laterally on the cephalic apodeme, this narrow and rather weak unit passes outward and slightly obliquely upward in front of the mandibular posterior adductor muscle. It is inserted by a long, flat tendon on the body wall medial to the large promotor muscle of the antenna.

Posterior dorso-ventral muscle (Fig. 8)

The course of this rather inconspicuous muscle is more horizontal than strictly dorso-ventral. It arises as a long, narrow, fibrous band laterally on the anterior fascia and, travelling dorsally over the muscles of the second maxilla, its few short fibres are inserted on the epimeron near the junction of the branchial and the prebranchial chambers and below the anterior end of the epimeral attractor muscle.

The function of these two muscles is obscure, but Berkeley (1928) has suggested that the two anterior and one posterior dorso-ventral muscles that occur in *Pandalus danae* probably strengthen the anterior fascia, while the anterior ones may also protect the viscera from compression by the large antennal muscles.

Ventral cephalic muscle (Fig. 8)

This is a tough, more or less tendinous strip, which arises on an antero-lateral process of the cephalic apodeme and is directed forward dorsally over the anterior apodeme of the mandible to an insertion on the posterior edge of the lateral apodeme of the epistoma close to the attachment of the depressor muscles of the antenna. As it is short and strong and fastens the cephalic apodeme to the epistoma, it probably provides some support for the anterior extremity of the endophragmal skeleton.

Thoracic superficial ventral muscles (Figs 8, 13)

Of the six pairs of these narrow, mid-ventral bands, the first four are clearly defined, but the last two pairs are weakly developed. The first pair bridges the gap between the anterior fascia and the mesophragms in the third thoracic segment and each of the other pairs is attached to the posterior border of the mesophragm of one segment and inserted on the anterior part of the next successive paired mesophragm. The attachments of the two muscles of a pair are usually fairly wide apart, but the muscles tend to spread out and the inner fibres slope medially towards each other and are adjacent at their insertions.

Like certain other small muscles, their usefulness is uncertain, but their better development in the immediate postcephalic region, where the mesophragms are not firmly united, indicates that they may help to sustain this part of the body or perhaps participate in any slight movements, while their rudimentary condition above the heavily-calcified posterior mesophragms may be correlated with the greater rigidity of the corresponding segments. Schmidt (1915) has also suggested that in *Astacus* they may be of some significance during ecdysis, but has offered no explanation of this supposition.

Superficial ventral thoraco-abdominal muscle (Figs 8, 13)

Generally considered as a continuation of the superficial ventral muscles of the thorax, this stouter pair of adjacent muscles is attached to the vertical sternal apodeme in the last thoracic segment and fills the posterior mid-ventral depression of this region. Although each muscle consists of fairly straight medial and more oblique lateral fibres, these are not identical with the parts distinguished in *Astacus* by Schmidt (1915) and in *Procambarus* by Pilgrim & Wiersma (1963). Instead of being divisible into one muscle inserted posteriorly on the first abdominal sternum and another having an insertion on the intersternal membrane between the thorax and abdomen, all the fibres are inserted on the medial sclerite of the first abdominal sternum below the insertion of the anterior thoracic muscle. This arrangement appears to provide for greater freedom of movement of the ventral thoraco-abdominal junction than would eventuate if these muscles were inserted directly on the proximal rim of the broad calcified first abdominal sternum immediately in front of the attachments of the second anterior oblique and some of the fibres of the third anterior oblique.

Apical muscles (Figs 60, 61)

In addition to the foregoing musculature, there is a pair of short, broad, anterior muscles, the omission of which by Schmidt (1915) seems to have resulted in some misconceptions regarding the homologies of certain muscles associated with the middle region of the fused eyestalks. The muscles in question were first briefly mentioned as the musculi compressores annuli by Baumann (1921) in his account of the circulatory system of *Astacus*. This term has been retained by Elofsson (1964), while Hanström (1947) referred to them as apical muscles innervated by the apical nerves, and his nomenclature seems appropriate for descriptive purposes. The eye muscles of *Jasus* (*Palinurus*) *edwardsii* studied by Parker & Rich (1893) are probably essentially similar to those of *J. lalandii* and, although their terminology is obsolete, it is likely that their levator of the basal sclerite is analogous to the apical muscle of *J. lalandii*.

The two flat apical muscles are located frontally in the middle cylinder of the fused eyestalks, and can only be clearly seen when the cephalic part of the nervous system has been exposed (fig. 61). They extend from the mid-dorsal surface outward and downward towards the junction of the eyestalk with the body near the ventral base of the pedate process (fig. 60): as Baumann's term suggests, they probably function as compressors of the eyestalk cylinder.

(b) *Abdominal muscles*

Movements of the abdomen are effected by powerful longitudinal muscles that are distinctly arranged into dorsal and ventral groups in each segment. The dorsal muscles, which lie between the terga and the intestine, are responsible for extending and straightening the abdomen, while contraction of the larger ventral muscles results in flexure of the segments.

(1) *Dorsal abdominal muscles*

The abdominal extensors are distinguished as two layers of paired muscles, which form an almost continuous series down the length of the abdomen. Herein, and also in Pilgrim & Wiersma's (1963) article, they are described as the superficial and deeper extensor muscles and correspond respectively to the musculi dorsales superficiales and the musculi dorsales profundi abdominis of *Astacus* (Schmidt, 1915). Situated above the anterior ends of the superficial extensors is another pair of rather inconspicuous bundles, which have been called the dorsal arthrodial muscles.

Dorsal arthrodial muscle (Fig. 12)

In describing the muscle receptor organs of *Homarus*, Alexandrowicz (1951) drew attention to the presence of paired, small, medio-dorsal muscles connected with the intertergal membranes, and his observations have been confirmed in *Procambarus* and *Astacus* by Pilgrim & Wiersma (1963), who have termed them the dorsal membrane muscles. In *Jasus* similar delicate muscle fibres form two fan-shaped elements in the first to the fifth segments immediately dorsal to the superficial extensors. Each is attached in the middle of the tergum of one segment and is inserted anteriorly on the next dorsal arthrodial membrane behind. Although weakly developed, they doubtless assist in movements of the intersegmental arthrodial membranes during extension and flexion of the abdomen.

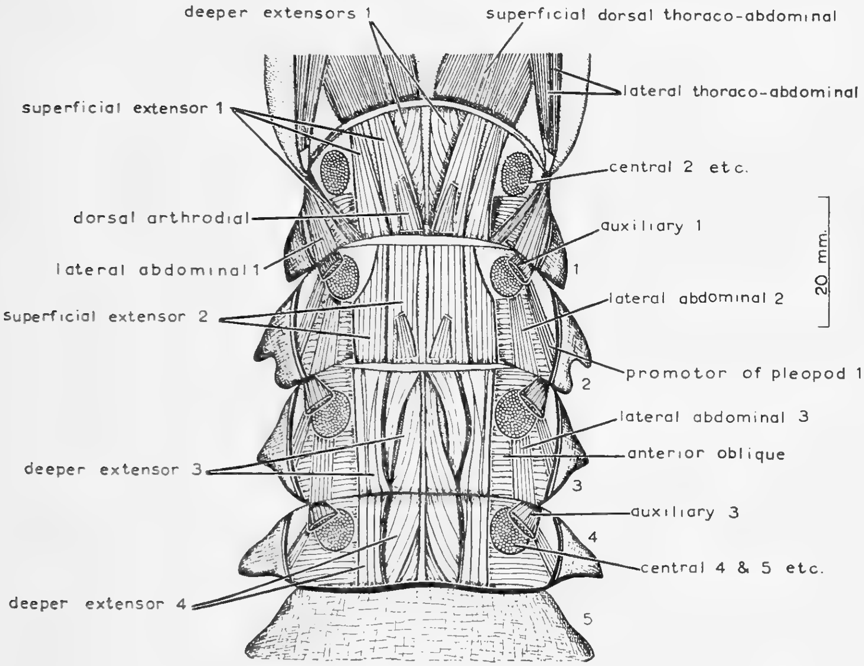


FIG. 12. Dorsal view of anterior part of abdomen, showing the dorsal musculature.

In their investigation of the thoraco-abdominal junction of *Procambarus*, Pilgrim & Wiersma (1963) have described certain other dorsal and lateral membrane muscles, but these appear to be similar to the muscles herein interpreted as intrinsic muscles of the pericardial pouches (p. 135–6).

Superficial extensors (Figs 8, 10, 12, 31, 54)

Mid-dorsally below the terga of the first five abdominal segments there are paired, strap-shaped muscles, each of which consists of medial and lateral bundles of almost straight fibres. Although they are uniformly arranged, they are not directly continuous, for each muscle originates near the anterior edge of the tergum and is inserted posteriorly on the next intertergal membrane, so that there is a slight gap between the insertion of one muscle and the attachment of the next one behind. As in *Procambarus* (Pilgrim & Wiersma, 1963), in most segments the lateral division is attached on an oblique tergal ridge postero-lateral to the level of the attachment of the medial portion.

The superficial extensors of the first abdominal segment arise immediately behind the insertions of the superficial dorsal thoraco-abdominal muscles, but the two of the pair are more widely separated than usual and do not adjoin in the mid-dorsal line. Furthermore, the lateral part of the superficial extensor of this segment is subdivided into two sections which tend to embrace the attachment of the axial column of ventral muscles, its narrower outer strip originating laterally on the first abdominal segment immediately posterior to the calcified triangular sclerite that supports the lateral thoraco-abdominal muscle.

In the sixth segment the superficial extensors are weakly developed and seem to be reduced to a few relatively short, medial fibres which are attached obliquely on the tergum and pass back beneath the medial remotor muscle of the uropod.

Deeper extensors (Figs 8, 12, 31, 54)

Being much thicker than the superficial extensors, this series almost fills the mid-dorsal part of the haemocoel above the intestine. Each muscle consists of closely-approximated medial and lateral parts and the consecutive units are practically continuous down the length of the abdomen, being attached anteriorly in one segment and inserted on the proximal border of the next segment behind. The *medial part* is composed of markedly oblique fibres which are separated into two main bundles; posteriorly the innermost bundle tends to overlap the outer bundle, but their insertions seem to be less complex than those observed in *Procambarus* by Pilgrim & Wiersma (1963). The *lateral part* consists of straight, longitudinal fibres and comprises several bundles, which are slightly superimposed on one another and so arranged that the insertion of the inner slip is somewhat dorsal to the outer fibres of the medial deeper extensor. Functionally they are similar to the superficial extensors and may be regarded as a continuation of the deeper thoraco-abdominal system. The last of the series, in the sixth segment, is narrower than usual, and is inserted on the proximal margin of the telson, of which it acts as an extensor.

(ii) *Ventral abdominal muscles*

The large, longitudinal flexor muscles practically fill the space below the intestine and are intricately arranged and intertwined to form thick, lateral, rope-like cords which are interconnected segmentally by transverse muscles. Daniel (1931, 1933), whose terminology has been applied to the component parts in *Jasus*, has shown that, despite varying degrees of complexity, the disposition of the abdominal muscles in the major groups of Malacostraca can be reduced to a basic plan. The main segmental constituent on each side is a thick *anterior oblique* muscle that twists around certain axial bundles distinguished as the *central* and the *oblique transverse* muscles, both of which enter into relationship with the major *transverse* muscle. A short, dorso-lateral *auxiliary* muscle is connected with most of the anterior oblique muscles, and just behind each of the latter is a narrow bundle, termed the *dorso-lateral* muscle. Additional to these, there is a comparatively long, flat *posterior oblique* muscle, which is usually attached on the tergum in front of the oblique transverse muscle, but travels beneath it and the central muscle to a ventral insertion. In most segments the attachments of all these muscles, except the anterior obliques, are grouped together on the tergum and form a conspicuous, rounded, tuft-like mass intercalated laterally between successive anterior obliques. The regular pattern formed on the sterna (fig. 14) by the attachments and insertions of the anterior oblique muscles and the insertions of the posterior oblique muscles suggests that concerted action is ensured down the length of the abdomen.

While each muscle is usually distinct, the plan becomes involved by occasional linkage of neighbouring units, and it seems pointless to describe the course of the individual muscles and their minor variations. Instead, a general account is given of each set of muscles and, in addition to superficial views of their arrangement (figs 8, 11), a grossly oversimplified scheme (fig. 13) has been included in an attempt to present a clearer impression of the system as a whole. In this plan the muscles represented are greatly attenuated and distorted and some interconnexions have been omitted. It was devised while endeavouring to compare the system of *Jasus lalandii* with Daniel's (1931, 1933) more realistic, but rather abstruse, diagrams of the abdominal muscles of other Malacostraca and, by coincidence, it is remarkably similar to figure 26 in Parker & Rich's (1893) beautifully illustrated account of the muscles of *Jasus edwardsii*, although this article was consulted after the present conclusions had been reached. The descriptions given by these authors therefore strengthen some of the following convictions regarding the composition of the ventral musculature and indicate that there is probably a uniform design in all species of *Jasus*.

Anterior oblique muscles (Figs 8, 10–13, 31, 54, 77, 78)

This group forms the principal flexors of the abdomen and comprises a series of strong paired muscles, all of which, except the last two pairs, occupy three successive segments. Typically each muscle arises ventro-laterally on or just in front of the anterior margin of one segment, practically in line with the lateral fibres of the superficial ventral muscles (fig. 14); it then arches dorsally in the pleural region and passes transversely across the segment towards the mid-line. After adjoining and sometimes, as in the last three segments, being connected by an aponeurosis with the contralateral muscle, it continues posteriorly as a broad ventral band and is inserted by tendinous material on the posterior sternal ridge of the second segment behind that in which it originates. Thus, for instance, anterior oblique muscle 4 (fig. 13) is attached near the proximal border of the third segment, but winds through the next two segments and has a broad insertion on the posterior bar of the fifth segment.

Compared with forms investigated by Schmidt (1915) and Daniel (1933), one pair of anterior oblique muscles is lacking, so that the first of the series in *Jasus* is equivalent either to the second or to the combined first and second anterior obliques of those Eucarida that possess seven pairs of these muscles. It bulges forward into the posterior region of the thorax as a conspicuous mass which, although composed of two broad bundles with separate origins, may be regarded as *anterior oblique* 1 (figs 8, 11, 13, 77). It differs from other anterior

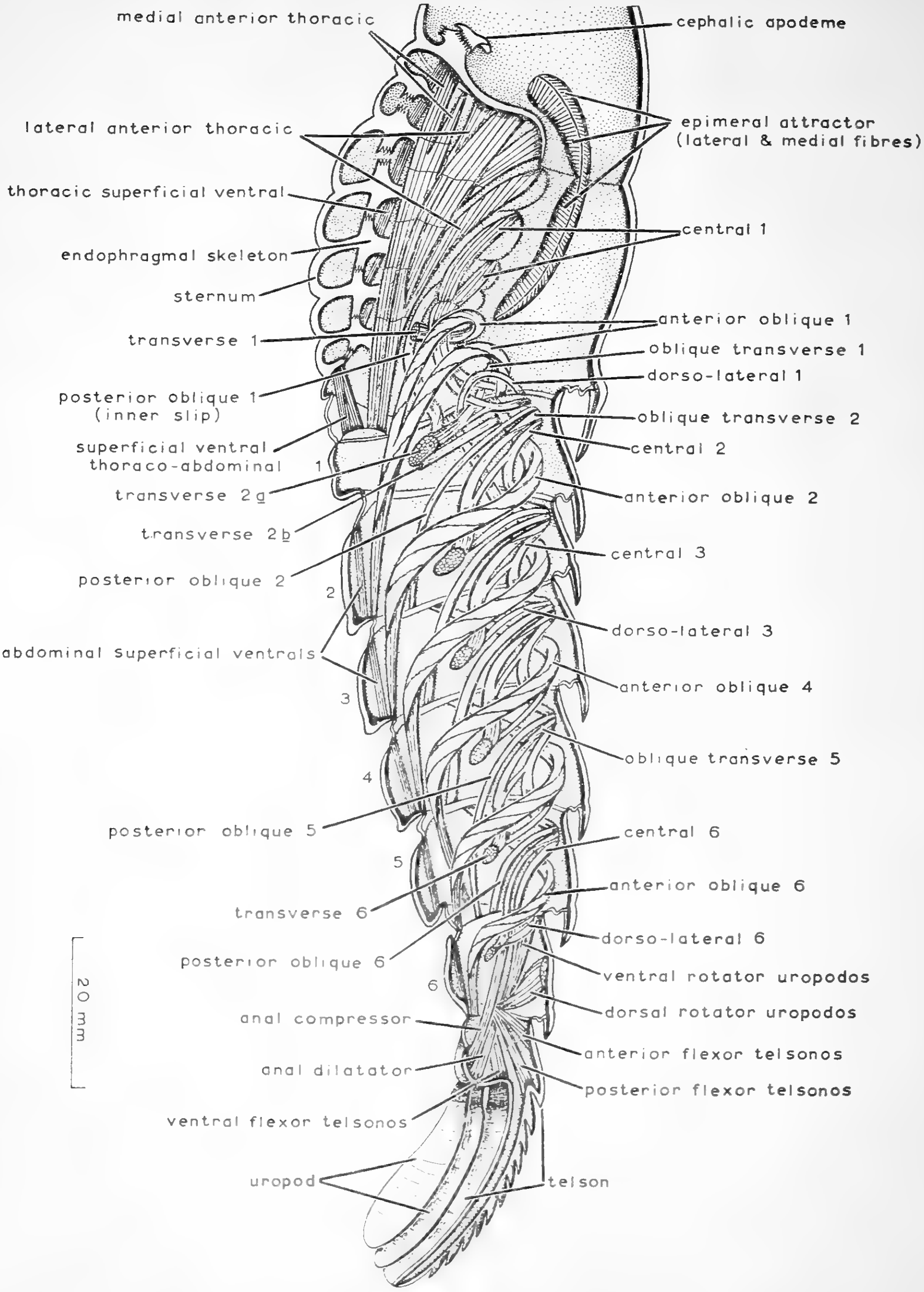


FIG. 13. Medial view of scheme of main right ventral muscles.

obliques in that its attachment is not essentially sternal; its anterior bundle is connected ventrally with the first transverse muscle and the posterior bundle mainly with an element identified as the first oblique transverse muscle, but some of its posterior fibres have a ventro-lateral attachment on the anterior margin of the first abdominal segment. The whole muscle curves dorsally over the first central muscle towards the mid-line before travelling ventrally to an insertion on the posterior sternal ridge of the second abdominal segment.

Anterior oblique muscle 3 has a normal attachment close to the anterior edge of the second abdominal segment, but some of its strong inner fibres arise proximally on the first abdominal sternum behind the attachment of the second anterior oblique muscle. This deviation from the norm may compensate in some measure for the absence of superficial ventral muscles in the first abdominal segment.

Although bulky, *anterior oblique muscles* 5 *and* 6 are relatively the shortest of the series and occupy two instead of the usual three segments. The former is inserted near the anterior margin of the sixth sternum, while the latter passes to the posterior sternal ridge of the same segment and its strong tendon is continued outward as far as the medio-ventral edge of the protopodite of the uropod.

Auxiliary muscles (Figs 11, 12, 77)

Antero-laterally in each abdominal segment, except the first, there is a short, stout muscle which arises by a tough tendon on the posterior sternal rib of the segment in front and near the origin of its corresponding anterior oblique muscle; it passes obliquely upward and backward, spreading out to a dorsal insertion on the tergum adjoining the attachments of the central muscles. The last of the series is the largest and projects into the sixth segment where it intervenes between the lateral and the medial remotor muscles of the uropod. Daniel (1931, 1933) has suggested that these are subsidiary to the anterior oblique muscles, and has also commented on the absence of auxiliary muscles in the first abdominal segment of *Homarus* and *Palinurus*. Similar muscles present in *Jasus edwardsii* were originally described by Parker & Rich (1893) as oblique flexors.

Central muscles (Figs 8, 11–13, 77)

Arranged intersegmentally and constituting part of the scaffolding around which the anterior oblique muscles twist, are curved dorso-lateral columns, distinguished as the central muscles by Parker & Rich (1893) and Daniel (1931, 1933). Although they form a regular series stretching from one segment to the next and are mostly fastened dorso-laterally to the tergum, they are not directly continuous, for the insertion of the posterior end of one muscle and the anterior attachment of the next in sequence are separated from each other and partly obscured by the attachments of the posterior oblique and the oblique transverse muscles.

Central muscle 1 (figs 8, 11, 13) acts as a support for the first anterior oblique muscle and, as previously indicated (p. 52), is considered to arise by two heads on the epimera approximately opposite the fifth and sixth thoracic segments, a conclusion that is substantiated by the observations of Parker & Rich (1893) and Daniel (1931, 1933). It is a somewhat twisted, double cord, the outer bundle of which joins the posterior fibres of the first anterior oblique, whereas the inner bundle is bridged to the second transverse muscle and is inserted antero-laterally in the first abdominal segment close to the attachment of the first dorso-lateral muscle.

Central muscle 2 is also bipartite at its origin in the first abdominal segment, its outer fibres arising antero-laterally, while its stout inner bundle attaches ventro-laterally behind the first central and the first dorso-lateral muscle.

Central muscle 6 (fig. 13) is a short, longitudinal column, practically confined to the fifth abdominal segment and inserted ventro-laterally at the anterior border of the sixth segment posterior to the insertions of the fifth anterior and the fifth posterior obliques and in proximity to the last auxiliary muscle.

The central muscles of *J. lalandii* may be compared to the lateral portions of the inter-tergal abdominal muscles of *Panulirus polyphagus* as described by George, Reuben & Muthe (1955), who have suggested that they assist the dorsal extensor muscles in straightening the abdomen, and consequently they and the major flexors (anterior obliques) relax and contract alternately. It is also of interest that central muscles have not been differentiated by either Schmidt (1915) or Berkeley (1928), but it seems likely that the longitudinal lateral parts of the transverse muscles of *Astacus* and *Pandalus* are their functional equivalents.

Transverse muscles (Figs 8, 11, 13, 54)

Daniel (1931, 1933) has recorded the presence of one thoracic and four abdominal transverse muscles in Eucarida, including the decapods *Homarus* and *Palinurus*. The arrangement in *J. lalandii* is substantially similar, with the possible addition of transverse muscles in the fifth and sixth segments, but in this detail there is agreement with *Astacus* (Schmidt, 1915) and *J. edwardsii* (Parker & Rich, 1893), in which transverse muscles also occur in the posterior segments.

Transverse muscle 1 (figs 8, 11, 13) is comparable to the thoracic transverse muscle described by Parker & Rich, Schmidt, and Daniel; it is a wide band that runs in the mid-line below the first central muscles and serves to connect the anterior bundles of the first pair of anterior obliques. In some respects, it is analogous to the minor transverse muscles in abdominal segments, especially that in the first abdominal segment.

In each abdominal segment there are major (transverse *a*) muscles, and in the first four segments additional minor (transverse *b*) muscles which correspond with the dorsal and the ventral transverse muscles of *Astacus* (Schmidt, 1915). The *major transverse* muscle may be described as an inter-segmental bridge composed of strands from the right and left anterior oblique, the central, and the oblique transverse muscles of the segment in front. The *minor transverse* muscles, on the other hand, are paired intrasegmental formations. With the exception of the first, each arises on the tergum (fig. 11) lateral to the origins of the posterior oblique and the oblique transverse muscles; it then bends inwardly below the posterior oblique and becomes thin and vertically flattened towards its mid-ventral insertion on the posterior face of the major transverse muscle. The first minor transverse muscle (transverse 2 *b*, fig. 13) stems from a broad inscription on the inner fibres of the second anterior oblique muscle, but its upper fibres also adjoin the ventral part of the second central muscle.

George, Reuben & Muthe (1955), although not recognizing discrete transverse muscles, have indicated that each inter-tergal muscle of *Panulirus polyphagus* has an inherent transverse portion which is responsible for the compression of the segment. From this it may be inferred that the inter-tergal muscles of *Panulirus* are homologous to the transverse muscles of *Astacus* (Schmidt, 1915) and *Pandalus* (Berkeley, 1928), while the latter in turn are evidently comparable to the combined transverse and central muscles defined by Parker & Rich (1893) and Daniel (1931, 1933).

Oblique transverse muscles (Figs 11, 13)

This name was applied by Daniel (1931, 1933) to certain rather inconspicuous muscle slips that usually unite neighbouring anterior oblique and central muscles in the anterior abdominal segments. In the present study these connections are considered to be relatively unimportant, and the term has been transferred to the elements described by Parker & Rich (1893) as oblique extensors and by Daniel (1931, 1933) as the dorso-lateral muscles, because each appears to be an oblique portion for the attachment of the major transverse muscle. Each member of the series arises on the tergum near the anterior head of the central muscle, and a small portion of it is visible dorsally adjacent to the posterior oblique muscle. Towards the mid-line, however, it becomes obscured as it bends below the central muscle and forms with it the saddle that supports the anterior oblique muscle; subsequently it merges with the major transverse muscle of the next segment.

A muscle, which may tentatively be identified as *oblique transverse* 1 (fig. 13), originates in the thorax at a ventral inscription on the posterior bundle of the first anterior oblique; it curves medially beneath the first central muscle to become confluent with the major transverse muscle in the first abdominal segment.

Dorso-lateral muscles (Figs 11, 13)

Associated with the transverse muscles of the first three abdominal segments, Parker & Rich (1893) distinguished paired accessory oblique extensors. These are homologous to the accessory dorso-lateral muscles described by Daniel (1931) in *Palinurus*, and the similar muscles of *J. lalandii* have simply been called the dorso-laterals.

On the whole, they are rather weakly-developed bundles that run parallel to the postero-dorsal fibres of the anterior oblique muscles and arch medially to join the major transverse muscles. Like the accessory oblique extensors mentioned by Parker & Rich, the first three have independent dorso-lateral attachments close to the posterior ends of the central muscles, but in the fourth and fifth segments the apparently analogous strands are connected with the anterior oblique muscles.

By reference to the relative positions of other muscles, a narrow bundle, which is closely applied to the sixth anterior oblique, may be determined as *dorso-lateral muscle* 6 (figs 11, 13), although it bears some resemblance to the ventral branch of the transverse muscle in the sixth abdominal segment of *Astacus* (Schmidt, 1915). It originates proximally in the sixth segment and bends medially to join the last transverse muscle.

Posterior oblique muscles (Figs 11, 13, 54)

Attached dorso-laterally on the first to the fourth abdominal terga, and perceptible in front of the heads of the oblique transverse muscles, are four of the six posterior oblique muscles. Each passes ventrally as a flat band adjacent to the oblique transverse muscle, but extends through two segments to insert distally in the second of these close to the tendon of the auxiliary muscle; as a rule, it also has a posterior slip connected with the neighbouring auxiliary muscle. Posterior obliques 2 and 5 (the first and fourth in the abdomen) are narrower than the other two, but they are all relatively strong and are capable of assisting the anterior obliques in flexing the abdomen.

Probably belonging to this series are two additional muscles, one in the posterior region of the thorax and the other in the fifth abdominal segment. The former consists of two flat strips attached to a ventral inscription on the anterior head of the first central muscle, and both are thought to represent *posterior oblique muscle* 1 (figs 8, 11, 13). The outer slip (fig. 11) passes below anterior oblique muscle 1 and is inserted somewhat dorso-lateral to the insertion of the lateral part of the anterior thoracic muscle on the medial sclerite of the first abdominal sternum. The inner slip (figs 8, 13) is more medial and continues into the first abdominal segment, where it becomes applied to the anterior face of the minor transverse muscle (transverse 2 *b*).

The other muscle of uncertain homology has provisionally been called *posterior oblique muscle* 6 (fig. 13). It is a somewhat fore-shortened, longitudinal element arising near and running parallel to the last oblique transverse muscle. It is inserted close to the last central muscle on the anterior margin of the sixth segment.

Flexor muscles of telson (Fig. 30)

While the telson is intimately linked to the uropod on each side by the telso-uropedal muscle (p. 105), it can also be bent forcibly beneath the last abdominal segment by the contraction of three pairs of strong flexor muscles. These are probably most frequently used when the animal is resting or walking to and fro or creeping backward into rock crevices. The telson and the uropods are then normally tucked under the abdomen, but the main driving force for rapid backward movement of an animal in flight is provided by the contraction of the powerful abdominal flexor muscles in conjunction with the scooping action of the tail-fan.

Most of the fibres of the short thick *anterior flexor muscle of the telson* spring from the postero-ventral face of the tendon of the dorsal rotator muscle of the uropod, but some are also attached to the tendon of the last anterior oblique muscle. The anterior flexor passes obliquely inward and backward and has a broad dorso-medial insertion in the proximal part of the telson.

The *posterior flexor of the telson* is a longer and a more conspicuous muscle which has its origin at the posterior end of the tendon of the last anterior oblique muscle. It extends below and slightly lateral to the anterior flexor of the telson, and its large insertion covers a considerable part of the antero-dorsal wall of the telson.

From an attachment on the tendon of the last anterior oblique muscle in the distal region of the sixth abdominal segment, the broad flat *ventral flexor of the telson* runs below the preceding muscle and is inserted ventro-laterally in the telson. This muscle is absent in *Astacus* (Schmidt, 1915), but in *Pandalus* (Berkeley, 1928) there are three pairs of flexor muscles resembling those of *J. lalandii.*

Anal compressor muscle (Figs 8, 13, 30, 63, 77)

Situated medio-ventrally in the last abdominal segment and the proximal part of the telson, this fairly strong muscle arises partly antero-ventrally on the sixth sternum and partly on the prolonged tendon of the last anterior oblique muscle. It inserts ventrally without tendinous material on a crescentic fold antero-lateral to the anus.

Anal dilatator muscle (Figs 8, 13, 30, 63)

Running parallel to the preceding muscle and having a somewhat similar attachment on the tendon of anterior oblique muscle 6, this equally strong, but more lateral, muscle has an insertion along the base of the anal lobe. While it serves to open the anus, contraction of the compressor muscle closes the aperture.

Abdominal superficial ventral muscles (Figs 8, 13, 14, 54)

The term ventral membrane muscles has been preferred by Pilgrim & Wiersma (1963) for this system of paired, segmentally-repeated elements, which operate during flexion of the abdomen. They are generally considered to be a continuation of the series of superficial ventral muscles in the thorax, but, strangely enough, there is none in the first abdominal segment of *J. lalandii.*

In each half of the other segments the muscles usually have a somewhat latero-ventral attachment on the intersternal arthrodial membrane, and are divisible into lateral and medial portions (fig. 14). The lateral band consists of fairly strong, almost straight fibres, which slightly overlap the medial fibres

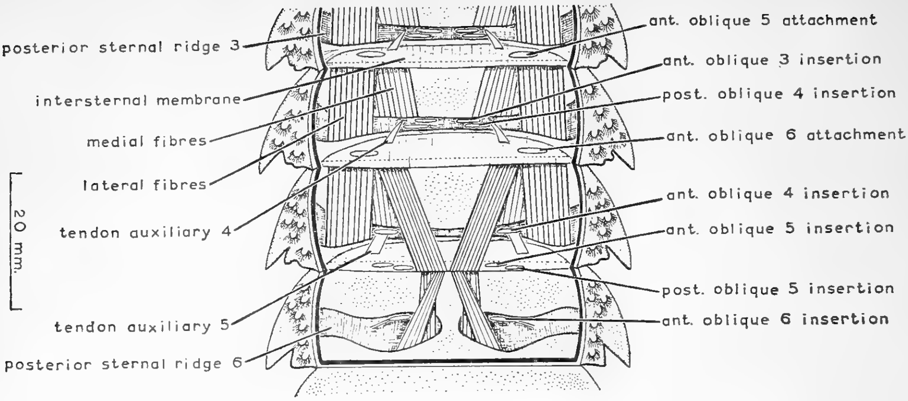


FIG. 14. Diagrammatic inner view of last three abdominal sterna, showing the approximate arrangement of the superficial ventral muscles.

and are inserted partly on the anterior and partly on the posterior edges of the posterior ridge of the sternum. The medial fibres are appreciably thinner and tend to slope inward to insert on the proximal part of the posterior sternal ridge in front of the insertions of the anterior and posterior oblique muscles and the tendon of the auxiliary muscle. In most segments, however, they do not reach the mid-ventral line, and a gap occurs between them and the ventral nerve cord.

As observed by Schmidt (1915) in *Astacus* and by Pilgrim & Wiersma (1963) in *Procambarus*, there is an additional strip of medial fibres in the fifth abdominal segment. This has a normal attachment on the intersternal membrane between the fourth and fifth segments but, while the outer medial fibres are inserted on the ridge of the fifth sternum in front of the tendon of the last auxiliary muscle, this inner bundle extends farther back and is inserted on the intersternal membrane between the fifth and sixth segments, practically meeting the one of the other side in the mid-ventral line. The reason for this modification is not immediately apparent, but it seems as though the medial fibres are usually more or less aligned with the insertions of the anterior and posterior oblique muscles. Consequently, the addition of another medial band stretching across the fifth sternum may be correlated with the foreshortening of the fifth anterior oblique and its insertion and that of the fifth posterior oblique near the proximal edge of the sixth sternum.

Perhaps owing to the complex musculature associated with the uropods and the telson, the superficial ventral muscles of the sixth segment (fig. 14) are reduced to relatively strong, medial fibres which underlie the last ganglion of the ventral nerve cord. Two rather narrow bundles are evident, the outer overlapping the inner; both arise anteriorly on the intersternal membrane between the fifth and sixth segments and are inserted distally on the broad sternal bar of the sixth segment.

(iii) *Lateral abdominal muscles*

Schmidt (1915) and Berkeley (1928) have described weak, serially-arranged lateral abdominal muscles attached to the hypodermis and inserted on the segmental articulations. Similar paired elements occur in the first three segments of *J. lalandii*, but in the posterior segments they seem to be replaced by fibrous tissue. The first (figs 11, 12) is an obvious band which originates on the proximal border of the first abdominal segment and is joined to auxiliary muscle 1 behind it by tough fibrous tissue that passes medial to the hinge joint. The muscles in the second and third segments are less conspicuous, and consist of delicate strands extending from the tergum behind the insertion of the central mass of muscles to the hinge joint but, like the first muscle, they are also connected by tendinous material with neighbouring auxiliary muscles. Lateral muscles were also observed by Daniel (1931) in the first three abdominal segments of *Homarus* and *Palinurus*, but the latter is exceptional in having two pairs, instead of a single pair, in each of these segments.

2. MUSCLES OF THE EYE (Fig. 15)

Each eye consists of a two-segmented peduncle and a swollen optic cup, at the distal extremity of which the darkly-pigmented visual portion is located. The optic cup and the peduncle are united by a thin, flexible, cuticular membrane, and the second peduncular segment, which has a calcified sclerite covering its exposed surface, is movable on the first segment. The latter projects laterally beneath the rostrum, and it and the base of the second segment are cushioned against the pedate process by a fairly wide, pliable membrane. The basal segments of the two eyestalks are confluent in the mid-dorsal line and together form the middle cylinder, which is located below the rostum and has a thickened dorsal wall. The *middle cylinder*, a term used by Berkeley (1928) and Cochran (1935), has been variously interpreted by different observers. Parker & Rich (1893) defined it as a mid-dorsal calcification of the arthrodial membrane of the eyestalks and named it the 'inter-ophthalmic sclerite . . . having the form of a half cylinder', while Schmidt (1915), Baumann (1921), and Elofsson (1963, 1964) have referred to it respectively as the 'mittleren Chitinring', the 'Augenring', and part of the 'bec ocellaire'. One of the features mentioned in Borradaile's (1907) key is that the eyes of Palinuridae 'are not enclosed in separate orbits formed by the edge of the carapace', a statement which probably alludes to the coalescence of the basal segments of the eyestalks. On the other hand, the comparatively small eyes of the Scyllaridae are separated by the wide frontal margin of the head and are lodged in individual sockets. The two eyestalks of *Jasus* and some other Decapoda are obviously fused mid-dorsally and are free from the overlying rostrum. Ventrally, however, the basal segments of both eyestalks are attached by a thin arthrodial membrane to the margins of the pedate processes and to the sclerite herein termed the antennal epimeron (fig. 3). The united eyestalks thus have a common articular cavity, called the ophthalmic fenestra by Parker & Rich (1893), and consequently the middle cylinder is incomplete ventrally.

As the eyes are normally laterally inclined and their stalks are almost at right angles to the longitudinal axis of the body, the terms medial and lateral, which are appropriate to the more porrect eyes of *Astacus* and *Pandalus*, are hardly applicable but have been retained, even though they are descriptive of the functional anterior and posterior surfaces. The eye musculature is complex and comparable with that of other Decapoda, but from observations of live animals movement of the eyestalk seems to be very slight and difficult to detect, although when the eyes are being cleaned by the pereiopods they are moved freely in various directions.

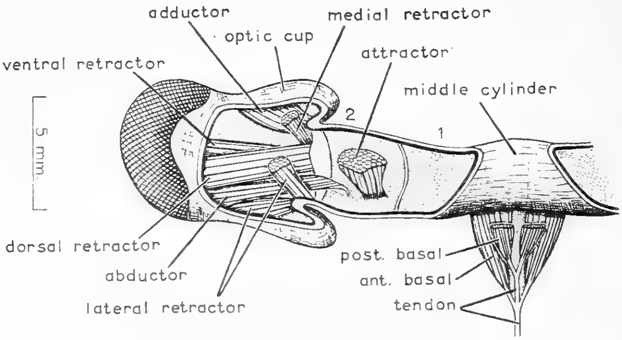


FIG. 15. Muscles of left eye, dorsal view.

Anterior basal

This fairly long, paired muscle arises on a strong median tendon from the median apodeme of the epistoma (fig. 8). The tendon subsequently bifurcates to support the two muscles which pass forward and upward on either side of the cerebral artery and are inserted adjacent to each other on the postero-dorsal edge of the subrostral cylinder of the fused eyestalks. As in other Decapoda, contraction of the two muscles may depress the cylinder and cause a slight rotation of the eyes.

Posterior basal

The median tendon of the previous muscle is continued forward and again divides to two shorter and more posterior muscles. These diverge somewhat as they extend upward to be inserted by tendinous material mid-dorsally on the body wall at the base of the rostrum and near the medial margin of the attachment of the anterior gastric muscle. On each side there is another long tendon which passes backward and outward from the insertion of each posterior basal muscle to a more distal part of the wall of the head.

As the median tendon runs between the two circum-oesophageal connectives and the two pairs of basal eye muscles overlie the cerebral ganglia, it would seem that the whole combines to support and protect the anterior part of the nervous system. At the same time, the posterior basal muscles are adjacent to the cor frontale at the anterior end of the median ophthalmic artery, and it is conceivable that their contraction may be correlated with the propulsion of blood from this arterial dilatation into the brain and the eyes.

Attractor

There are no muscles associated with the projecting part of the first segment of the eyestalk, but the second segment contains a short, stout, rather conical muscle, which has been identified with the musculus oculi attractor of *Astacus* (Schmidt, 1915). It is attached ventrally near the junction of the two segments and passes slightly obliquely upward and forward to a broad dorsal insertion in the distal part of the second segment. A somewhat similar muscle has been described by Parker & Rich (1893) as the rotator muscle of the basal sclerite in *Jasus edwardsii*. Probably it is partly antagonistic to the basal eye muscles in rotating and perhaps slightly compressing the second segment.

According to Berkeley (1928) and Cochran (1935), the attractor eye muscle of the animals dissected by them is located in the middle cylinder, but this is obviously a misinterpretation of the paired apical muscle and, following on this, the muscle identified by them as the adductor is in all probability the attractor eye muscle as defined by Schmidt.

Two pairs of musculi compressores annuli have been described in Natantia by Elofsson (1964), who maintains that both are innervated by the apical nerves, but admits that the supply to the musculus compressor annuli anterior is usually indistinct. It seems likely that Elofsson's posterior compressor muscles are homologous to the apical muscles of *Jasus*, and these are certainly supplied by the apical nerves (fig. 61). Specific structural and myological differences doubtless exist and, while not wishing to dogmatize, it may be suggested that the anterior pair of mm. compressores annuli observed by Elofsson in Natantia are analogous to the attractor eye muscles of Reptantia. In *Jasus*, at least, the attractor muscle of each eye is located in the eyestalk proper, and its innervation by the second oculomotor nerve (figs 59, 61) may account for Elofsson's difficulty in tracing the nerve supply in sections of Natantia.

Abductor

As in *Astacus* (Schmidt, 1915), this muscle is attached ventrally by a short tendon in the second segment of the eyestalk near the origin of the attractor muscle and is inserted distally in the optic cup. It rotates the latter backward relative to its longitudinal axis and appears to be less substantial than that of *Astacus*.

Adductor

Arising dorso-medially at the junction of the optic cup and the eyestalk, this relatively broad muscle runs obliquely forward to a medial insertion on the wall of the optic cup. In moving the eye forward, it opposes the abductor muscle, but differs from the analogous muscle of *Astacus* in being confined to the optic cup and not to the second peduncular segment.

Retractor muscles

As in the species investigated by Schmidt (1915), Berkeley (1928), and Cochran (1935), retraction and rotation of the eye about its longitudinal axis are accomplished by four conspicuous muscles, all of which originate on the flexible membrane between the eyestalk and the optic cup and are inserted in the latter at different levels.

Dorsal retractor

This is one of the most prominent of the eye muscles; it arises dorsally and slants slightly backward to a dorso-lateral insertion in the distal part of the optic cup. In addition to moving the optic cup upward, it is somewhat antagonistic to the adductor muscle.

Ventral retractor

Being located below the optic ganglia, this is the only ventral muscle of the eye. It lies opposite the dorsal retractor, but is rather broader and pursues a straighter course from the articular membrane to the ventro-distal region of the optic cup. Unlike the other retractor muscles, it does not participate in the rotation of the optic cup.

Lateral retractor

The two distinct, relatively stout bundles of this muscle are attached laterally to the cuticular membrane. The anterior or inner portion is the shorter of the two and is inserted proximally in the optic cup above the dorsal retractor muscle; the broader posterior or outer section partly obscures the abductor muscle and is applied to the lateral wall of the optic cup. Both parts effect a strong outward and backward movement of the cup.

Medial retractor

Partly overlapping the adductor muscle, this short element originates close to the dorsal retractor and passes obliquely to a medial insertion in the proximal part of the optic cup. It is the weakest of the eye muscles and probably plays a minor part in the rotation of the optic cup.

3. MUSCLES OF THE APPENDAGES

The nomenclature applied by Schmidt (1915) to the appendicular musculature of *Astacus* has been adhered to as closely as possible and, to abridge the descriptions and obviate unnecessary repetition of the function of homologous muscles, a brief explanation of Schmidt's usage of the terms may be given. Berkeley's (1928) account of the myology of *Pandalus* has also been based on Schmidt's investigations, while Cochran (1935) has compared her findings in *Callinectes sapidus* with those of Schmidt and Berkeley. Reference to the observations of these authors is therefore implied in comparisons made between *J. lalandii* and any of these three decapods.

In the second and third maxillipeds and in the five pairs of pereiopods the action of the segments of the protopodite and the endopodite is to some extent governed by articulating joints (fig. 16) and, as a rule, each segment moves about an axis perpendicular to that of the segment proximal to it. The disposition of the muscles effecting these movements is thus fairly uniform in most of the thoracic appendages, and the terminology is descriptive of their function.

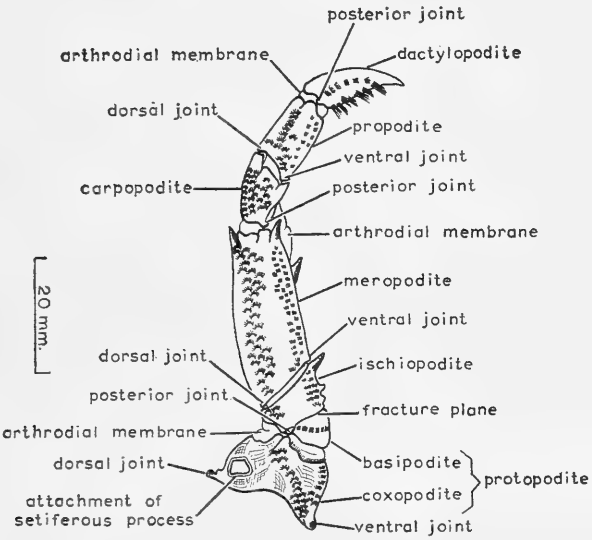


Fig. 16. Right first pereiopod of small female, posterior (caudal) view.

The main muscles which move the protopodite of any appendage are usually attached to parts of the endophragmal skeleton, particularly to the endopleurites and the endosternites, and they occupy the upper or pleural and the lower or sternal muscle chambers (figs 2, 7). Whereas the terms *promotor* and *remotor* are assigned to the muscles which respectively rotate the coxopodite forward and backward about an axis almost perpendicular to the sagittal plane, the names *levator* and *depressor* are reserved for the muscles which raise and lower the basipodite in a dorso-ventral plane. Similar movements are apparent in the segments of the endopodite but, to distinguish their muscles from those of the two segments of the protopodite, a different set of terms has been devised. Thus, the muscles which are analogous to the promotors and the remotors are respectively called the *productors* and the *reductors*, while those which correspond to the levators and the depressors are termed the *abductors* and the *adductors*. Brief mention must also be made of the terms used in connexion with the attachments and insertions of the muscles described in the following account. As most of the appendages are somewhat flattened against the ventral surface of the body, their upper and lower surfaces are obviously dorsal and ventral. The coxopodites of the pereiopods are, however, set at an angle to the horizontal axis of the body, and the limbs tend to be poised more obliquely outward, especially when they are supporting the body during ambulation; as is customary, the anterior and posterior surfaces of the segments are called rostral and caudal respectively.

The appendicular muscles were dissected in sequence from the anterior to the posterior end of the specimen and, while the mouth-parts and the pereiopods are most easily examined from the dorsal or the frontal aspect after removal of the thoracic trunk musculature, the pleopods are more directly approached from the ventral surface. The individual muscle attachments and insertions were carefully ascertained and each appendage, with its related exoskeletal and endoskeletal elements, was removed upon completion of the observations of its muscles. The conclusions have been diagrammatically represented in the accompanying figures, but in some of the larger appendages the full extent of the massive proximal muscles has not been indicated, and the joints and the arthrodial membranes have been omitted.

(a) *The antennule* (Fig. 17)

The basal segment of this slender, active appendage has no external articulations with the head, but is attached by an extensive arthrodial membrane and is capable of rotation in various directions. There is, however, a strong internal process from the dorsal base of the first peduncular segment. This articulates with a lateral projection of the medial partition between the two antennulary sockets, and has been termed a hinge (fig. 60). The three peduncular segments are interconnected by relatively wide membranes and the second and third segments are almost as mobile as the first; the second segment has a slight dorsal joint and can be moved outward at an acute angle on the first segment, while the third segment has small lateral and medial joints and bends sharply upward and downward on the second segment. The muscles operating the segments cannot be homologized easily with those of a typical stenopodium, but the fact that there is a duplication of antagonistic muscles associated with the proximal segment seems to suggest that this segment may represent a fusion of the coxopodite and basipodite of a generalized appendage.

Promotor

This strong muscle arises on the dorsal wall of the head below the pedate process and is inserted dorsally by a long flat tendon on the proximal margin of the first segment of the peduncle above its dorsal hinge. By its contraction the antennule is raised in the sagittal plane.

Remotors (a, b)

Two muscles, which are unrepresented in *Astacus* and *Pandalus* but seem to be present in *Callinectes sapidus*, are considered to be antagonistic to the promotor muscle and, like the remotor muscles of other appendages, have their origin in the body.

At its attachment on the lateral ridge of the antennulary socket, *remotor a* is wide, but it narrows appreciably towards its lateral insertion by a broad tendon on the proximal margin of the first segment.

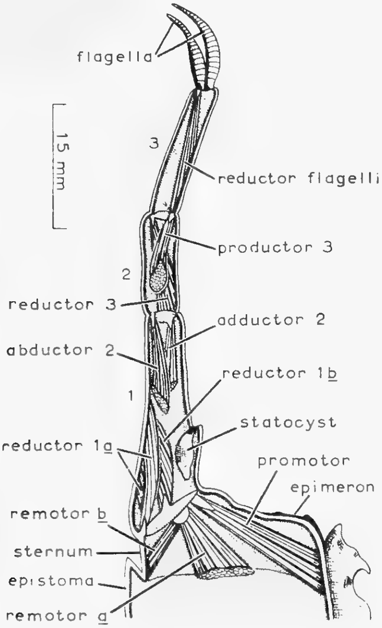


Fig. 17. Muscles of left antennule, lateral view.

Remotor b is much shorter but, nevertheless, is fairly broad and strong. It arises ventrally at the junction of the antennulary sternum and the epistoma, and passes slightly obliquely upward and forward to be inserted laterally on the first segment adjacent to remotor *a*.

Reductor 1 (*a*, *b*)

An adductor and two abductor muscles have been observed by Berkeley (1928) in the first antennulary segment of *Pandalus*, but they do not seem to be homologous to two muscles that occur in *Jasus*. The latter bear a closer resemblance to the two muscles described as remotors in *Astacus* and *Pandalus* and are similarly disposed in the first segment. As their action is probably antagonistic to that of the promotor muscle, they are complementary to the remotor muscles in lowering the appendage.

Reductor 1 *a* is attached latero-ventrally by a strong, blunt tendon on the proximal edge of the first segment. Its fibres are unequal in length and are inserted along the ventro-lateral wall of the proximal half of the first segment.

Lying below the level of the statocyst, the comparatively shorter *reductor* 1 *b* originates medio-ventrally on a strong tendon on the proximal margin of the first segment. It spreads out somewhat and is inserted medio-ventrally in the middle of the segment. There is a tendency for the two reductor muscles to split into two heads at their insertion in such a way that the ventral section of each is distinct from the lateral or the medial portion, as the case may be.

Abductor 2

In *Astacus* and *Pandalus* the second antennulary segment is raised and lowered in the sagittal plane respectively by a productor and a reductor muscle, but in *Jasus* the two antagonistic muscles appear to function more in the outward and inward movements of the segment. They have therefore been labelled as the abductor and adductor muscles, and it is of interest that in *Callinectes sapidus* the second segment is operated by four muscles and seems to combine the features of *Astacus* and *Pandalus* on the one hand with those of *Jasus* on the other.

Distal to the statocyst in the first segment is the broad lateral attachment of *abductor* 2, while its insertion takes place ventro-laterally by a fairly stout tendon on the proximal margin of the second segment.

Adductor 2

The broad attachment of this somewhat smaller muscle is also in the distal half of the first segment, but on its medial wall; it is inserted medially by a short tendon on the proximal border of the second segment.

Productor 3

The third segment is raised dorsally in the sagittal plane by a rather short muscle, which arises laterally about the middle of the second segment and is inserted dorso-laterally by a short tendon on the proximal edge of the third segment.

Reductor 3

The action of the previous muscle is opposed by this somewhat longer and stronger one, which originates dorso-medially in the proximal part of the second segment. It passes obliquely across the segment and is inserted ventrally by a long flat tendon on the proximal margin of the third segment.

Reductor flagelli

Only one muscle is associated with the activity of the antennulary flagella, neither of which has any intrinsic flexor muscles. The single muscle is attached dorsally and medially in the proximal part of the third segment and is inserted ventrally by a long tendon on the proximal edge of the outer flagellum. It moves the latter outward and downward about an axis somewhat inclined to the sagittal plane, and is responsible for its constant vibration against the more inert inner flagellum.

(b) *The antenna* (Fig. 18)

As there has been a reduction in the number of segments in the antennal peduncle in all Scyllaridea, the proximal antennal muscles can hardly be likened to those of the few decapods that have previously been described. In his account of the antennal musculature of *Astacus*, Schmidt (1915) assigned certain small basal muscles to the basipodite and an ill-defined ischiopodite, and identified the three remaining segments as the meropodite, the carpopodite and the propodite, and the flagellum as the dactylopodite but, according to Balss (1940), Schmidt misconstrued the proximal components of the antennal peduncle and, consequently, his terminology is inaccurate. The disposition of the antennal muscles of *Jasus* suggests that the epistoma and the antennal coxopodite are fused and that the basal segment is twofold but, to obviate confusion, the three segments have simply been numbered and their muscles named according to their supposed functions.

The segments of the peduncle articulate with one another by strong joints which are so arranged that each segment moves in a plane different from that of the preceding member. The segments are also set slightly obliquely on one another and, when the antenna is fully extended, the arrangement of the intersegmental joints seems to differ from that of the pereiopods. It is possible, however, that the dorsal and ventral antennal joints are functionally similar to the anterior and posterior leg joints and that the medial and lateral antennal joints are comparable with the dorsal and ventral joints of the leg. The first segment, which has wide arthrodial membranes at its base, articulates dorso-medially with the frontal tubercle of the head and ventro-laterally at the junction of the epistoma with the head exoskeleton and is raised and lowered slightly obliquely in the sagittal plane. Between the first and second segments there are also fairly wide membranes and the joints are dorso-lateral and ventro-medial in position; the second segment moves easily, being tilted inward and upward on the one hand and outward and downward on the other. The third segment has dorsal and ventral joints and pivots freely inward and forward and outward and backward. The joints of the flagellum are almost medial and lateral in position, and the movements tend to be obliquely upward and backward and downward and forward, but the inclination of the segments and differences in the planes of their articulations with one another also affect the orientation of the flagellum. On the whole, however, the dorso-ventral movements of the antenna are more vigorous than its lateral ones.

The main muscles operating the antenna as a whole are associated with the basal segment, but the muscles of the other segments are equally powerful and are characterized by long supporting tendons.

Promotor

Being superficial, this is a conspicuous element, but it also happens to be flatter than most of the antennal muscles. It is attached by a wide surface dorsally on the wall of the head (fig. 8) immediately in front of the cervical groove, and passes forward as a broad band along the side of the fore-gut medial to the mandibular minor abductor muscle and above the antennal gland. It is inserted dorsally by a long, flat, strong tendon on the proximal margin of segment 1 and, as it serves as the principal muscle for raising the

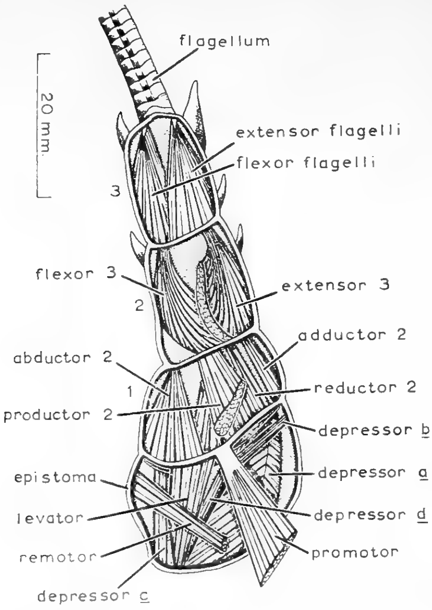


FIG. 18. Muscles of left antenna, dorsal view.

appendage, it is comparable to the antennal promotor muscle of *Astacus* and *Pandalus*.

Remotor

In *Astacus* and *Pandalus* the remotor muscle is at least subequal to the promotor, but what appears to be the corresponding muscle in *Jasus* is a narrow slip that hardly seems capable of participating in movements of the antenna. It originates laterally on the head wall between the attachments of the two lateral adductors of the mandible and, passing downward and outward across the main lobe of the labyrinth of the antennal gland (fig. 38), it spreads out a little as it inserts laterally on the rim of the epistoma slightly antero-lateral to the level of the excretory aperture. It thus extends between two immovable skeletal parts and its function is obscure; perhaps it acts as a support for the labyrinth and part of the bladder, or it may in some way be concerned in regulating the elimination of urine from the ureter.

Levator

Arising by strong tendinous material on the outer face of the lateral apodeme of the epistoma anterior to the ventral cephalic muscle, this substantial muscle runs upward and is inserted by a broad surface dorso-laterally on the proximal border of the first segment.

Depressors (*a*, *b*, *c*, *d*)

There are four muscles which oppose the promotor and levator muscles by lowering and rotating the antenna. Four antennal depressors have also been described by Schmidt (1915) in *Astacus* while, according to Berkeley (1928), three occur in *Pandalus*. It is uncertain if these are homologous to the muscles of *Jasus*, but it seems probable that depressors *a* and *b* of *Astacus* and *Jasus* are essentially similar and that the other two may be subject to specific differences.

Depressor a consists of two large heads, each with slanting fibres. The outer head arises on the inner face of the lateral apodeme and the inner head on the outer border of the medial apodeme of the epistoma, and they pass respectively to the lateral and medial faces of a large, flat, vertical tendon located medio-ventrally on the proximal margin of the first segment.

Contrasted with the other antennal muscles, *depressor b* is a short, rather inconspicuous element lying near the postero-medial corner of the first segment. It is attached close to the medial edge of the tendon of the promotor muscle and slopes forward to its insertion by a fairly long and strong tendon below the dorso-medial joint of the first segment.

Depressor c is a thick bundle arising anteriorly on the lateral apodeme of the epistoma. Running forward below the levator muscle, it is inserted ventrally by a flat tendon on the proximal border of the first segment.

Largely concealed dorsally by depressor *a*, *depressor d* is attached to the anterior edge of the lateral apodeme of the epistoma medial to depressor *c*, and is inserted close to depressor *a* by a short tendon.

Productor 2

The second antennal segment is operated by four muscles, the presence of which is suggestive of its compound nature and reminiscent of the musculature described by Schmidt (1915) in the basal parts of the antennal peduncle of *Astacus*. Like the first segment, it is set obliquely, and the movements promoted by its muscles involve production and abduction on the one hand, as against reduction and adduction on the other hand.

Productor 2 is a broad muscle arising dorsally on the proximal margin of the first segment and, after narrowing somewhat, it is inserted dorsally on the proximal edge of the second segment, on which it exerts an upward pull.

Reductor 2

This, the stronger of the two medial muscles, is attached dorsally and ventrally on the proximal margin of the first segment and is inserted medio-dorsally by a long, flat tendon on the proximal border of the second segment. Its ventral fibres pass obliquely upward from their attachment and are mainly responsible for the downward movement of the segment.

Abductor 2

Somewhat larger than the productor of the second segment, this muscle has its origin both dorso-laterally and ventro-laterally in the proximal part of the first segment, its ventral fibres being particularly strong and slanted. It is inserted ventro-laterally by a long, angled tendon on the proximal margin of the second segment and pulls the latter outward.

Adductor 2

Arising medially on the proximal border of the first segment and inserted medially on the proximal edge of the second segment, this relatively smaller muscle supplements reductor 2 and draws the second segment inward towards the mid-line.

Flexor 3

The third segment is moved outward by this thick muscle which occupies the outer half of the second segment and is comparable to the flexor of the antennal propodite in Schmidt's (1915) account of *Astacus*. Its dorso-lateral, lateral and ventral attachment covers a large area, but the muscle narrows as it passes distally to insert ventro-laterally by a strong, somewhat folded tendon on the proximal edge of the third segment.

Extensor 3

Like its antagonist, this larger and more powerful muscle has a wide attachment, but arises dorsally and medially in the proximal part of the second segment. It is inserted medially on the proximal margin of the third segment by a long, flat tendon with a raised median spine.

Flexor flagelli

Corresponding to the flexor of the dactylopodite of *Astacus*, this muscle moves the flagellum outward and backward relative to the third segment. Its fibres are unequal in length and originate dorso-laterally and ventro-laterally in the third segment. They all converge on a long, flat, vertical tendon located laterally on the proximal edge of the flagellum.

Extensor flagelli

The fibres of this muscle also have a somewhat pinnate appearance, but spring from the medio-dorsal and medio-ventral walls of the third segment. They are inserted medially by a long, narrow, vertical tendon on the proximal margin of the flagellum and oppose the action of the flagellar flexor muscle.

(c) *The mandible* (Fig. 19)

Because the heavy calcified body of the mandible articulates postero-laterally by a condyle with the mandibular epimeron and is also attached anteriorly to the supralabral ridge, its axis of movement is obliquely transverse and it is practically incapable of true rotation. Its muscles are all extrinsic and, like the proximal muscles of other appendages, arise either on the exoskeleton or on the endoskeleton. They have been likened by Snodgrass (1938, 1950) to the promotors and the remotors of a typical arthropod leg but, as they produce movements towards and away from the mid-line in decapod Crustacea, they serve essentially as adductors and abductors. Snodgrass (1950) concluded, however, that the variation in the number and functional adaptation of the mandibular muscles in different groups of Arthropoda did not warrant the introduction of a functional terminology, but recognized the prevalence of three primary groups of muscles, namely, an antero-dorsal (*A*), a postero-dorsal (*P*), and a ventral group (*V*), in each of which there may be one or more muscles. Nevertheless, these are comparable to the mandibular muscles of *Jasus*, for which Schmidt's (1915) nomenclature has been followed and, with the abbreviations used by Snodgrass in brackets, the homologies may be summarized thus: lateral adductors (1*A*, 2*A*); minor abductor (3*A*); anterior adductor (1*V*); major abductor (2*V*); and posterior adductor (*P*).

In a comparative study of the jaw mechanisms of representatives of all the major groups of arthropods, Manton (1964) has indicated that many of the earlier conclusions relating to the basic structure and function of the arthropod mandible are inaccurate. She has recognized two structural types of mandibles, Types A and B, and two types of mandibular movements, Types I and II. The mandibles of *J. lalandii* clearly belong to structural type A, in which the body of the mandible represents a modified gnathobase and the basal part of the coxopodite. Furthermore, owing to their strong gripping action in the transverse plane they are examples of type II, in which the movement is described by Manton as a direct or primary abductor–adductor one. Type II movement found in the more advanced Crustacea is, however, considered to be a modification of the rolling type I movement which is characteristic of the grinding mandibles of the Branchiopoda and the more primitive Malacostraca, and the antagonistic muscles producing the type II movement are remotors (adductors) and promotors (abductors). Thus, the muscles described in *J. lalandii* as antero-lateral, postero-lateral, and posterior adductors are respectively remotor (adductor) muscle 1, remotor (adductor) muscle 2, and remotor (adductor) muscle 4 in Manton's account of *Astacus* and *Carcinus*, while the minor and major abductors in *J. lalandii* are the promotor (abductor) muscle 3 and the promotor (abductor) muscle 6 of the crayfish and the crab; the remaining muscle, the anterior adductor of *J. lalandii*, is comparable with the transverse muscle 5 *a*, which is attached to the head endoskeleton in the crayfish and is small in the crab.

Posterior adductor

This is the strongest and most conspicuous muscle of the mandible and is its main adductor. It consists of two bundles of fibres which originate one behind the other postero-laterally on the wall of the head anterior to the cervical groove. The two bundles meet on a long, slender posterior apodeme which extends downward at the side of the fore-gut and is articulated with the posterior rim of the body of the mandible.

Anterior adductor

Attached to and supported by the transverse mandibular tendon which juts antero-laterally below the cephalic apodeme, this broad muscle spreads

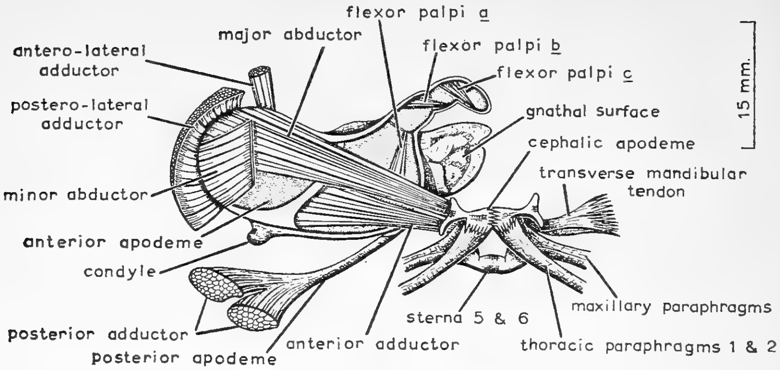


FIG. 19. Muscles of left mandible, dorsal view. The major abductor and the anterior adductor muscles have been inordinately lengthened to indicate their attachments respectively on and below the cephalic apodeme.

out and is inserted on the inner face of the posterior part of the body of the mandible, practically filling this region, while the rest of the mandibular concavity is occupied by digestive gland. It is complementary to the posterior adductor and approximates the gnathal surface of the mandible to that of its fellow.

Lateral adductors

Two of these muscles occur dorso-laterally on the anterior apodeme of the mandible. The *postero-lateral adductor* is the more important of the two and consists of numerous short, closely-packed fibres which have a widespread origin on the antero-lateral part of the hepatic region of the wall of the head and are inserted over the outer convex surface of the anterior apodeme. The *antero-lateral adductor* is short and flat and quite distinct from the postero-lateral adductor, arising on the head wall antero-dorsal to it and being inserted on the rim of the anterior apodeme close to the insertion of the major abductor muscle. These two muscles assist the anterior adductor by tilting the anterior part of the mandible towards the mid-line, and Snodgrass (1950) and Manton (1964) have indicated that the strong gripping action of the decapod mandibles is largely dependent on the development of the anterior apodeme which provides leverage for the adductor muscles.

Abductors

The action of the adductor muscles is opposed by two distinct muscles which are conformable with the major and minor abductors in *Astacus*. Arising on the blunt antero-lateral extremity of the cephalic apodeme antero-dorsal to the attachment of the anterior adductor, the broad *major abductor* passes forward and outward to insert antero-laterally on the inside of the anterior apodeme. In front of the cervical groove there is a row of short, flat muscle fibres, which originate on the dorso-lateral gastric ridge of the head exoskeleton and extend laterally to the upper rim of the anterior apodeme medial to the postero-lateral adductor muscle. They are probably equivalent to the *minor abductor* of *Astacus* which, however, tapers towards its insertion by a short tendon on the outside of the mandible.

Flexores palpi (*a*, *b*, *c*)

The three-segmented mandibular palp is joined to the body of the mandible by a pliable arthrodial membrane and is moved actively in front of the mouth by one extrinsic and two intrinsic flexor muscles. As in *Astacus*, the palp has no extensor muscles, but Schmidt (1915) has suggested that the elasticity of the arthrodial membrane probably provides the necessary opposing force.

Flexor palpi a is relatively strong and originates medio-ventrally on the posterior inner face of the body of the mandible beneath the medial part of the anterior adductor muscle. It tapers towards its insertion by a short tendon on the medial proximal edge of the first segment of the palp. The last segment of the palp of *Astacus* is furnished with a flexor muscle, but in *Jasus* there are two such muscles, *flexores palpi b* and *c* which bend the two distal palpal segments. Each arises in one segment and is inserted medio-ventrally in the proximal part of the next segment.

(d) *The first maxilla* (Fig. 20)

As it plays an important part in the manipulation of the food, this small flat appendage has well-developed muscles, most of which are thick and cylindrical and cause strong rotation of the appendage on its slack arthrodial membrane.

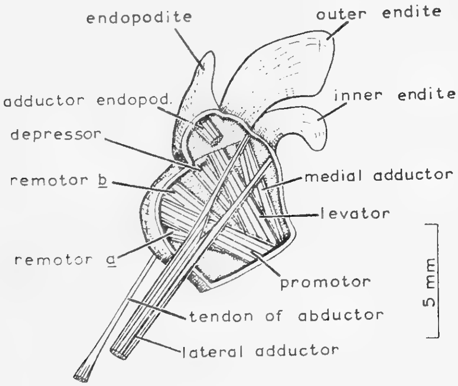


Fig. 20. Muscles of left first maxilla, dorsal view.

Promotor

This is a fairly stout muscle attached by a small tendon laterally on the anterior fascia below the fused paraphragms of the fifth and sixth cephalic segments and close to the sternal region. It passes somewhat obliquely outward across the base of the appendage and is inserted dorso-laterally in the coxopodite. It raises the appendage and rotates it forward about an axis slightly inclined to the sagittal plane.

Remotor (a, b)

As in *Astacus* and *Pandalus*, remotion of the appendage is effected by adjacent dorsal and ventral muscles, which are ventral to the promotor and are inserted laterally in the proximal part of the coxopodite. The dorsal remotor, *remotor a*, arises close to the promotor and also has a short pointed tendon, while the somewhat larger ventral muscle, *remotor b*, originates without tendinous material below both the dorsal remotor and the promotor.

Levator

Attached to the anterior fascia by tendinous tissue medial and ventral to the promotor and inserted dorsally by a very short, broad tendon on the proximal margin of the basipodite, this muscle raises the larger outer endite and also moves it inward about an axis slightly inclined to the sagittal plane.

Depressor

Counteracting the levator muscle and running ventrally parallel to it, this rather stronger unit has its origin ventrally on the anterior fascia and is inserted ventrally on the proximal border of the basipodite.

Abductor

To compensate for its rather remote origin on the wall of the head dorsal to the lateral adductors of the mandible, this small, conical muscle has a very long, slender tendon which passes downward between the mandible and the first maxilla and inserts laterally on the proximal edge of the coxopodite. Its function is to pull the appendage away from the mouth. The presence of an abductor tendon seems to be characteristic of *Jasus*, for one similar to that of *J. lalandii* has also been reported in the first maxilla of *J. edwardsii* by Parker & Rich (1893).

Adductors

Two adductors, a lateral and a medial, oppose the abductor muscle and approximate the endites to the mouth.

The *lateral adductor* is the stronger of the two and is attached to the wall of the head near, but slightly postero-dorsal to, the origin of the abductor muscle. It runs for some distance parallel to the tendon of the latter muscle, but enters and traverses the coxopodite dorsally. As it travels medially, it splits into two tendons, the posterior and stronger of which is inserted medially at the base of the inner endite, while the anterior tendon passes to the base of the outer endite. Apparently this muscle is slightly variable in different species. In *Astacus* it arises by a long thin tendon and is inserted medio-dorsally in the coxopodite, and the abductor muscle has no tendinous material. Two slender muscles, called the m. adductor anterior and the m. adductor posterior coxopoditis I maxillae by Cochran (1935), occur in *Callinectes* and are suggestive of the separate insertions of the lateral adductor of *Jasus*.

Closely applied to the posterior border of the lateral adductor, there is another bundle which, at first sight, seems to belong to the first maxilla. Its long, slender tendon, however, extends across the maxillary muscles and is inserted at the lateral base of the paragnath, of which it is probably an adductor.

The short, rather broad *medial adductor* arises on the anterior fascia near the fused cephalic sterna. It runs below and parallel to the levator muscle and is inserted medially at the junction of the inner and outer endites.

Adductor endopoditis

Only one comparatively strong and almost cylindrical muscle operates the endopodite and moves it towards the mid-line. It originates close to the base of the outer endite and is inserted laterally in the proximal part of the endopodite.

(e) *The second maxilla* (Fig. 21)

This much flattened appendage is largely thin-walled and the boundaries of the coxopodite and basipodite are rather indistinct. The scaphognathite, however, has a conspicuous, swollen, dorso-laterally sclerotized base, on which it swings dorso-ventrally with a slight rotary action. The proximal muscles almost fill the space between the fused paraphragms of the last two cephalic segments and those of the first two thoracic segments, and the majority constitute the so-called *respiratory muscles* which are generally considered to be the chief agents controlling the movements of the scaphognathite.

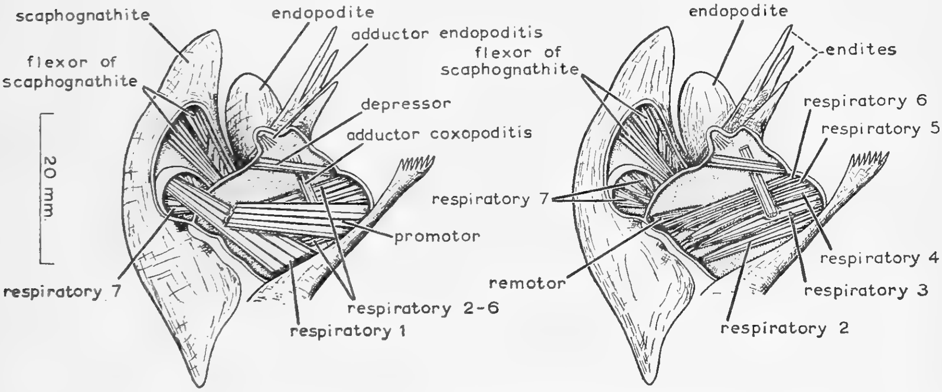


FIG. 21. Muscles of left second maxilla, dorsal views; the promotor and respiratory muscle 1 have been removed in the diagram on the right.

Promotor

This thick strong muscle arises below the cephalic apodeme and passes somewhat obliquely outward above the respiratory muscles. It is inserted dorso-laterally on the proximal border of the coxopodite close to the posterior skeletal swelling of the scaphognathite. It raises the coxopodite and also the posterior half of the scaphognathite, so that in some respects it functions as a respiratory muscle.

Remotor

A fairly strong remotor muscle has been reported in the second maxilla of other decapods, but was not observed in all specimens of *J. lalandii.* It springs medio-ventrally from the sternal region below the cephalic apodeme and runs to the ventro-lateral margin of the coxopodite. It underlies the respiratory muscles, and is not so markedly separated from them as is the promotor muscle.

Adductor coxopoditis

Attached ventro-medially below the fused cephalic paraphragms, which are omitted in figure 21, this narrow, straight, but fairly strong element passes dorsally over the respiratory muscles. It has a ventral insertion on the proximal border of the coxopodite, and pulls the latter inward and backward.

Depressor

In *Astacus* and *Callinectes* the depressor muscle has two heads, but in *Pandalus* and *J. lalandii* it is a single, fairly broad muscle which arises medially in the sternal region. It proceeds outward and forward through the coxopodite and is inserted mid-dorsally on the proximal margin of the basipodite. It causes an inward and downward movement of the basipodite, and, as in other decapods, it has no antagonistic levator muscle.

Adductor endopoditis

This muscle is inconspicuous in most specimens and consists of only a few very short fibres which are attached dorso-medially in the basipodite and are inserted ventrally in the proximal part of the endopodite. It has no antagonistic muscle, but this also applies to *Astacus*, *Pandalus*, and *Callinectes*, and Schmidt (1915) has suggested that its action is opposed by the resiliency of the flexible arthrodial membrane. Nevertheless, the endopodite of the second maxilla of *Jasus* seems to have little independent movement, and may be influenced by the contraction of the depressor muscle.

Flexor muscle of scaphognathite

The anterior half of the scaphognathite contains a relatively strong muscle which is partly responsible for the sinuous movements of this part of the appendage. Its two bundles, which may be analogous to the superior and inferior flexor muscles of the scaphognathite of *Pandalus*, originate at the junction of the protopodite and the scaphognathite and, on passing into the latter, some of the anterior fibres become slightly twisted.

Respiratory muscles

In common with other decapods, there is a complex set of seven muscles, most of which are inserted in the swollen base of the scaphognathite. Together with the flexor muscle, they are thought to bring about the undulatory movements of the scaphognathite whereby the respiratory current of water is swept out of the prebranchial chamber.

It is doubtful if they are all identical with those that have been described in *Astacus*, *Pandalus*, and *Callinectes*, but the broad *first respiratory muscle* is essentially similar in all four species. In *Jasus* it arises laterally on the fused thoracic paraphragms and extends forward and outward beneath the lateral part of the promotor muscle. It has a dorsal and somewhat distal insertion in the base of the scaphognathite, and appears to be one of the main muscles for raising the scaphognathite.

The *second* to the *sixth respiratory muscles* are so compressed that, upon cursory examination, they appear as two transverse bands lying below the promotor muscle in the angle formed by the last cephalic and the first thoracic paraphragms. Arising in a row on the anterior fascia, they run outward parallel to one another, and laterally they lie ventral to the first respiratory muscle. They are fairly easily separated, however, and the third, fourth, and fifth of the series are distinguished by distinct tendons at their insertions on different levels of the basal swelling of the scaphognathite. Of this group, the second and the third are the most conspicuous, while the fifth is a narrow slip, partially obscured dorsally by the sixth muscle.

The *seventh respiratory muscle*, like that of *Pandalus*, is short, broad, and practically confined to the scaphognathite. It is covered dorsally by the insertion of the first repiratory muscle and consists of three small wedge-shaped bundles which are attached to the distal margin of the coxopodite and spread out as they insert ventrally and distally in the scaphognathite posterior to the flexor muscle.

(f) *The first maxilliped* (Fig. 22)

The muscles of this appendage are hardly consistent with those of the other two maxillipeds and present a closer resemblance to the arrangement in the maxillae because, apart from the more or less cylindrical and freely movable exopodite, the parts are markedly flattened. Endites 1 and 2 are medial lobes of the protopodite, probably respectively representing expansions of the coxopodite and the basipodite. The endopodite, which is also flattened and joined medially to endite 2, has little independent movement; in fact, some of the muscles seem capable of moving the appendage as a whole rather than its individual parts, and none of them has supporting tendons. They are broadly similar to those of the first maxillipeds of *Astacus* and *Pandalus*, but the arrangement appears to vary with the species and the homologies of some of the muscles are uncertain. Several muscles, which are unrepresented in other forms, occur in *Callinectes*; Cochran (1935) has numbered these and made tentative suggestions as to the resemblances between some of them and the muscles of *Astacus*.

Promotor medialis

This broad muscle is attached medially on the endosternite and not on the fused thoracic paraphragms as in *Astacus* and *Pandalus*. It is inserted dorsally on the proximal margin of the coxopodite and, while it moves the latter forward

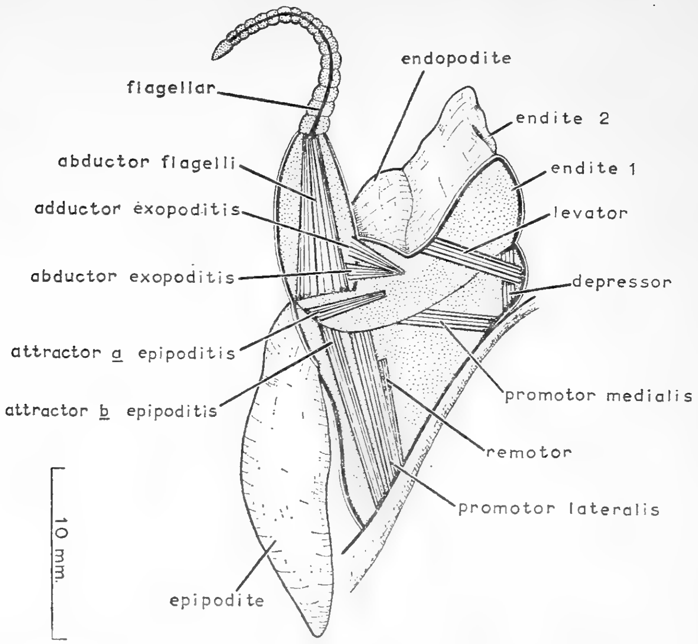


FIG. 22. Muscles of left first maxilliped, dorsal view.

or upward, to some extent it may also be adducent in function. It is directed more laterally than the medial promotor of *Astacus*, and in some respects resembles the levator muscle described by Schmidt (1915).

Promotor lateralis

Originating laterally on the fused paraphragms of the first two thoracic segments, this rather longer and narrower muscle is inserted dorso-laterally on the proximal edge of the coxopodite. It doubtless assists the previous muscle in raising the appendage, but may also be slightly antagonistic to it by causing an outward movement.

Remotor

Jasus resembles *Pandalus* and differs from *Astacus* in having a remotor muscle, which arises below the lateral promotor on the fused thoracic paraphragms. It has a ventro-lateral insertion on the proximal border of the coxopodite and, although weaker than either of the promotor muscles, it is capable of opposing their action by lowering the appendage.

Attractores epipoditis (*a*, *b*)

As in *Pandalus*, elevation of the epipodite is effected by two muscles. ***Attractor epipoditis a*** is a conical element arising ventrally in the coxopodite and passing outward to insert near the shoulder of the epipodite. Unlike *Pandalus*, however, this muscle is not repeated in other thoracic segments, although the epipodite is joined to the setiferous process of the coxopodite by a flexible membrane. In both the adult and the puerulus stage blood channels and strands of fibrous tissue, but no recognizable muscle fibres, occur at the base of the epipodite, and any necessary changes in its position will probably be produced by movements of the limb.

The much stronger *attractor epipoditis b* is attached laterally to the fused thoracic paraphragms close to the lateral promotor, to which it runs parallel and inserts at the junction of the epipodite with the coxopodite. Schmidt (1915) suggested that in *Astacus* this muscle might have replaced the non-existent remotor muscle but, as Berkeley (1928) has indicated, this opinion is nullified by the presence of attractors of the epipodite, as well as a remotor, in the first maxilliped of other species.

Levator

From a medial attachment on the endosternite near the base of endite 1, this conspicuous muscle extends outward through the coxopodite to the proximal border of the basipodite and is concerned with the outward movement of the appendage.

Depressor

Opposing the action of the levator muscle and attached medio-ventrally below it, this short muscle is directed forward to its medio-ventral insertion on the proximal margin of endite 1. In *Astacus* and *Pandalus* it has a more normal insertion at the proximal edge of the basipodite, but the position of muscle number 75 in *Callinectes* is somewhat similar to that of the depressor in *Jasus*, and was considered by Cochran (1935) to be reminiscent of the depressor of *Astacus* and *Pandalus*.

According to Berkeley, two *adductor* muscles are associated with the endopodite of *Pandalus*, while a single muscle in *Astacus* was identified by Schmidt as a *reductor* of the endopodite. None of these is present in *Callinectes* or *Jasus*, but the muscle in *Astacus* is suggestive of attractor epipoditis *a* of *Pandalus* and *Jasus*.

Abductor exopoditis

Originating ventro-laterally in the basipodite, this relatively short entity passes into the ventral proximal region of the exopodite and causes an outward and backward movement of this part of the appendage. A similar muscle is present in *Pandalus*, but not in *Astacus* or *Callinectes*.

Adductor exopoditis

This equally short but rather thicker muscle is attached close to its antagonist and is inserted medially in the proximal part of the exopodite.

Abductor flagelli

In all three maxillipeds there is a single, fairly strong muscle which practically fills the peduncle of the exopodite and, being inserted ventrally at the proximal end of the flagellum, it functions in the outward movement of this structure. The abductor flagelli of the first maxilliped is stouter than that of the other two maxillipeds and pursues a straighter and more medial course through the peduncle, its insertion being mid-ventral, while that of the second and third maxillipeds tends to be ventro-lateral.

Flagellar muscle

In each of the three maxillipeds, the flagellum of the exopodite has an intrinsic muscle which is responsible for its active movements in various directions. It consists of thin muscle strands arising from the base and annulations of the flagellum and extending down its length to an insertion in the terminal segment.

(g) *The second maxilliped* (Fig. 23)

The second and third maxillipeds differ from the first in being pediform and in having the same number of segments in the well-developed endopodite as in the pereiopods. Because of the coalescence of the basipodite and ischiopodite, the latter is immobile and no muscles pass into it from the basipodite. Productor and reductor muscles have, however, been established in the ischiopodite for the slight forward and backward movements of the meropodite, and the arrangement of the whole system resembles that of other Decapoda.

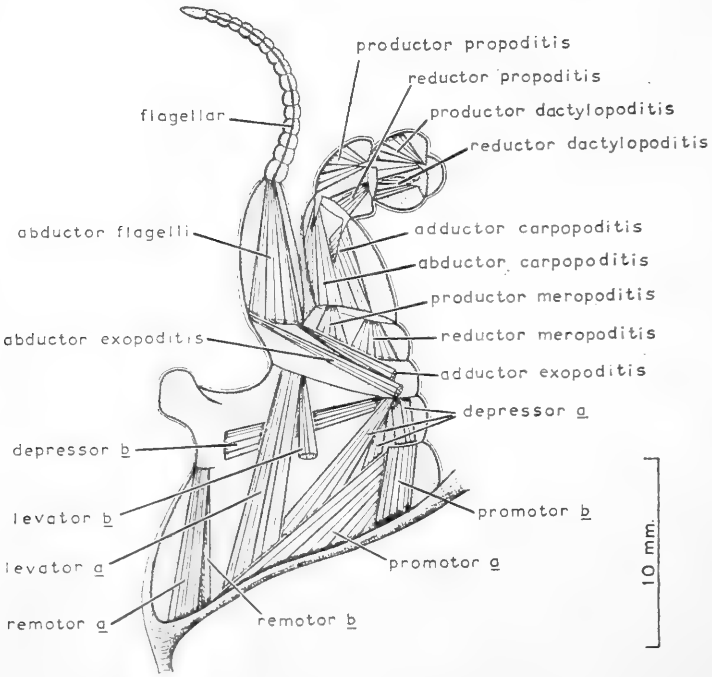


Fig. 23. Muscles of left second maxilliped, dorsal view.

Promotor

This relatively short but powerful dorsal muscle lies anteriorly in the sternal muscle chamber. It apparently consists of two partly superimposed bundles which have broad attachments on the anterior face of the paraphragm and the endopleurite between the second and third thoracic segments and may correspond to promotors *a* and *b* of the third maxillipeds and pereiopods. The insertion takes place dorso-medially by a fairly long, flat tendon on the proximal margin of the coxopodite, and contraction of the muscle directs the coxopodite forward and inward.

Remotor (*a*, *b*)

Although narrower than the promotor, this muscle is clearly divisible into two bundles which arise in the small pleural muscle chamber.

Remotor a is fairly robust and extends latero-dorsally from the endopleurite near the epimeron. It is inserted ventro-laterally on the proximal margin of the coxopodite by a fairly long tendon.

Remotor b is subequal in size to remotor *a* and is inserted with it, but passes below it from a more ventral attachment on the endopleurite.

Levator (*a*, *b*)

The two heads of this muscle have separate origins, but are inserted dorso-laterally on the proximal margin of the basipodite by a common, strong, flat tendon; together they pull the basipodite outward about a slightly inclined angle.

Levator a is fairly long, originates on the endopleurite below the lateral fibres of the promotor muscle, and runs forward parallel to the remotor muscle.

Levator b is considerably shorter, passes somewhat obliquely forward from a dorso-medial attachment on the proximal border of the coxopodite, and becomes applied to levator *a* distally.

Depressor (*a*, *b*)

Situated behind the promotor muscle in the sternal muscle chamber, this, like the two previous muscles, is also distinctly bipartite.

Depressor a is a compound of three bundles, two of which arise medially and laterally on the anterior face of the fairly large endosternite separating the second and third thoracic segments, while the third is attached medially on the proximal margin of the coxopodite. All three bundles are inserted ventro-medially by a strong tendon on the proximal edge of the basipodite.

Depressor b is a smaller, single bundle that originates laterally in the coxopodite. It passes inward beneath the levator muscles and becomes fixed to the side of the tendon of depressor *a*. The two depressors are antagonistic to the levator muscle and produce a downward and inward movement of the basipodite.

Productor meropoditis

The relatively long meropodite is moved forward by this rather small muscle, which is attached laterally in the ischiopodite and is inserted dorso-laterally on the proximal margin of the meropodite by a short tendon.

Reductor meropoditis

This is proportionally broader and stronger than its antagonist, the productor muscle of the meropodite. It arises dorso-medially in the ischiopodite and narrows somewhat at its insertion by a short ventro-medial tendon on the proximal edge of the meropodite.

Abductor carpopoditis

While the action of the meropodite is decidedly limited, the carpopodite is freely movable and its two antagonistic muscles occupy a large part of the meropodite.

The *abductor* muscle originates dorso-laterally in the proximal part of the meropodite and is inserted laterally by a fairly long tendon on the proximal border of the carpopodite.

Adductor carpopoditis

Attached ventro-laterally in the proximal part of the meropodite, this equally strong, but flatter, muscle is inserted medially on the proximal edge of the carpopodite by a strong tendon running down the length of its fibres.

Productor propoditis

From a wide area of attachment dorso- and ventro-laterally on the wall of the carpopodite, this muscle narrows considerably towards its dorso-lateral insertion by a broad, flat tendon on the proximal margin of the propodite; it moves the latter forward.

Reductor propoditis

This rather smaller muscle occupies the medial half of the carpopodite, along the ventro-medial wall of which it is attached. It is inserted ventro-medially on the proximal border of the propodite by a narrow tendon.

Productor dactylopoditis

The terminal segment is pulled forward by this muscle which springs from the dorso-lateral wall of the propodite and is inserted dorso-laterally by a relatively long, flat tendon on the proximal margin of the dactylopodite.

Reductor dactylopoditis

This antagonist of the preceding muscle is slightly weaker, arises ventro-medially in the propodite, and is inserted almost mid-ventrally on the proximal edge of the dactylopodite by a relatively strong tendon.

Abductor exopoditis

The only muscles located in the basipodite are the two for moving the exopodite, the rest of this segment being filled with connective tissue and blood. The *abductor* muscle of the exopodite is attached medially in the basipodite and finds its insertion by a relatively long, flat tendon on the proximal lateral border of the exopodite.

Adductor exopoditis

Lying close to the former muscle, this weaker one arises more ventrally in the basipodite and, passing obliquely outward, is inserted by a short tendon medially on the proximal margin of the exopodite. There is no corresponding muscle in *Astacus* or *Callinectes*, but the latter has an attractor muscle for the epipodite.

The remaining muscles, namely the *abductor flagelli* and the *flagellar*, are similar to those of the first maxilliped.

(h) *The third maxilliped* (Fig. 24)

The third maxilliped is longer and more robust than the second maxilliped, and has a closer resemblance to the pereiopods in the shape of its segments. As in the second maxilliped, the carpopodite swings easily on the meropodite and it and the two more distal segments can be flexed ventrally towards the mouth and so directed that their heavily setose medial margins meet those of the other third maxilliped in the mid-line. The exopodite is shorter than that of the second maxilliped, but has similarly-arranged abductor and adductor muscles and, as there is also a general agreement in the disposition and function of the other parts of the system, brief comments only are given on some features of the main muscles.

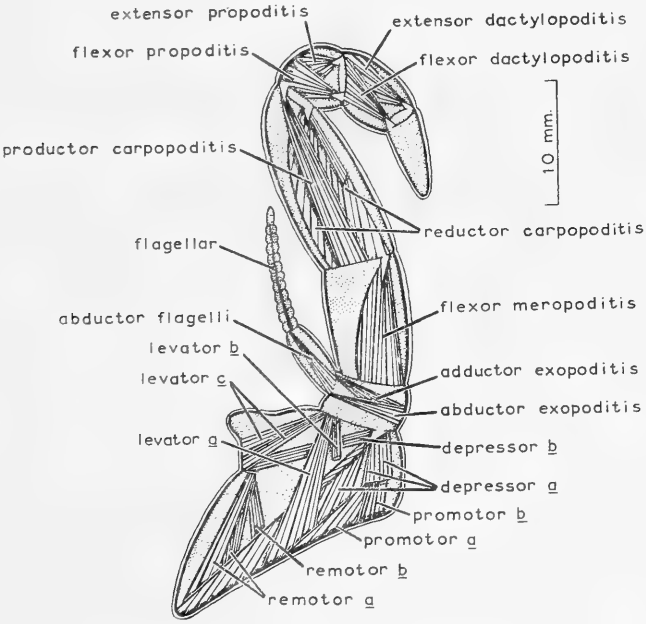


FIG. 24. Muscles of left third maxilliped, dorsal view.

Promotor (a, b, c)

As in the second maxilliped, this is a comparatively short but substantial muscle which, however, is divisible into three heads having attachments laterally on the endopleural invagination (*promotor a*), on the paraphragm between the second and third thoracic segments (*promotor b*), and on the frontal side of the mesophragm and the endosternite between the third and fourth segments (*promotor c*, fig. 27). A broad, heavy tendon inserts it medio-dorsally on the proximal border of the coxopodite.

Remotor (a, b)

At least two heads and possibly the makings of a third head may be distinguished in this muscle, which is again characteristically the most lateral of the proximal muscles.

The large lateral bundle, *remotor a*, has a curved attachment high up on the epimeron, but it also spreads on to the under surface of the shaft of the endopleurite between the third and fourth segments; it is inserted ventro-laterally on the proximal margin of the coxopodite by a long tendon which supports the muscle and extends well into the pleural muscle chamber.

The more medio-ventral *remotor b* originates on the surface of the posterior process of the endopleurite between the second and third epimera and is inserted near the tendon of remotor *a*.

Levator (a, b, c)

The main branch, *levator a*, arises behind the promotor muscle on the anterior face of the endosternite and endopleurite and is inserted dorso-laterally on the proximal edge of the basipodite by a spatulate tendon.

Levator b is essentially similar to that of the second maxilliped and is inserted by a short tendon medial to levator *a*.

Levator c consists of two superimposed parts which arise laterally and ventro-laterally in the proximal region of the coxopodite and are inserted by a short tendon adjacent to that of levator *a*.

Depressor (a, b)

Relative to the levator, this is a more powerful muscle, but its two main heads resemble those of the second maxilliped.

Depressor a consists of at least four bundles, the attachments of which spread over the proximal border of the coxopodite, the medial area of the endosternite, the endopleurite, and the epimeron. Its dorso-lateral fibres (fig. 27) overlap the remotor muscle in the pleural muscle chamber, obscuring it in a medial view, while its shorter ventro-lateral slip extends from the anterior face of the vertical plate of the endopleurite between the third and fourth segments.

Depressor b arises laterally in the proximal part of the coxopodite, a small spur-like projection of which separates it from levator *c*. It is inserted on a slight ridge of the proximal margin of the basipodite adjoining the long, sabre-like, ventro-lateral tendon of depressor *a*.

Pilgrim & Wiersma's (1963) observations on living *Procambarus* demonstrate that the promotor and not the depressor muscles, as suggested by Schmidt (1915), are mainly instrumental in bringing the medial edges of the basipodites and ischiopodites together when food is clasped between the two third maxillipeds. The remotor muscles are evidently responsible for withdrawing the appendages from the mid-line, but when they and the depressors contract simultaneously the maxillipeds are said to retain their hold on the food.

Flexor meropoditis

As in *Astacus* and *Callinectes*, there is no extensor muscle of the meropodite, and only one muscle, a relatively strong flexor, is developed for moving this segment inward and upward. Originating proximally in and occupying the medial half of the long ischiopodite, it is inserted dorso-medially by a long, strong tendon on the proximal edge of the meropodite.

Each of the three distal segments of the endopodite is provided with two antagonistic muscles, which differ slightly in function from the analogous muscles of the second maxilliped. Thus, while the *carpopodite* is moved forward and backward by a *productor* and a *reductor* muscle, the *propodite* and the *dactylopodite* are operated by *extensor* and *flexor* muscles, which respectively produce forward and outward and contrary backward and inward movements of the segments. Although there is a functional similarity between these and the corresponding six muscles of *Astacus*, some differences are evident in their attachments and insertions. In *Jasus* (fig. 24) it may be noted that the extensor muscles of the propodite and the dactylopodite originate ventro-laterally and their flexors are dorsal; the tendinous insertions of the productor of the carpopodite and the extensors of the propodite and dactylopodite are lateral, as opposed to the medial insertions of their antagonistic muscles. The reductor of the carpopodite also differs from that of *Astacus* in being composed of short dorso-medial and long ventral fibres, but this probably foreshadows the arrangement in the pereiopods.

(i) *The pereiopods*

The musculature of all five pairs of pereiopods is fairly uniform and, apart from the absence of the exopodites and their associated muscles, the main elements are almost identical with those of the third maxillipeds. Most of them are inserted and supported by strong flat tendons (fig. 25), each of which usually has a flexible attachment at some point on the proximal edge of a segment, and may run through the middle of its particular muscle, receiving fibres at intervals along its length.

(a) *First pereiopod of the male* (Fig. 26)

The muscles of the sturdy first pereiopod of the male, although somewhat shorter and broader than those of the other pereiopods, may be used to illustrate the basic arrangement in any of the walking legs.

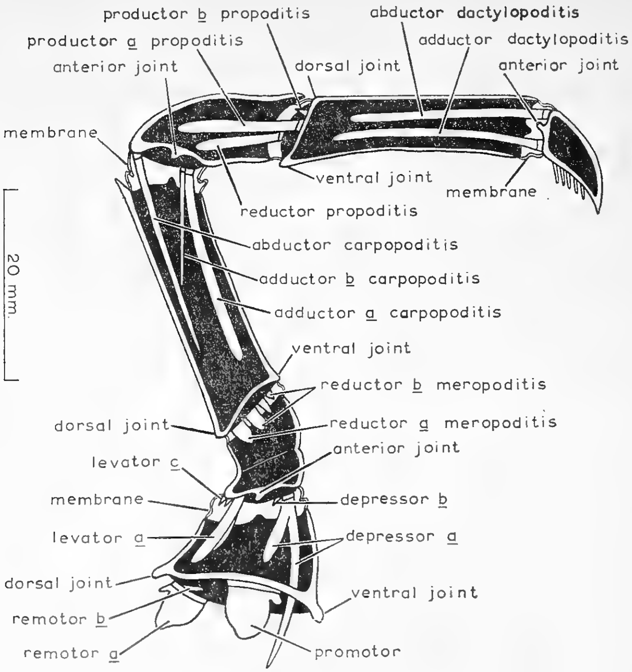


FIG. 25. Diagram of the tendons, some of the joints and intersegmental arthrodial membranes of the left fourth pereiopod of male; in each segment all but the proximal margin of the anterior (rostral) surface has been removed.

Promotor (*a*, *b*, *c*)

Located rostrally in the sternal muscle chamber, the promotor muscle is bulky and even more distinctly divisible into three heads than that of the third maxilliped.

The fairly long lateral head, *promotor a,* arises on the shaft of the endopleurite between the third and fourth epimera, and is obvious in sagittal view (fig. 27) as it passes downward over the bifurcation of the endopleurite into its anterior and posterior processes.

The rostral head, *promotor b,* is short and flat and is attached to the paraphragm between the third and fourth segments.

The caudal head, *promotor c,* is more cylindrical and passes downward from the mesophragm and the frontal face of the endosternite between the fourth and fifth segments; its attachment is visible in an inner view (fig. 27) in the region bounded by the mesophragms and the rostral and caudal paraphragms of the fourth segment. The whole muscle is inserted rostrally by a broad, flat, heavy tendon which projects from the proximal rim of the coxopodite, and contraction of the muscle pulls the leg forward.

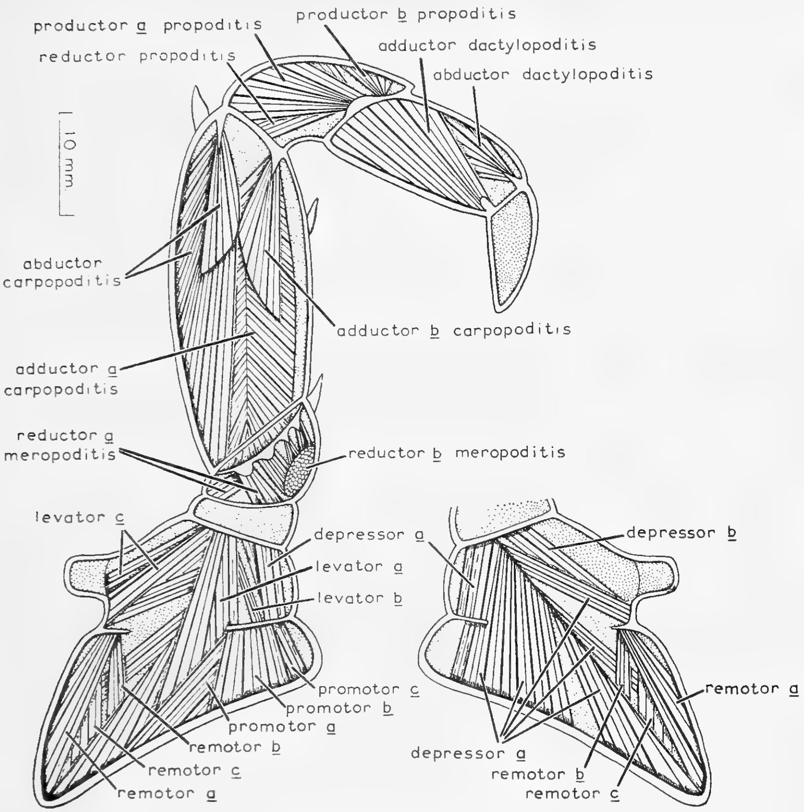


FIG. 26. Rostral views of muscles of first pereiopods of small male.

Remotor (a, b, c)

While the remotor muscle of all the pereiopods in *Pandalus* and that of the first four legs in *Callinectes* is apparently undivided, the arrangement in *Jasus* is comparable to that of *Astacus* in which Schmidt (1915) distinguished three distinct branches.

The main part of the muscle, *remotor a*, is a large leaf-shaped, almost vertical bundle, with a dorso-lateral attachment on the epimeron of the fourth segment.

Remotor b is fairly broad, but shorter than remotor *a*. It is located rostrally in the pleural muscle chamber and arises somewhat ventrally on the outer face of the vertical part of the posterior process of the endopleurite between the third and fourth epimera.

Remotor c, which occurs between the other two heads, originates on the under surface of the stem and the anterior process of the endopleurite projecting from the junction of the fourth and fifth epimera. The fibres of all three parts of the muscle are inserted caudo-laterally on the proximal border of the coxopodite, those of remotor *a* and remotor *c* on a long flat tendon and those of remotor *b* on a separate, small, adjacent tendon. In the last two pereiopods the main remotor tendon (fig. 25) is usually broad and short, while in the last pereiopod there is commonly no separate tendon for remotor *b*.

Levator (*a*, *b*, *c*)

The three divisions of this muscle are essentially similar to those of the third maxillipeds, levators *a* and *c* being conspicuous, while the much weaker levator *b* arises rostrally on the proximal edge of the coxopodite and becomes progressively more insignificant in posterior pereiopods.

The attachments of *levator a* are widely distributed on the anterior face of the endosternite between the fourth and fifth segments and on the broad vertical plate of the posterior process of the endopleurite that projects inward between the third and fourth epimera and separates this muscle from those in the pleural muscle chamber. It passes through the sternal muscle chamber caudal to the promotor muscle, and in all the pereiopods is inserted rostrolaterally on the proximal margin of the basipodite. As previously indicated, (p. 36), it is by the excessive contraction of this muscle that autotomy of the limb is effected.

Levator c is rather short and thick and, as in the third maxilliped, is divisible into two bundles originating laterally and caudo-laterally in the proximal part of the coxopodite near the root of its setiferous process. They are inserted one above the other by short, separate tendons at the side of levator *a* on the proximal edge of the basipodite. The whole levator muscle forms a powerful element for elevating the basipodite and, with it, the whole appendage.

Depressor (*a*, *b*)

As in the second and third maxillipeds, this is one of the strongest and most extensive of the extrinsic muscles of the pereiopod, but it is still fundamentally bipartite.

Its main portion, *depressor a*, occupies most of the caudal half of the sternal muscle chamber and has several subdivisions arising medially and laterally on the proximal margin of the coxopodite, and ventrally behind levator *a* on the rostral face of the endosternite between the fourth and fifth segments. In addition, it invades the pleural muscle chamber: its dorso-lateral slip is attached to the fourth epimeron and the under surface of the endopleurite stem between the fourth and fifth epimera and covers the inner surface of the remotor muscle; its ventro-lateral slip arises deep in the pleural muscle chamber on the anterior face of the vertical plate of the endopleurite between the fourth and fifth epimera and thus travels behind the remotor muscle. All its various bundles collect on a strong bifurcated tendon projecting caudo-medially from the proximal margin of the basipodite.

By comparison, *depressor b* is rather weak and short. It is attached caudolaterally in the coxopodite below levator *c*, and is inserted near the main depressor on the proximal border of the basipodite by a very small tendon.

Schmidt (1915) has indicated that in *Astacus* the depressor is the largest of the protopodite muscles and is effective in raising the body when it pulls the endopodite forcibly downward while the dactylopodite is in contact with the substratum. In this connexion, the various joints of the segments also play an important part in the complex movements of the limb during ambulation. The action of the promotor and remotor muscles rotates the extended limb forward and backward on the dorsal and ventral joints of the coxopodite. The leg is bent between the carpopodite and the meropodite but, owing to the rigidity of the latter, the fusion of the basipodite and ischiopodite, and the presence of anterior and posterior joints on the basipodite, contraction of the levator and depressor muscles also affects the limb as a whole.

Reductor (a, b) meropoditis

In both *Astacus* and *Pandalus* a reductor muscle of the ischiopodite has been reported in all the pereiopods, but it is lacking in the cheliped of the former, in which the basipodite and ischiopodite are fused. This muscle does not occur in any of the pereiopods of *Callinectes*, and is also absent in *Jasus*. In the latter the basipodite is filled with connective tissue, but a fairly complex musculature for the movement of the meropodite occupies the relatively short ischiopodite. Only reduction seems to be effected and, although the components are inserted by a row of four tendons on the caudal proximal margin of the meropodite, they may be considered to constitute two main muscles comparable to the dorsal and ventral reductors of the meropodite of *Astacus*.

Reductor a is short and broad with two subequal heads, one arising caudo-dorsally and the other caudo-ventrally in the ischiopodite. Both are inserted caudo-dorsally on the proximal edge of the meropodite by a strong, flat tendon.

The stronger *reductor b* has a conspicuous, broad attachment rostro- and caudo-ventrally, and superficially appears to form a compact muscle, but it separates into three bundles which are inserted caudally by individual tendons on the proximal margin of the meropodite. Of the three, the uppermost is the largest and the ventral one the smallest.

Abductor carpopoditis

Lying rostro-dorsally, but also having some attachments distally in the meropodite, this long, rather flat muscle is inserted dorsally by a narrow, tapering tendon on the proximal border of the carpopodite. Its function is to raise and extend the latter segment.

Adductor (a, b) carpopoditis

Relative to its antagonist, this muscle is larger and more powerful and, as in *Astacus*, is divisible into two parts, the proportions of which, however, seem to be reversed in the two species.

Adductor a is attached caudally along the length of the meropodite and fills the caudal half of the segment. Supporting it is a broad, strong, horizontal tendon from the mid-ventral proximal rim of the carpopodite.

Adductor b is much weaker and adjoins the abductor of the carpopodite in the distal half of the meropodite. It originates rostro-ventrally in the meropodite and is inserted in front of adductor *a* by a long, slender tendon.

Productor (a, b) propoditis

As in the preceding muscle, two heads may be recognized. The dense fibres of *productor a* are attached practically along the whole rostral wall of the carpopodite and are inserted rostrally about the middle of the proximal margin of the propodite by a strong, flat, vertical tendon.

Productor b is inconspicuous and hardly distinguishable from the much larger main productor of the propodite. It lies dorsally in the distal part of the carpopodite and is inserted rostrally next to the other muscle by a small tendon. Contraction of these muscles produces a forward movement of the propodite.

Reductor propoditis

Opposing the action of the productor of the propodite, this somewhat smaller and flatter muscle is attached caudally in the carpopodite and is inserted caudally on the middle of the proximal edge of the propodite by a broad, almost horizontal tendon.

Abductor dactylopoditis

The fibres of this muscle spring mainly from the dorsal wall of the propodite and insert mid-dorsally by a strong tendon on the proximal margin of the dactylopodite.

Adductor dactylopoditis

This is the stronger of the two muscles of the terminal segment and originates partly rostrally and partly caudally in the propodite. It has a very broad, flat tendon for its ventral insertion on the proximal margin of the dactylopodite. It serves to move the dactylopodite downward and inward, while the abductor muscle has the opposite effect.

(b) *Variation in attachments of muscles of posterior pereiopods*

Although the intrinsic musculature of the segments of the endopodite is consistently arranged in all the pereiopods, several modifications are apparent in the attachments of the proximal muscles of the last three pereiopods. In sagittal view (fig. 27) *promotors a* and *c* are evident dorsally in the sternal muscle chambers between the anterior and posterior paraphragms of the thoracic segments. While the former usually occurs latero-dorsally with its fibres arising near the inner anterior edge of the corresponding pleural muscle chamber, promotor *c* is located more medially and caudally in the angle between the mesophragm and the posterior paraphragm; it is also frequently divisible into three bundles which, in the third maxilliped and first three pereiopods, pass forward and downward towards their insertion. In the last pereiopod there is a slight transposition of the lateral head of the promotor muscle, its attachment being effected nearer the posterior rim of the pleural muscle chamber of the

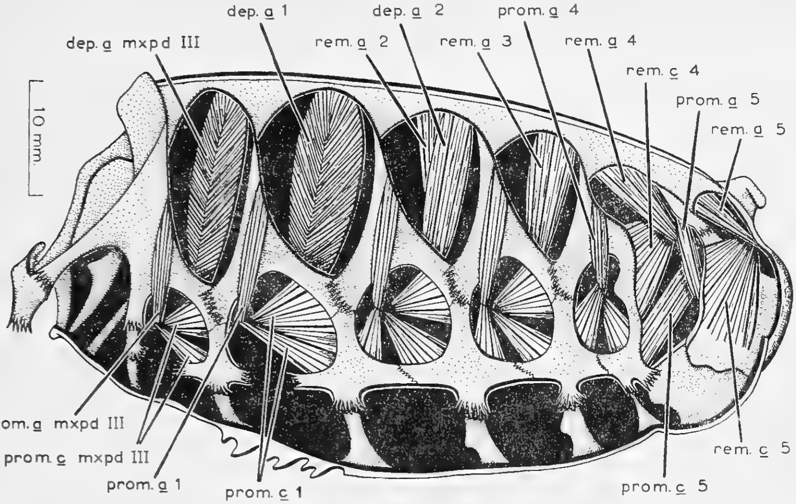


FIG. 27. Diagrammatic inner view of right half of endophragmal skeleton and proximal muscles of right third maxilliped and right pereiopods; *prom.*, promotor; *rem.*, remotor; *dep.*, depressor muscle; numbers 1 to 5 are applicable to the muscles of the five pereiopods.

fourth pereiopod than the anterior border of the last pleural muscle chamber. Promotor *c* of the last two pereiopods tends to be anterior to promotor *a* and is directed obliquely backward and outward to the respective appendages.

The origins of the three heads of the *remotor* muscle are practically identical in the first three pereiopods, but there is a gradual expansion and flattening of remotors *b* and *c* from the second to the last pereiopod. Consequently, the large remotor *c* of the fourth pereiopod arises partly on the caudal face of the paraphragm and the endosternite between the seventh and the eighth segments and is visible in a median view (fig. 27) in front of remotor *a* of the fourth pereiopod and promotor *c* of the fifth pereiopod. The attachment of remotor *c* of the last pereiopod is spread over a wide area of the caudal or upper face of the posterior endosternite, medial to the corresponding remotor *a*. There is also a tendency for the insertions of remotors *b* and *c* of the last two legs to extend on to the proximal caudal margin of the coxopodite. Certain differences are obvious between this arrangement and that described for *Procambarus* by Pilgrim & Wiersma (1963), but these may be attributed to specific dissimilarities of the skeletal framework and the movability of the eighth sternum in *Procambarus*.

The disposition of the *levator* muscle is less variable, and its main head, *levator a*, is hidden dorsally by promotor *c*.

The criticism levelled by Pilgrim & Wiersma (1963) against Schmidt's (1915) assumption that the lateral portion of *depressor a* of all the pereiopods arises from the epimeron is supported by the present observations. It certainly has this origin in the third maxilliped and in the first pereiopod, in each of which it is so large that it obscures remotor *a*. In the second pereiopod the dorso-lateral slip of depressor *a* is also attached to the epimeron, but it is reduced and passes between remotors *a* and *c*, partly covering the former. From the third to the last pereiopod there is a progressive diminution of the lateral section of depressor *a* and it is no longer seen in an inner view. That of the third pereiopod is attached to the under surface of the strut of the endopleurite between the sixth and seventh epimera and, as in the second pereiopod, it travels between remotors *a* and *c* on its way to its insertion on the pereiopod. Depressor *a* of the last two pereiopods does not appear in the pleural muscle chamber and all its lateral fibres arise on the proximal margin of the coxopodite.

(j) *The pleopods* (Figs 28, 29)

Although the pleopod of the male differs from that of the female in being uniramous and in having a proportionally smaller exopodite lamella, the musculature is remarkably similar in both sexes. Moreover, the disposition of the muscles in the four pairs of biramous female pleopods is fairly consistent, and the only noticeable effect of the presence of the endopodite lamella in the first pair (on the second abdominal segment) is the addition of a flagellar or lamellar muscle. In the other three pairs of female pleopods the endopodite is a cylindrical, two-segmented rod which has a wide membranous connexion with the medial expansion of the basipodite. In both sexes the coxopodite is incomplete ventrally and the basipodite and the exopodite lamella articulate by a small ventral joint and are interconnected by a relatively wide arthrodial membrane. The exopodite is not clearly differentiated from the broad exopodite lamella and may be incomplete, but between the lamella and the basipodite there is a dorso-lateral sclerotized area for the insertion of some of the muscles of the exopodite. All the pleopods are attached to the abdominal sterna by flexible membranes and are capable of rotation.

(a) *Muscles common to the male and the female pleopods*

The following is a general account of the musculature of any one of the pleopods, excluding the muscles of the endopodite of the female. Perhaps owing to the size of the lamellae, the system is more complex than that of either *Astacus* or *Pandalus* with which, however, some similarities are evident.

Promotor

In *Astacus* Schmidt (1915) observed three proximal muscles which he named the musculi remotor, rotator dorsalis basipoditis, and rotator ventralis basipoditis. Analogous muscles occur in *Jasus* but, in addition, there is a conspicuous *promotor* muscle, which arises dorso-laterally on the tergum in proximity to the auxiliary muscle (figs 11, 12) and is more powerful in the female than in the male. It is obviously separated into a more or less cylindrical anterior head and a broader, flatter, more posterior portion consisting of two bands of widely spread fibres. The whole narrows somewhat towards its dorso-lateral insertion by a fairly strong tendon on the proximal margin of the coxopodite, and on contraction pulls the appendage forward.

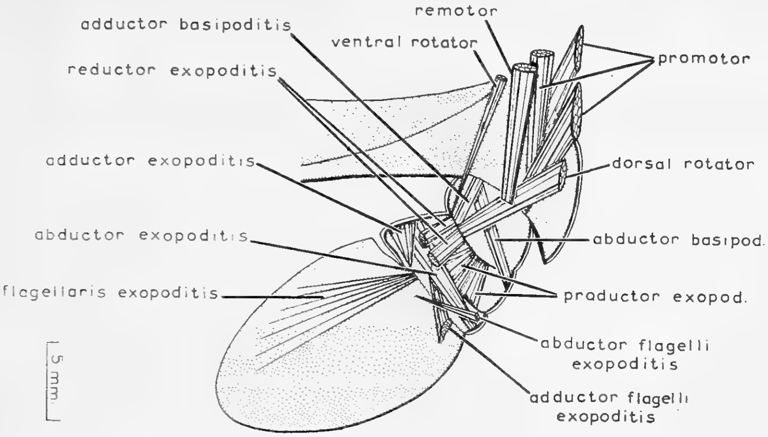


FIG. 28. Ventral view of muscles of left third pleopod of male.

Remotor

Backward movement of the pleopod is effected by this muscle, which differs in the two sexes, being slender in the male but comparatively wide and composed of three bundles in the female appendage. In both sexes it is ventral to the promotor muscle, and is attached antero-laterally on the pleuron and inserted ventrally by a short tendon on the proximal border of the coxopodite.

Dorsal rotator

This is a thick band, divisible into upper and lower bundles which originate postero-laterally on the tergum behind the promotor muscle. It slants obliquely inward dorsal to the remotor muscle and, traversing the coxopodite, is inserted ventrally on the middle of the proximal border of the basipodite by a conspicuous, flat tendon. It is comparable to the musculus rotator dorsalis basipoditis of *Astacus* and *Pandalus*, but differs in having a ventral and not a dorsal insertion.

Ventral rotator

Arising at the anterior junction of the sternum and pleuron, this muscle tapers rapidly towards its medial insertion by a slender tendon on the proximal edge of the basipodite. In the male pleopod it is feebly developed and consists of only a few fibres, but in the female there is an additional, more substantial bundle that practically obscures the weaker element ventrally. The two rotator muscles probably correspond to the levator and depressor muscles of the thoracic appendages, and are functionally antagonistic, the dorsal one turning the appendage outward and forward and the ventral one pulling it inward and forward.

Abductor basipoditis

Some specific variation is apparent in the number of remaining muscles associated with the basipodite. In *Astacus* there is a single reductor of the basipodite, but *Pandalus* also has a productor and an adductor of this segment. Two muscles, considered to be an abductor and an adductor, are concerned respectively with further outward and inward movements of the basipodite of *Jasus*.

The origin of the long, narrow *abductor basipoditis* takes place medio-dorsally on the proximal border of the coxopodite, through which it runs obliquely outward to a lateral insertion in the basipodite.

Adductor basipoditis

Lying approximately parallel to the medial margin of the coxopodite and dorsal to the ventral rotator muscle, this much shorter unit is attached near the abductor of the basipodite and extends medio-ventrally to the proximal margin of the basipodite near the insertion of the dorsal rotator muscle.

Productor exopoditis

Crowded into the short basipodite are four muscles, which are responsible for the movements of the narrow basal part of the exopodite and are distinct from those of the broad lamella. The *productor* muscle occupies the dorso-lateral half of the basipodite and moves the exopodite forward. It is usually divisible into two bands stretching between the proximal margins of the basipodite and the exopodite, but an additional bundle may occur in the larger pleopods of the female.

Reductor exopoditis

Like the previous muscle, this is also bipartite or tripartite, its somewhat thicker bundles arising side by side ventrally on the proximal border of the basipodite. They insert ventrally on the proximal margin of the exopodite and oppose the action of the corresponding productor muscle.

Abductor exopoditis

There appear to be more muscles associated with the exopodite of the pleopod than in other Decapoda previously investigated. The productor and reductor muscles have not been reported in *Astacus* and *Pandalus* and, while the former has no adductor muscle, the exopodite of the latter resembles that of *Jasus* in being provided with antagonistic abductor and adductor muscles.

Arising dorso-medially in the basipodite, the fairly thick and relatively long *abductor* muscle of the exopodite passes outward and backward between the productor and reductor muscles of the exopodite. It is inserted laterally in the exopodite and serves to tilt it and the broad lamella outward.

Adductor exopoditis

This shorter muscle has a wide attachment medio-ventrally in the basipodite, but tapers acutely before being inserted medially by a slender tendon on the proximal edge of the exopodite.

Abductor flagelli exopoditis

As the flat, unsegmented lamella of the exopodite is analogous to the flagellum of the three maxillipeds, the terminology applied to the musculature of the latter may be repeated in describing the remaining muscles of the pleopod. Abduction and adduction of the lamella, however, are effected by muscles which have no homologues in either *Astacus* or *Pandalus*.

The exopodite lamella is moved forward and outward by a very small *abductor flagelli exopoditis*, which is attached laterally in the exopodite ventral to the insertion of the abductor exopoditis. It tapers rapidly towards its dorsal insertion by a strong tendon in the middle of the proximal region of the lamella.

Adductor flagelli exopoditis

Inward movement of the exopodite lamella is accomplished by this rather thicker and more obvious muscle, which arises dorsally in the exopodite and spreads out ventro-laterally in the proximal part of the lamella.

Flagellaris exopoditis

In both sexes the thin exopodite lamella is provided with a number of strong fibres which are attached dorsally at its proximal margin. They fan out into the medial part of the lamella and cause it to bend in various directions.

(b) *Additional muscles in the female pleopod*

The endopodite is a conspicuous ramus of the female pleopod and its movements are produced by several intrinsic muscles, all of which are repetitions of the musculature of the exopodite.

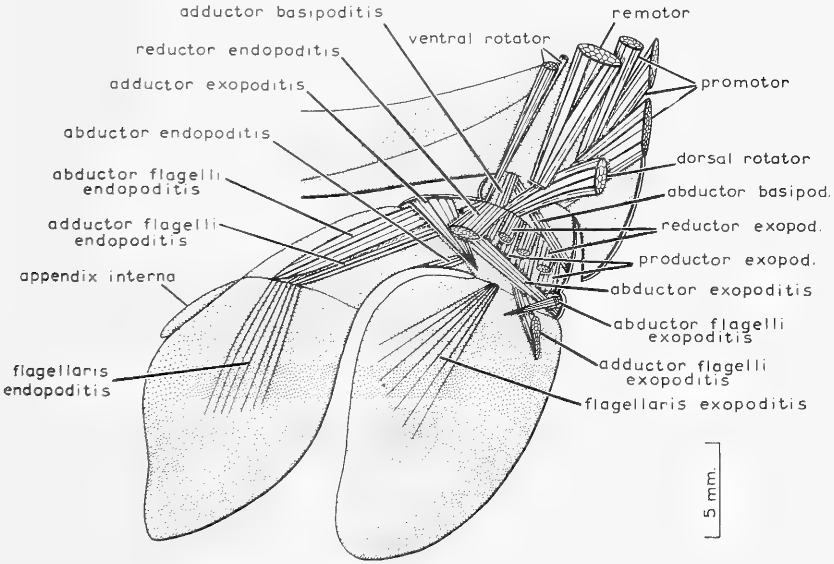


FIG. 29. Ventral view of muscles of left first pleopod of female.

Productor and reductor endopoditis

The connexion between the basipodite and the endopodite is largely membranous, but obvious medial bundles in line with the productor and reductor muscles of the exopodite appear to be inserted more particularly on the endopodite and may be distinguished as elements contributing to its forward and backward movements.

Abductor and adductor endopoditis

Located in the lower, outer angle of the endopodite are probable abductor and adductor muscles of the endopodite, which are weakly developed in the first pleopod, but are more apparent in the other three pleopods. They arise dorsally on the distal margin of the basipodite near the corresponding muscles of the exopodite and spread out slightly along the lower proximal wall of the endopodite, the abductor muscle being ventral to the adductor at its attachment and insertion; the adductor muscle has been omitted in figure 29.

Abductor and adductor flagelli endopoditis

The large inner lamella of the first pleopod of the female is provided with two subequal antagonistic muscles that are more conspicuous than those of the exopodite lamella. They are attached dorsally one above the other at the junction of the basipodite and the endopodite and proceed close together through the basal segment of the endopodite, but are distinguished from each other by the fact that the abductor has a ventral and the adductor a dorsal insertion on the proximal edge of the lamella.

Although the endopodite lamella is lacking in the remaining female pleopods, these muscles are retained. The abductor, however, is foreshortened and inserted proximally in the basal segment, while the adductor muscle extends to the distal region of the segment in line with the appendix interna.

Flagellaris endopoditis

The intrinsic muscle of the endopodite lamella of the first pleopod of the female resembles that in the exopodite lamella, but it is rather smaller and situated more in the middle of the lamella. It is, of course, non-existent in the other three pleopods of the female.

(k) *The uropod* (Fig. 30)

The last pair of abdominal appendages differs from the pleopods in being larger and biramous in both sexes and, although the coxopodite and basipodite are fused, thin arthrodial membranes allow of easy rotation of the undifferentiated protopodite and its appended flat, foliaceous exopodite and endopodite. The overall plan of the musculature is practically identical with that of *Astacus* and *Pandalus* and, as in these species, the muscles of the protopodite and exopodite are well developed and intricately arranged.

Lateral remotor of uropod

Located dorso-laterally and partly overlapping the last auxiliary muscle, this broad, fan-shaped muscle is composed of several bundles attached dorsolaterally behind the hinge near the proximal margin of the sixth abdominal segment. As it passes posteriorly, it narrows appreciably and is inserted dorso-

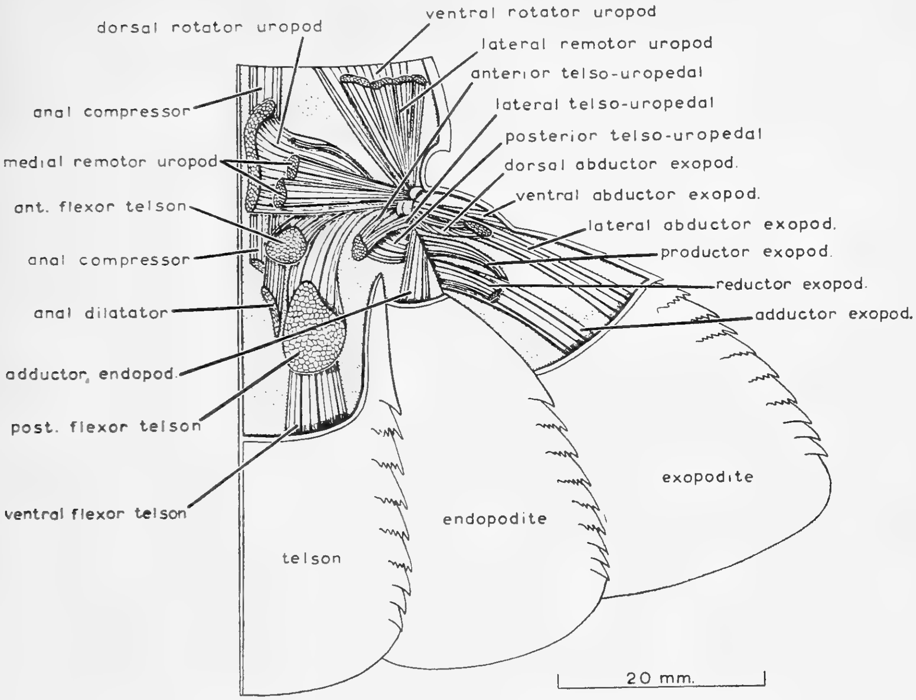


FIG. 30. Dorsal view of muscles of right uropod and right half of telson.

laterally on the proximal border of the protopodite by a broad, flat tendon, and effects a backward or upward movement of the appendage.

Medial remotor of uropod

The two contiguous bundles of this muscle arise dorso-medially in the posterior half of the sixth abdominal segment, and are separated from the lateral remotor by auxiliary muscle 5. The whole muscle lies superficially above the segmental extensor muscles and runs transversely across the segment to insert on the same tendon as the lateral remotor, to which it is similar in function, but also serves partly as an abductor.

Dorsal rotator of uropod

Apart from a narrow anterior slip arising in front of the medial remotor muscle above the extensor muscles of the sixth abdominal segment, this strong element originates mid-dorsally on the sixth abdominal tergum in the gap between the right and left extensor muscles. It slopes ventro-laterally below the latter and narrows rapidly towards its medio-ventral insertion by a very distinct, slightly curved tendon on the proximal edge of the protopodite. It pulls the uropod ventrally and thus turns it forward and inward.

Ventral rotator of uropod

On the whole, this broad, rather flat muscle is about equal in strength to the dorsal rotator of the uropod, and is situated beneath the lateral remotor of the uropod and auxiliary muscle 5. It is attached ventrally near the anterior border of the sixth abdominal segment and is inserted antero-ventrally on the tendon of the dorsal rotator of the uropod, but also spreads on to the adjacent tendon of the last anterior oblique muscle.

Abductors of exopodite

The expansion of the uropod to form the tail-fan is assisted by three muscles, which occupy the lateral parts of the protopodite and correspond to the lateral, dorsal, and ventral abductors of the exopodite in Schmidt's (1915) account of the musculature of *Astacus*.

The most conspicuous of the three is the long *lateral abductor*, which arises dorso-laterally on the proximal edge of the protopodite and extends through the latter to insert ventro-laterally in the exopodite some distance from its proximal border.

The *dorsal abductor* of the uropod is medial to and much shorter than the lateral abductor and, as in *Astacus*, is composed of two parts. In addition to a weak, narrow, dorso-lateral band, there is a thicker bundle arising ventro-laterally in the proximal region of the protopodite, so that it practically embraces the attachment of the lateral abductor of the exopodite. All its fibres congregate at a relatively wide insertion medio-dorsal to the lateral abductor muscle on the proximal margin of the exopodite.

The lateral abductor overlies the small *ventral abductor* of the exopodite both at its ventro-lateral origin on the proximal margin of the protopodite and at its ventro-lateral insertion on the proximal edge of the exopodite.

Adductor of exopodite

This is the only muscle that directly opposes the abductors of the exopodite and lessens the width of the tail-fan. It is attached ventrally in the distal part of the protopodite and curves into the exopodite parallel to the lateral abductor muscle, medial to which it has a broad, dorsal insertion.

Productor of exopodite

Arising dorsally by a broad surface in the proximal half of the protopodite, this fairly substantial muscle narrows appreciably as it bends round the outer margin of the adductor of the exopodite and passes to a thin ventral tendon located just beyond the proximal border of the exopodite. It pulls the latter forward in a ventral direction.

Reductor of exopodite

The origin of this somewhat shorter and weaker muscle is posterior to the previous muscle and dorsal to the adductor of the exopodite. It passes dorso-laterally over the latter and is inserted dorsally without a tendon near the proximal edge of the exopodite.

Adductor of the endopodite

As in *Astacus* and *Pandalus*, the endopodite has no abductor muscle, there being only a rather weak adductor, which causes an inward movement of the endopodite. It is attached dorso-medially in the protopodite in line with the productor muscle of the exopodite, and is inserted ventro-medially on the proximal margin of the endopodite.

Telso-uropedal

This muscle agrees with that of *Astacus* in originating by a broad surface dorso-laterally near the proximal border of the telson and in being divisible into three parts.

The *anterior head* is narrow and passes from the antero-lateral corner of the telson into the proximal part of the protopodite where it is inserted medio-ventrally on the posterior edge of the tendon of the dorsal rotator muscle of the uropod.

Slightly broader than the former, the *lateral head* is inserted laterally in the proximal region of the protopodite near the dorsal abductor of the exopodite.

The strongest of the three is the *posterior head*, which passes below the other two bundles and inserts medio-ventrally in the protopodite opposite the productor muscle of the exopodite.

Although the telso-uropedal muscle originates dorso-laterally in the telson, some of the fibres of the lateral and posterior bundles are connected by fibrous material with the tendon of the last anterior oblique muscle. By contributing to the outward and forward or ventral orientation of the uropod, the entire muscle is complementary to some of the other muscles in effecting movements of the tail-fan.

D. ALIMENTARY TRACT

In common with the majority of free-living triploblastic Invertebrata, the alimentary tract, which is a straight tube, may be differentiated into three regions, the stomodaeum, the mesenteron, and the proctodaeum.

The *stomodaeum* or *fore-gut* is lined with epicuticle (Dennell, 1960) and consists of a short *oesophagus* (figs 32, 33) extending vertically upward from the antero-ventral mouth (figs 4, 31), and a large *proventriculus* (figs 10, 31, 77, 78) which occupies the greater portion of the anterior part of the body cavity. Following the nomenclature used by Pearson (1908), the proventriculus may be divided into a large, almost spherical, flat-roofed *cardiac fore-gut* and a smaller *pyloric fore-gut*, in the latter of which anterior and posterior regions are recognizable. The inner wall of the proventriculus is furnished with a number of strong teeth which constitute the so-called 'gastric mill' for grinding the food; it also has groups of setae which form a filtering apparatus for straining the food and ensuring that only the finest particles and liquids are passed back into the mid-gut.

The *mesenteron* or *mid-gut* (figs 32–34) is a short, soft-walled chamber, the epithelium of which is endodermal in origin and absorptive in function. Opening into it on each side is the duct from the large, paired *digestive gland* (figs 10, 31, 77, 78), while postero-dorsally it gives off a short, inconspicuous,

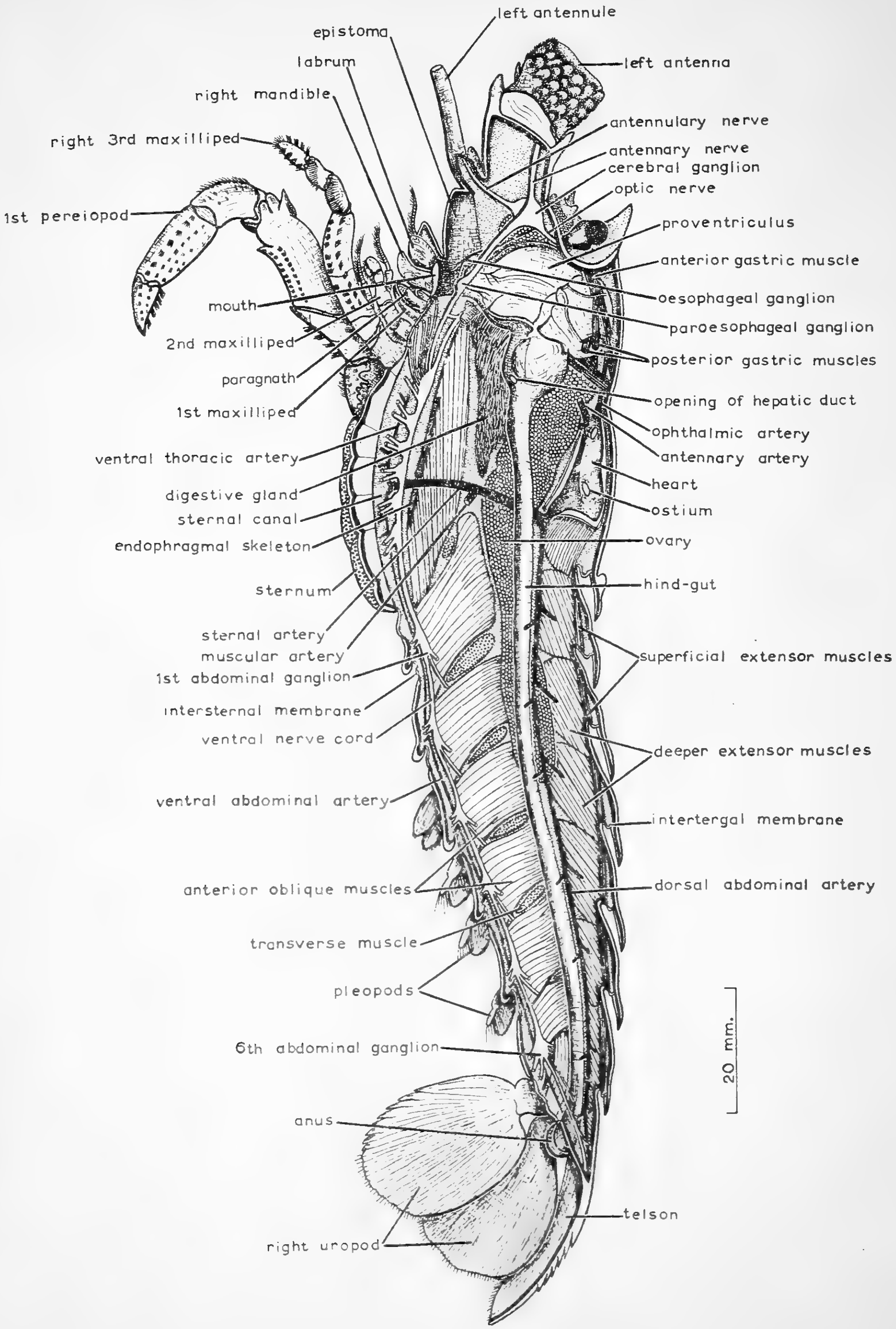


Fig. 31. General anatomy of small female, dissected from the left.

forwardly-directed *caecum* (figs 33, 37) which is closely adherent to the dorsal wall of the posterior part of the pyloric fore-gut.

The *proctodaeum, intestine,* or *hind-gut* (figs 31–34, 77, 78) is the longest part of the alimentary tract and, like the fore-gut, is lined with epicuticle. It is a straight narrow tube which lies beneath the pericardial cavity in the cephalothorax and extends down the length of the abdomen below the extensor muscles to open at the slit-like *anus* (fig. 31) located ventrally on the telson.

1. OSSICLES AND TEETH OF THE PROVENTRICULUS (Figs 32–34)

The cardiac and pyloric chambers of the fore-gut differ not only in relative size, but also in that, whereas the wall of the former serves as an internal masticatory 'gastric mill', the latter functions chiefly as a filtering or sieving mechanism; consequently the structural modifications in each region are considerable.

(a) *Cardiac fore-gut*

While this is relatively thin-walled laterally and ventrally, it is supported dorsally and dorso-laterally by a number of *ossicles*, which are thickenings of its cuticular lining. The ossicles not only provide attachment for the extrinsic and the intrinsic muscles of the fore-gut, but certain of them are produced into conspicuous *teeth* which form the grinding apparatus for triturating the food. The various structures of the cardiac fore-gut are distributed much as are those of other Reptantia described by Pearson (1908) and Patwardhan (1935).

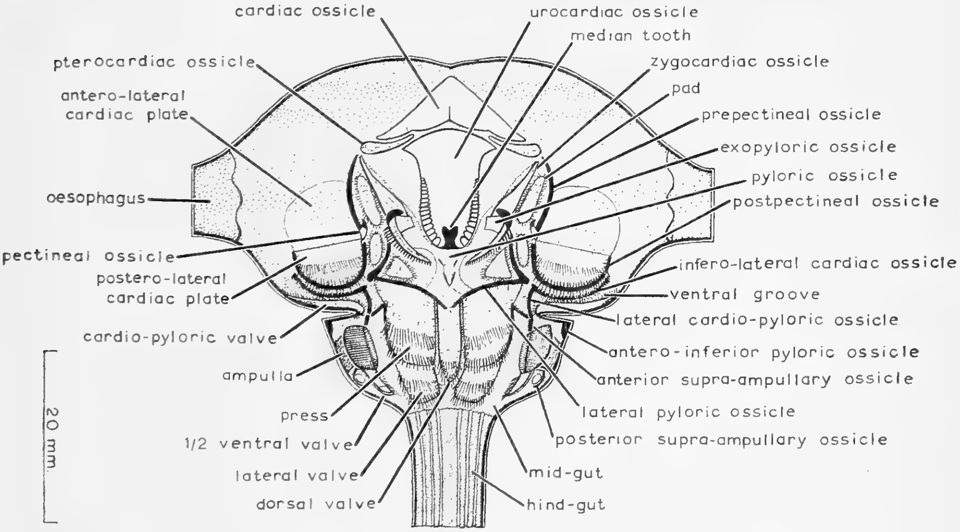


FIG. 32. Inner view of fore-gut, cut mid-ventrally to expose the ossicles, teeth, valves, etc.

The postero-lateral walls are strengthened by a pair of conspicuous, more or less semicircular *postero-lateral cardiac plates* (figs 32–34). The surface of each is provided with several rows of setae which project into the lumen.

In front of these areas there is a pair of ill-defined *antero-lateral cardiac plates* (figs 32, 34); these are more membranous and are not setose.

The *cardiac ossicle* (figs 32–34) is a fairly large, dorso-median, roughly triangular piece with an indented posterior margin and a slight, outer, postero-median ridge for the insertion of the anterior gastric muscles.

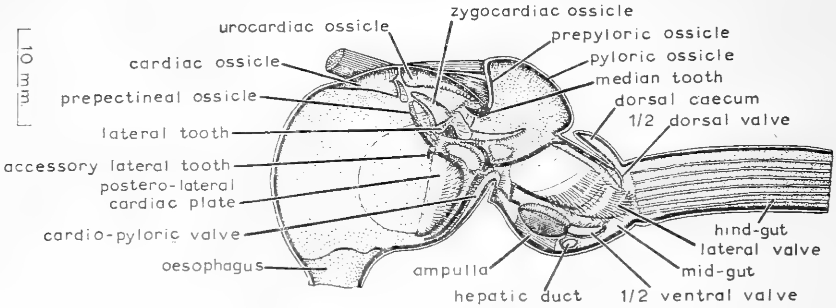


FIG. 33. Median view of fore-gut.

The *pterocardiac ossicles* (figs 32, 34) are paired, rather small, slender, lateral sclerites articulating with the postero-lateral border of the cardiac ossicle and extending inward towards its postero-lateral notch.

The greater part of the roof of the cardiac fore-gut is formed by the flat *urocardiac ossicle* (figs 32–34). It is broadest anteriorly at its articulation with the cardiac and the pterocardiac ossicles and narrows perceptibly at its posterior extremity, where it is continued into a downwardly-directed, forwardly-

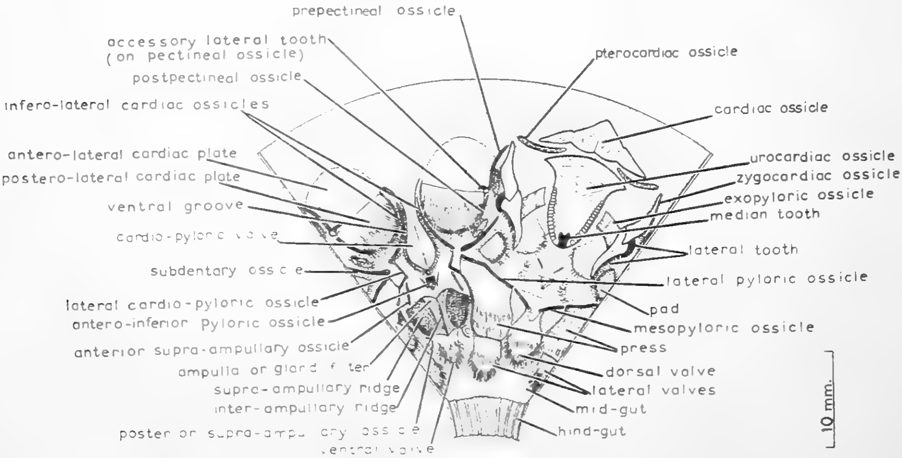


FIG. 34. Plan of inner view of fore-gut, spread out after lateral incision.

curved, brownish and slightly bifid *median tooth* (figs 32–34). In the posterior two-thirds of the ossicle the lateral margins are marked by a series of blunt, transverse ridges.

Paired, thickly-sclerotized *zygocardiac ossicles* (figs 32–34) occur dorso-laterally and articulate anteriorly with the outer ends of the pterocardiac ossicles. Each arches backward and downward and tapers anteriorly and posteriorly; at its widest point it supports a large, blunt denticle which curves inward towards the median tooth. In addition, there are about 21 acutely-pointed smaller denticles along the lateral border of the posterior half of the zygocardiac ossicle; these decrease progressively in size from the large denticle backward and, combined with the latter, constitute the *lateral tooth* (figs 33, 34).

The *exopyloric ossicles* (figs 32, 34) are a pair of small, somewhat rectangular plates, which are intercalated between the posterior part of the zygocardiac ossicle and the pyloric ossicle and virtually lie between the cardiac and pyloric portions of the fore-gut.

Located in the wall of the cardiac fore-gut lateral to the large denticle on the zygocardiac ossicle and at the inner end of the curvature of the postero-lateral cardiac plate is a small, rather inconspicuous, paired *pectineal ossicle* (fig. 32). It is characterized by the presence of a minute, hooked, backwardly-directed *accessory lateral tooth* (figs 33, 34).

The *prepectineal ossicles* (figs 32–34) are long, narrow, curved rods which lie parallel to the outer edge of the zygocardiac ossicles and extend forward from the pectineal ossicles to the outer ends of the pterocardiac ossicles.

Two slender *postpectineal ossicles* (figs 32, 34) run backward from the pectineal ossicles round the posterior margin of the postero-lateral cardiac plates in the direction of the oesophagus.

The *infero-lateral cardiac ossicles* (figs 32, 34) are also thin, arched bars, which lie behind and parallel to the postpectineal ossicles but, unlike the latter, they are fringed with setae and each forms the anterior boundary of a paired *ventral food groove* (figs 32, 34) leading from the oesophagus to the pyloric fore-gut.

On each side a narrow, slightly bent *subdentary ossicle* (fig. 34) passes from the large denticle on the zygocardiac ossicle to the upper end of the infero-lateral cardiac ossicle with which it is loosely articulated.

Paired, short, curved *lateral cardio-pyloric ossicles* (figs 32, 34) extend from the posterior ends of the infero-lateral cardiac ossicles below the cardio-pyloric valve into the ventro-lateral part of the pyloric fore-gut.

The side-wall of the cardiac fore-gut is provided with three fairly conspicuous *pads* or cushions, the surfaces of which are beset with short setae. One is an anterior, elongate-oval swelling between the zygocardiac and prepectineal ossicles (fig. 32), and the other two are more posterior and are located on either side of the subdentary ossicle. According to Yonge (1924), similar pads in the cardiac fore-gut of *Nephrops norvegicus* guard the entrance into the pyloric fore-gut.

(b) *Pyloric fore-gut*

This somewhat bent posterior part of the proventriculus, although possessing fewer ossicles, is structurally just as complex as the cardiac fore-gut. Continuous with the latter is a thin-walled, antero-dorsal pyloric chamber, while postero-ventrally the second half of the pyloric fore-gut communicates with the extremely short mid-gut and leads almost directly to the hind-gut.

(i) *Anterior part of pyloric fore-gut*

Two main median ossicles, the *prepyloric* and the *pyloric*, occur in this region: the *prepyloric ossicle* (fig. 33) is a small, triangular, vertical plate, extending upward from the posterior end of the urocardiac ossicle to join the *pyloric ossicle*. The latter (figs 32, 33) forms the arched, thin-walled roof of this chamber, and articulates with the prepyloric ossicle anteriorly and with the exopyloric ossicles more laterally.

In addition to the above two ossicles, the narrow ventral wall is supported by a small *antero-inferior pyloric ossicle* (figs 32, 34). This is a median, somewhat triangular plate, lying immediately behind the cardio-pyloric valve and flanked on each side by a short, rod-shaped *pre-ampullary ossicle*, which is represented but not labelled in figure 34.

(ii) *Posterior part of pyloric fore-gut*

This is rather more compact than the anterior part and, owing to the intricate arrangement of plates, valves and other structures, its lumen is much smaller. Its most striking feature is the presence of a pair of ventro-lateral pockets, each of which contains a remarkable semicircular organ, termed the *pyloric ampulla* by Pearson (1908) and the *gland filter* by Yonge (1924). Each *ampulla* (figs 32–34, 36) consists essentially of a thick, ventro-lateral, concave, plate, which is internally produced into parallel, longitudinal, cuticular rods, capped with setae. The two ampullae meet mid-ventrally in an obvious sloping *inter-ampullary ridge* (figs 34, 36, 37), which lies behind the antero-inferior pyloric ossicle and projects upward into the very narrow lumen, its summit being furnished with two parallel rows of setae. Fitting into the concavity of the ampulla is a pronounced, convex *supra-ampullary ridge* (figs 34, 36), the dense setose covering of which forms part of the filtering apparatus.

Immediately in front of each supra-ampullary ridge is a short, rod-shaped *anterior supra-ampullary ossicle* (figs 32, 34), which supports the wall between the ridge and the lateral cardio-pyloric ossicle.

In the vicinity of the supra-ampullary ridge, there is also at least another short bar, the *posterior supra-ampullary ossicle* (figs 32, 34), which partly embraces the opening of the hepatic duct in the anterior region of the mid-gut.

Each lateral wall is occupied by a flat, relatively broad plate, partially covered with setae; the two plates have been identified as the *press* (figs 32, 34, 36, 37), as they are comparable to the structure so described by Yonge (1924) in his account of the fore-gut of *Nephrops norvegicus*. The anterior margin of each half of the press is strengthened by a narrow, transverse bar, which extends almost to the posterior extremity of the subdentary ossicle, and may conveniently be termed the *lateral pyloric ossicle* (figs 32, 34). Articulating with the latter is another, paired, horizontal rod, the *mesopyloric ossicle* (fig. 34), which seems to be the only obvious support of the dorsal wall and may correspond to the paired posterior mesopyloric ossicle of crabs (Pearson, 1908; Patwardhan, 1935).

The arrangement of most of the aforementioned proventricular structures broadly reflects the findings of Pearson (1908), Yonge (1924), and Patwardhan (1935) in other Decapoda. Pearson, however, has mentioned several additional, small, supporting ossicles in the lateral walls of the pyloric fore-gut of *Cancer*; although these have not been detected in *Jasus*, it is possible that some of them have been replaced by the press.

2. PROVENTRICULAR VALVES (Figs 32–34, 37)

In addition to ossicles and teeth, the proventriculus is equipped with five conspicuous valves whose main function is to guide food particles along definite channels, but some of them may also act as a protection for the soft-walled mid-gut.

The cardiac and pyloric regions of the proventriculus are incompletely separated by a relatively large *cardio-pyloric valve*. This is a thickened infolding of the postero-ventral wall of the cardiac fore-gut and, like many other parts of the inner lining of the proventriculus, it is fringed with closely-set setae. It lies in proximity to the two posterior pairs of cardiac pads and, forming a spout-like projection in front of the press, it partly obstructs the entrance into the posterior half of the pyloric fore-gut.

Extending from the posterior division of the pyloric fore-gut into the lumen of the mid-gut are the following four cuticular, flat, setose valves: the *dorsal valve* is a tongue-shaped flap attached to the medial ends of the mesopyloric ossicles; a similar, but slightly smaller, *ventral valve* is continuous with the ampullary region; and two elongate *lateral valves* pass back from the press. As Pearson (1908) has remarked, these four valves may serve as a protective lining for the very short mid-gut, ensuring the direct passage of hard particles from the fore-gut into the hind-gut and guarding the delicate epithelium of the mid-gut against injury. Yonge (1924), however, has indicated that this function cannot be realized in *Nephrops norvegicus* which has a relatively long mid-gut. He has therefore suggested that the valves and the filter apparatus ensure that only liquids and fine food particles will enter the hepatopancreas and, from an examination of their disposition in *Jasus*, it seems likely that they may also be partly adapted for this purpose in decapods with an extremely short mid-gut.

3. MUSCLES OF THE FORE-GUT (Fig. 35)

The several parts of the fore-gut are dilated and constricted by a complicated musculature which, as in *Cancer pagurus* (Pearson, 1908) and in *Paratel-*

phusa guerini (Patwardhan, 1935), may be divided into two main categories. The *extrinsic muscles* are those which originate outside the fore-gut, generally on different parts of the exoskeleton; most of them are inserted on the ossicles of the fore-gut and serve to dilate its parts. On the other hand, the *intrinsic muscles* function as constrictors and usually have their attachments and insertions on the proventricular ossicles; it has been shown by Manton (1928, 1934) that many of the intrinsic muscles are derived from the preantennulary mesoderm. The arrangement of the muscles in *J. lalandii* closely resembles that of *Cancer* and *Paratelphusa*, and the terminology used in the following account is in accordance with that of Pearson (1908).

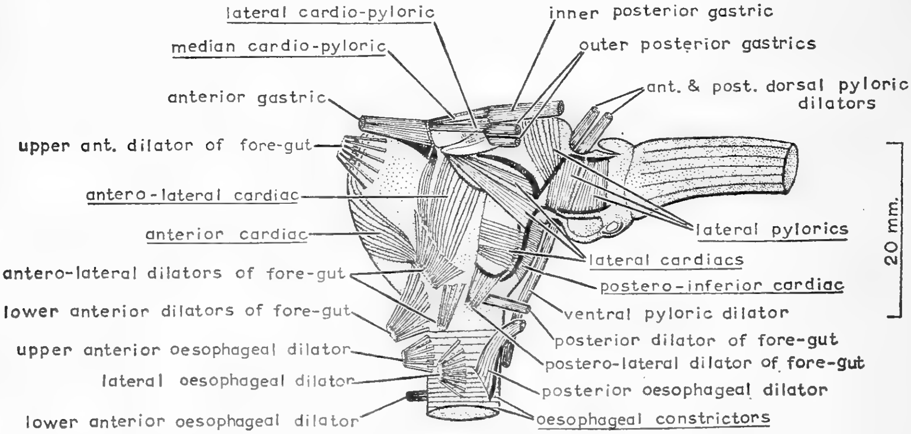


FIG. 35. Left lateral view of fore-gut, showing position of muscles; intrinsic muscles are underlined.

(a) *Extrinsic muscles*

Anterior gastrics: one pair of broad muscles attached to the procephalic processes. Each passes somewhat obliquely backward and is inserted on the posterior half of the cardiac ossicle. As some of the fibres are inserted on the median ridge of the cardiac ossicle, there is only a slight gap between the posterior ends of the two muscles.

Posterior gastrics. These comprise one pair of *inner* and two pairs of *outer* muscles, all of which arise posteriorly on the gastric region of the wall of the head. The *inner posterior gastrics* are attached close together near the mid-dorsal line and medial to the posterior bundle of the mandibular posterior adductor muscle. Each is inserted on an antero-lateral ridge of the pyloric ossicle, just behind the margin of the prepyloric ossicle. The *outer posterior gastrics* arise more laterally on the head wall and pass obliquely forward and inward between the two bundles of the mandibular posterior adductor muscle. On each side the two muscles are contiguous and are inserted on the exopyloric ossicle, one above the other.

Upper anterior dilators—one pair. These are not compact muscles, each being composed of a number of separate strands, which arise close together on the ventro-lateral surface of the procephalic process beneath the anterior gastric muscle. The muscle strands diverge as they pass backward, inward and downward, and are inserted separately on the anterior and antero-lateral wall of the upper part of the cardiac fore-gut.

Lower anterior dilators: one pair, each of which consists of long, thin strands, and the whole is subequal in size to the upper anterior dilator muscle. The fibres originate on the median apodeme of the epistoma and spread to each side of the ventral antero-median wall of the cardiac fore-gut.

Antero-lateral dilators. In *Cancer* Pearson (1908) has described a single pair of narrow compact muscles, but in *Jasus* there appear to be two pairs, one above the other. They are attached near each other on the mandibular epimeron in the prebranchial chamber close to the lateral margin of the epistoma. They consist of long, slender muscle strands inserted on the lateral wall of the cardiac fore-gut in the region of the antero-lateral cardiac plate. The lower muscle is the smaller of the two and its fibres are inserted slightly behind and below the upper muscle.

Postero-lateral dilators: one pair, which are less compact than those of *Cancer*. Each arises behind the antero-lateral dilator muscles towards the anterior end of the mandibular epimeron and passes inward and backward, spreading out as a broad sheet of fibres which are inserted on the ventral margin of the postpectineal ossicle.

Posterior dilator. This paired muscle, which is absent in *Cancer* and *Paratelphusa*, is short, narrow, and compact, and is attached to the postero-dorsal border of the cephalic apodeme. Crossing over the outer surface of the ventral pyloric dilator muscle, it passes forward and is inserted postero-laterally on the wall of the cardiac fore-gut below the postero-lateral cardiac plate and near the upper limit of the oesophagus.

Dorsal pyloric dilators: two pairs, the anterior and posterior, arising from the postero-median part of the gastric region of the body wall, a short distance in front of the cervical groove and just behind the attachment of the inner posterior gastric muscles. On each side the two muscles pass forward and downward parallel to each other, the anterior muscle being inserted on the dorsal wall of the pyloric fore-gut behind the pyloric ossicle and the posterior muscle on the mesopyloric ossicle in front of the dorsal valve.

Ventral pyloric dilator. There is a single pair, corresponding with the inner of the two pairs of *Cancer* (Pearson, 1908). Each is a long, strap-shaped band originating anteriorly on the base of the anterior mandibular apodeme. It runs slightly backward and abruptly upward medial to the ventral cephalic muscle, and is inserted on the antero-inferior ossicle in the ventral wall of the pyloric fore-gut.

Upper anterior oesophageal dilators: one pair, attached to the median apodeme of the epistoma ventral to the lower anterior dilator muscles of the cardiac fore-gut. Each consists of a number of separate fibres which pass backward and slightly upward and are inserted on the anterior wall of the oesophagus.

Lower anterior oesophageal dilators: one pair of narrow inconspicuous muscles, arising below the origins of the previous pair and passing directly backward to the anterior wall of the oesophagus.

Lateral oesophageal dilators—one pair. Each muscle originates on the postero-lateral corner of the epistoma, passes backward and slightly obliquely upward, its separate fibres diverging as they are inserted along the lateral wall of the oesophagus.

Posterior oesophageal dilators: one pair, each of which is a relatively strong muscle composed of a series of muscle strands arising together on the anterior margin of the cephalic apodeme above and medial to the attachment of the mandibular major abductor muscle. It runs forward and acutely downward and is inserted on the posterior wall of the oesophagus. Like the posterior dilator of the cardiac fore-gut, this muscle crosses over the ventral pyloric dilator.

(b) *Intrinsic muscles*

Cardio-pylorics. These occur in the dorsal depression above the urocardiac ossicle and comprise a median and two lateral bundles extending backward from the posterior border of the cardiac ossicle. The *median* muscle is inserted on the dorsal margin of the prepyloric ossicle, while the *lateral* muscles pass obliquely outward to the antero-lateral corner of the exopyloric ossicles.

Lateral cardiacs. As in *Cancer* (Pearson, 1908) and *Paratelphusa* (Patwardhan, 1935), three pairs of these muscles occur on each side of the posterior region of the cardiac fore-gut. The *upper* muscle arises from the posterior end of the subdentary ossicle and passes upward and forward to the dorso-lateral edge of the zygocardiac ossicle as a narrow band of fairly stout fibres.The *middle* muscle is slightly longer than the preceding one and also consists of rather thick fibres. It is attached to the infero-lateral cardiac ossicle and runs obliquely upward and forward below and parallel to the upper muscle. It is inserted partly on the antero-lateral corner of the zygocardiac ossicle but mainly on the pre-pectineal ossicle. The *lower* muscle forms a broad sheet of delicate strands which partly cover the postero-lateral cardiac plate, being inserted along its anterior border and originating on the anterior edge of the infero-lateral cardiac ossicle.

Mocquard's (1883) suggestion, cited by Pearson (1908), that the lateral cardiac muscles serve to raise the cardio-pyloric valve is doubtless a true interpretation of their function but, at the same time, it is also probable that their contraction will be instrumental in widening the ventral food grooves which lie between the cardio-pyloric valve and the infero-lateral cardiac ossicles.

Postero-inferior cardiac. In *Cancer* (Pearson, 1908) and in *Paratelphusa* (Patwardhan, 1935) this is a median muscle stretching between the two infero-lateral cardiac ossicles. In *Jasus* it is effectively similar, but appears to be paired, the short fibres passing on each side from the posterior edge of the infero-lateral cardiac ossicle to a slender, mid-ventral rod which supports the floor of the cardio-pyloric valve. It seems likely that they are antagonistic to the lateral cardiac muscles and are capable of compressing the cardio-pyloric valve and the ventral food groove.

Anterior cardiac. As it arises on the anterior margin of the cardiac ossicle, the dorsal part of this median muscle is obscured by the anterior gastric and the upper anterior dilator muscles. Its delicate fibres spread over the anterior wall of the cardiac fore-gut and, like the next pair of muscles, serve to constrict this part of the proventriculus.

Antero-lateral cardiacs. This name was given by Pearson (1908) to a pair of muscles passing upward from the antero-lateral cardiac plates towards the mid-dorsal wall. In *Jasus* somewhat similar muscles are inserted on these plates above the extrinsic antero-lateral dilator muscles and are attached to the prepectineal and pterocardiac ossicles.

Lateral pylorics. The wall of the pyloric fore-gut is constricted by a number of fibres which seem to be arranged on each side into three main muscles. The *anterior* muscle forms a sheet of delicate strands attached to the anterior margin of the lateral pyloric ossicle; they pass obliquely forward and upward across the anterior chamber of the pyloric fore-gut and are inserted on the pyloric ossicle. The *middle* muscle consists of rather stronger fibres arising on the lateral cardio-pyloric and the anterior supra-ampullary ossicles. They run almost vertically upward to the posterior margins of the lateral pyloric and meso-pyloric ossicles and thus cover the anterior part of the press. The *posterior* muscle is located in the wall of the posterior half of the press, extending from its lateral to its dorsal border and being subequal in strength to the middle bundle.

The *oesophageal constrictors* are fine circular fibres which run in the wall of the oesophagus and serve, as their name denotes, to reduce the lumen of this tubular part of the fore-gut.

4. SIGNIFICANCE OF THE PROVENTRICULUS

An internal masticatory apparatus, the so-called 'gastric mill', is a feature of the malacostracan proventriculus, and it has been demonstrated by Patwardhan (1935) and Reddy (1935) that its elaboration in the Decapoda is directly correlated with the types of mandibles in the different subdivisions of the order. Possessing well-defined incisor and molar processes, the mandibles of most Natantia are efficient masticatory organs and, while a filtering apparatus is present in the pyloric fore-gut, a complicated gastric mill is usually lacking in the cardiac fore-gut, being replaced by spinous valves. Contrasted with these circumstances, the mandibular incisor and molar processes are indistinct in Reptantia and, to compensate for the inadequate fragmentation of the food by the mouth-parts, an ingenious internal mill has been designed for the final comminution of the food. The foregoing account of the complex structures and the intricate musculature of the proventriculus of *Jasus* is a measure of the importance of this part of the alimentary tract as a grinding and filtering mechanism for reducing the food and directing the finer particles towards the mid-gut and the digestive gland.

Once the food has been dealt with by the mouth-parts and forced into the mouth, it travels up the short, vertical oesophagus, its transit being controlled by the antagonistic action of the oesophageal dilatator and constrictor muscles. At the junction of the oesophagus and the capacious cardiac fore-gut a ventral and two lateral valvular folds assist in narrowing the passage and in retaining the food in the cardiac chamber. Within the latter the food is pulverized by the strong median and lateral teeth (figs 32–34), after which there is a separation of the finer from the larger particles, which then flow along different routes through the pyloric fore-gut.

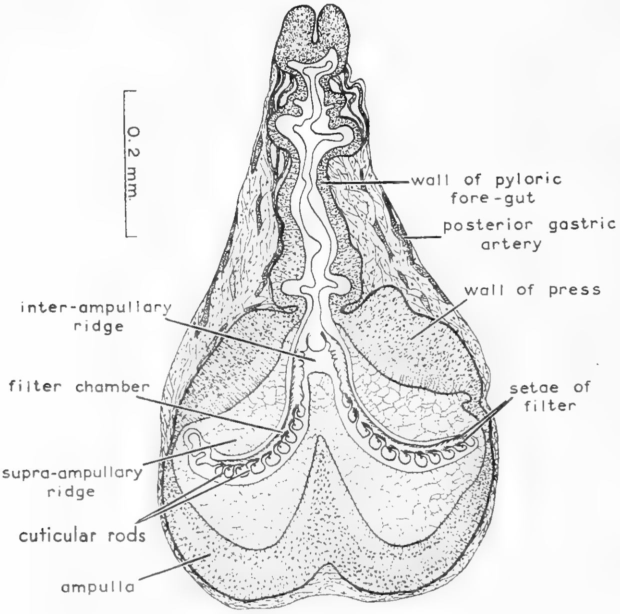


Fig. 36. Puerulus stage: transverse section through posterior part of pyloric fore-gut.

A reasoned exposition of the passage of food through the alimentary canal of *Nephrops norvegicus* has been given by Yonge (1924), and a similar course of events in the proventriculus is applicable to *Jasus*. Owing to the disposition of the ossicles, pads and folds of the proventricular wall, certain *food grooves* or channels are clearly demarcated. A pair of *ventral grooves* (figs 32, 34), extending from the oesophagus to the posterior half of the pyloric fore-gut and supported by the closely-approximated postpectineal and infero-lateral cardiac ossicles, form a gutter on each side of the cardio-pyloric valve and lead towards the ampullae. Running backward from the median tooth to the base of the dorsal

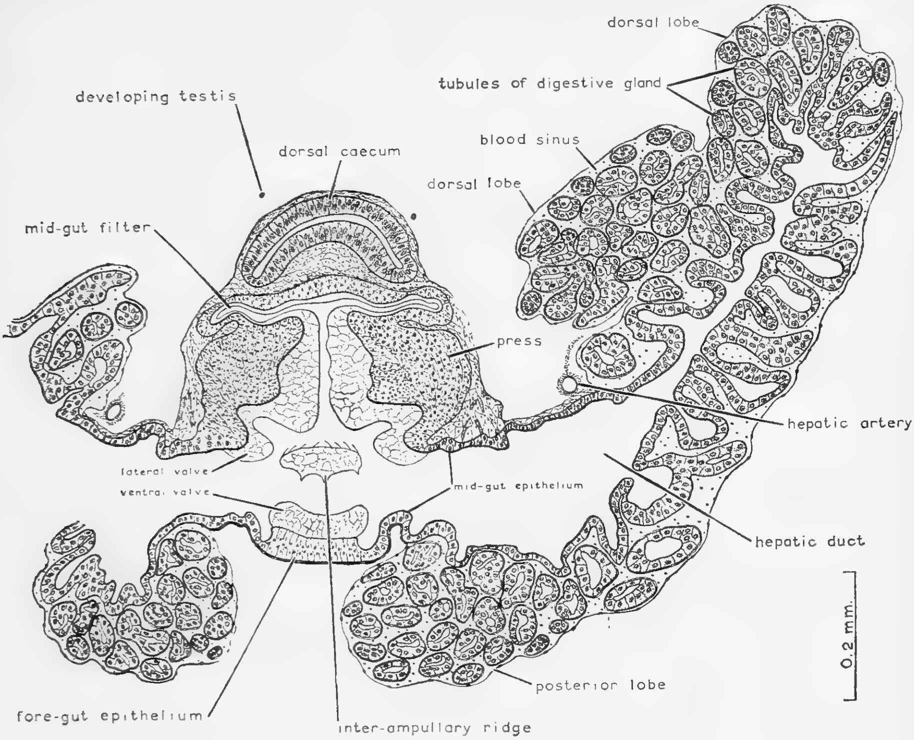


FIG. 37. Puerulus stage: transverse section through hepatic ducts.

caecum of the mid-gut and lying above the press, are two dorso-lateral channels which, according to Yonge (1924), may be described as the *mid-gut filter* (fig. 37). *Lateral grooves*, bounded by the zygocardiac and subdentary ossicles and by the pads at the sides of the postero-lateral cardiac plates, communicate with the press in the posterior part of the pyloric fore-gut.

It has also been demonstrated by Yonge (1924) that the secretions from the digestive gland pass forward along the ventral grooves and become mixed with the food during mastication in the cardiac chamber. Digested and fine particulate matter is then conveyed backward via the ventral grooves and traverses the *filter chamber* (fig. 36) which is bordered by the setae of the ampullae and their supra-ampullary ridges. On leaving the filter chamber, the sifted material passes into the mid-gut and enters the digestive gland, in the tubules of which absorption and storage of good substances takes place. Simultaneously, the larger undigested fragments are swept along the lateral grooves and the mid-gut filter into the press and thence, in *Jasus*, are guided through the pyloric valves into the hind-gut.

The mechanism of the gastric mill and the flow of food through the fore-gut are governed by the previously-described sets of muscles. Based on Huxley's

(1881) account of the gastric mill of *Astacus*, it is generally assumed that the anterior and posterior gastric muscles are mainly responsible for the approximation of the median and lateral teeth, the gnashing action of which is effective in triturating the food. When the anterior gastric muscles contract, the cardiac and urocardiac ossicles are pulled forward; as this also adjusts the prepyloric ossicle, the median tooth on the urocardiac ossicle is brought forward and directed vertically downward. Added to this operation, the backward pull on the pyloric and exopyloric ossicles, exerted by the contraction of the posterior gastric muscles, and perhaps to some extent by the constriction of the wall by the lateral cardiac muscles, affects the inclination of the zygocardiac ossicles, causing them to be rotated inward. Thus, when the anterior and posterior gastric muscles contract simultaneously, the large denticles of the lateral teeth are brought into contact with the median tooth, and their concerted grinding action disintegrates the food. Evidence quoted by Pearson (1908), Yonge (1924), and Balss (1944) suggests that, when the gastric muscles relax, the ossicles revert to their normal resting position with the teeth apart, partly owing to the elasticity of the walls at their points of articulation, and partly as a result of the contraction of the intrinsic cardio-pyloric muscles.

5. DIGESTIVE GLAND (Figs 10, 31, 51, 53, 77, 78)

The digestive gland, hepatopancreas, or 'liver', is a paired, voluminous, yellowish organ, composed of numerous, discrete, digitiform tubules and enclosed in a delicate syncytial membrane. It is primarily an outgrowth of the mid-gut and occupies a considerable portion of the cephalothoracic body cavity, each half of the gland lying mainly between the alimentary tract and the lateral body wall and being divisible into anterior, dorsal, and posterior lobes.

The *anterior lobe* (figs 38, 51, 77) is situated below the antennal promotor muscle and lateral to the proventriculus. It extends almost to the anterior limit of the body cavity and projects ventro-laterally into the concavity of the anterior apodeme of the mandible.

The middle or *dorsal lobe* (figs 37, 38, 51, 77), which partly overlaps the other two lobes, lies chiefly in front of the cervical groove and practically in line with the two bundles of the mandibular posterior adductor muscle. It is widest anteriorly, where it spreads out laterally between the anterior part of the branchiostegite and the roof of the prebranchial chamber.

The *posterior lobe* (figs 37, 51, 77) is larger and more ventral than the other two lobes. It stretches approximately from the cervical groove to the end of the sixth thoracic segment and is located ventro-laterally below the pericardial septum.

On each side the digestive gland communicates with the mid-gut by a relatively wide *hepatic duct* (figs 31, 33, 37), which branches into each of the three lobes and therein forms a system of ramifying ductules that are ultimately continuous with the lumina of the tubules of the gland (fig. 37).

It has been shown by Yonge (1924), Van Weel (1955), and Vonk (1960) that the digestive gland of decapod Crustacea has several functions; it is not only concerned with the secretion of various enzymes such as proteases, lipases, and carbohydrates, but it is also an important organ for the absorption of nourishment and for the storage of glycogen, fat, and sometimes calcium.

E. Excretory Organs

In a discussion of facts concerning excretion in Crustacea, Parry (1960) has shown that the urine produced by the antennal glands of Decapoda generally contains relatively small quantities of nitrogenous substances, and that other organs and tissues contribute towards the elimination of waste products. It has also been demonstrated by Parry (1960) and Robertson (1960) that, while the antennal glands of some fresh-water decapods are osmoregulatory in function, in marine species the antennal glands mainly participate in the ionic regulation of the body fluids.

1. ANTENNAL GLANDS

The two antennal glands are situated at the bases of the antennae on either side of the cardiac fore-gut. Each gland may be exposed by removal of the lateral part of the head exoskeleton, but satisfactory dissection of the entire organ is somewhat difficult owing to the fact that it is wedged between the anterior viscera, particularly between the powerful muscles of the antenna. The whole is a compact structure which lies rather superficially beneath the body wall and occupies the haemocoelic space bounded by the mandibular lateral adductor muscles, the cardiac chamber of the fore-gut, and the base of the antennal peduncle. Dorsally it is largely obscured by the antennal promotor muscle which, however, can easily be removed; but intervening between the anterior and posterior parts of the gland is the strong levator muscle of the antenna, careful excision of which is required before all the parts of the organ can be displayed.

Marchal's (1892) article on the antennal glands of decapod Crustacea is one of the most comprehensive reports on the subject. Not only has it formed the basis of subsequent accounts of the so-called 'green gland' of the fresh-water crayfish, *Astacus*, but it also contains factual descriptions of the excretory organs of a variety of species representative of the main subdivisions of the Decapoda. Later investigations, such as Waite's (1899) observations of the antennal glands of *Homarus* and the comparative study of the excretory organs of *Astacus* and *Homarus* by Peters (1935), have largely substantiated Marchal's findings, while surveys by Parry (1960), Robertson (1960), and Lockwood (1962) disclose the current research interest in various aspects of the physiology of the antennal glands.

Marchal (1892) has shown that the essential parts of the decapod antennal gland are the *end sac*, the *labyrinth*, and the *bladder* or vesicle. These three structures usually intercommunicate consecutively, and transmission of the

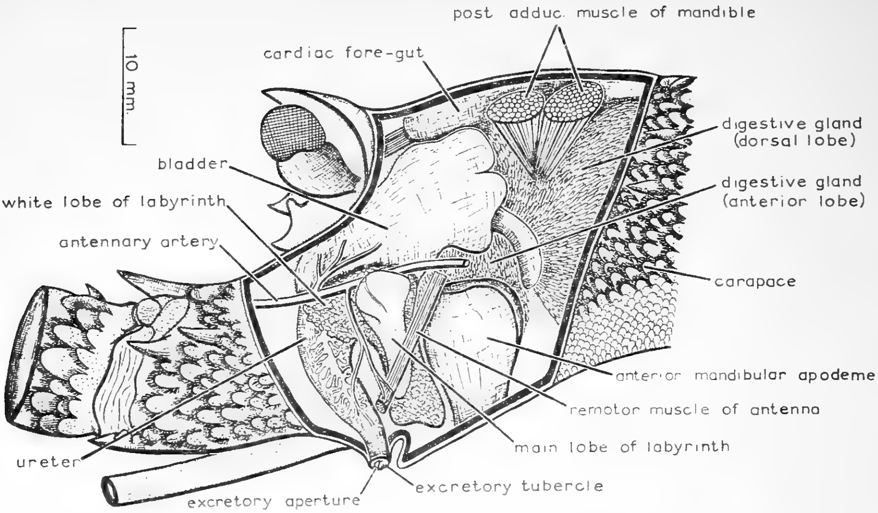


FIG. 38. Diagram of left antennal gland *in situ*.

excretory products to the exterior is effected by the *ureter*, which is continuous with the bladder and discharges on an excretory tubercle at the base of the antenna. The arrangement of the parts is variable, especially in the Macrura Reptantia and, although the antennal gland of *Astacus* is sometimes regarded as typical of Decapoda, Marchal considered it to be somewhat exceptional, but he made the important observation that the structural differences between it and the gland of marine species might signify adaptive modifications to their respective external media. Even among marine species, however, there is

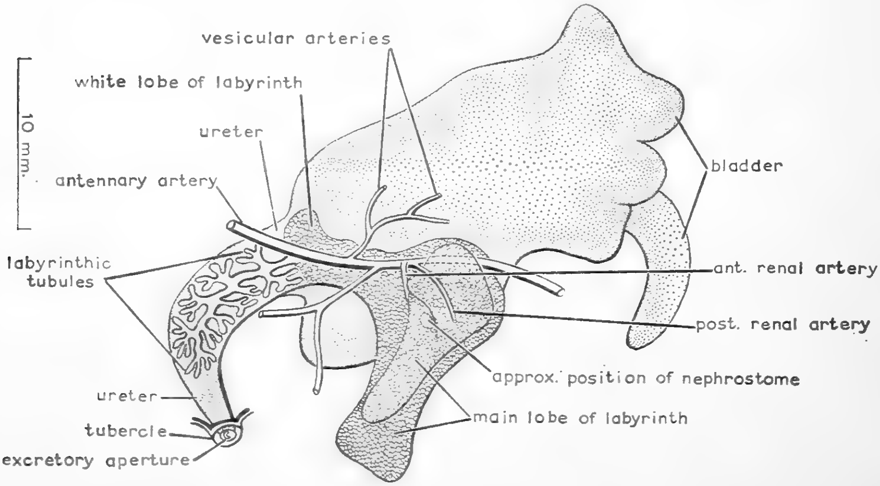


FIG. 39. Diagrammatic side view of left antennal gland, removed from the body.

apparently no uniform structural plan, and some of the most interesting variations elucidated by Marchal relate to the morphology of the end sac and the labyrinth.

In *Palaemon*, *Astacus*, and the Brachyura the end sac is distinct and perceptible on the dorsal surface of the labyrinth. Frequently, however, the end sac and the labyrinth are either intricately branched or the lumen of both may be subdivided by partitions, which develop as infoldings of the walls and obviously increase the surface area of these parts. Unlike that of *Astacus*, the end sac of the majority is ventrally prolonged into a number of processes which burrow deeply between the convolutions of the labyrinth wall and, in what may be regarded as extreme examples of this interdigitation of the two parts (Galatheidae, Thalassinidea, and Paguridae), the end sac may be so completely embedded in the labyrinth that even its dorsal wall is no longer visible on the surface of the gland. The bladder is also variously modified and, while in many Macrura it is a relatively simple sac, in the Anomura, the Brachyura, and in *Palaemon* among Natantia it may be extensively and intricately lobed.

Marchal's (1892) exhaustive studies indicate that the antennal gland of nearly every decapod species presents its own structural peculiarities and, in this respect, *J. lalandii* is no exception. From the following account, which is based on dissections and serial sections of the glands of adult specimens, it is apparent that, although there is some resemblance to the organs of *Homarus* and *Palinurus*, the parts are not morphologically identical with those of any other species so far described.

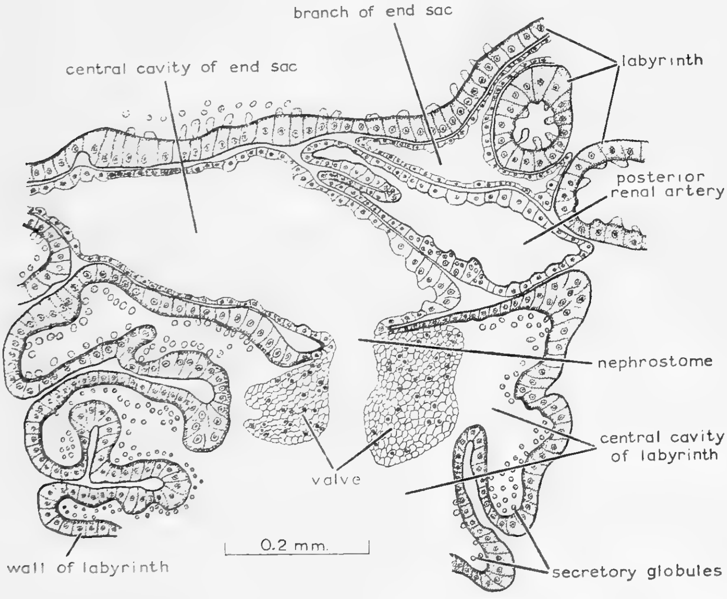


FIG. 40. Part of transverse section of antennal gland.

(a) *The end sac*

The *end sac* differs from that of the well-known *Astacus* in not being exposed on the dorsal surface of the labyrinth. As in Anomura and *Palinurus* (Marchal, 1892), it is completely enveloped by the labyrinth and therefore can only be properly identified in sectioned material (figs 40, 41). It is relatively voluminous and has a fairly distinct central cavity (fig. 40) which is located more or less dorso-laterally in the middle of the main lobe of the labyrinth. From this numerous branches radiate in all directions into the interstices of the labyrinth, so that the body of the gland is a compound of both the end sac and the labyrinth.

Waite's (1899) statement that in *Homarus* the end sac is a derivative of the embryonic coelom and that the remainder of the gland is ectodermal in origin has been quoted in several subsequent publications; but Manton (1928, 1934) has shown that both the duct and the end sac are mesodermal and that only the tube which leads to the exterior is ectodermal. Functional differences of the parts may account for the marked histological contrast between the walls of the end sac and the labyrinth in *J. lalandii*. The wall of the end sac is formed by a delicate layer of rather irregular cells (fig. 41), each of which contains a large nucleus and faintly staining granular contents and is 11·5 to 14·3 μ high.

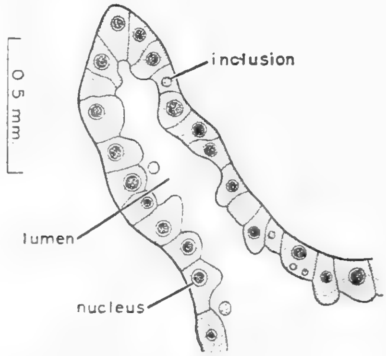


Fig. 41. Transverse section of wall of end sac.

(b) *The labyrinth*

The labyrinth is the spongy mass forming the bulk of the antennal gland and which, for descriptive purposes, may be divided into a main lobe and a white lobe.

The *main lobe* (figs 38, 39) constitutes the posterior part of the labyrinth lying adjacent to the anterior apodeme of the mandible. It is cream coloured, and when viewed laterally is roughly quadrangular in outline with its antero-ventral extremity usually curved forward almost to the level of the excretory pore. In most of specimens examined, an anterior fissure demarcates a more or less leaf-shaped lateral area from the larger more medial part of the main lobe and marks the approximate position of the underlying central cavities of the end sac and the labyrinth. It is also in this region that the end sac communicates with the labyrinth by an opening, which is sometimes termed the '*nephrostome*' (fig. 40). In many marine species (Marchal, 1892; Peters, 1935) this orifice is furnished with a valve-like structure which, however, is apparently absent in fresh-water forms, such as *Astacus* (Peters, 1935) and *Procambarus* (Maluf, 1941). Sections of the antennal gland of *Jasus* reveal that the *valve* (fig. 40) is conspicuous and essentially similar to that described by Peters (1935) in *Homarus* in that it is composed of relatively large cells which stain feebly and resemble the epithelial cells of the end sac. It therefore seems likely that, as Peters suggested, the valve represents a mass of modified end-sac cells which, by hanging into the central cavity of the labyrinth, forms a closing device between the two principal parts of the gland and prevents regurgitation of fluids into the end sac. It is also noteworthy that in the vicinity of the valve there is a conspicuous accumulation of haemocytes. These have been omitted in figure 40, but occur in a dilatation of the thin-walled renal vein, into which blood from the posterior renal artery (figs 39, 40) drains at the hinder limit of the valve. The venous channel runs parallel to the central cavity of the end sac and leaves the antennal gland in front of the valve.

The lumen of the labyrinth is broken up into numerous irregular channels by invaginations of its wall, but in the neighbourhood of the valve there is a central cavity (fig. 40) which communicates directly with the end sac through the 'nephrostome'. The epithelium of the labyrinth (fig. 42) is easily distinguished from that of the end sac, not only by its larger, more columnar cells which are from 18 to 22 μ high, but also by its more intensely stained cytoplasm. The nuclei are fairly large and almost centrally placed, and the granular cytoplasm is characterized by fine, but obvious, longitudinal striations. It is particularly noticeable that the free margin has the appearance of a striated border, which is comparable with the 'Porensaum' of *Astacus* and *Homarus* (Peters, 1935) and is surmounted by numerous globules of various sizes and

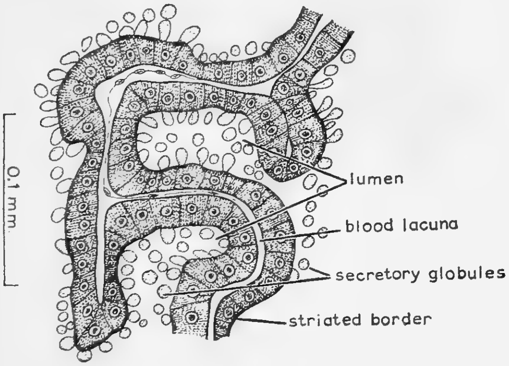


FIG. 42. Transverse section of wall of labyrinth.

shapes. These project into the lumen and, as most of the ramifications of the labyrinth are practically filled with free globules, it seems as though they have been detached from the epithelial cells as products of active secretion. Occasional cells are slightly larger than normal and are conspicuous by their paler staining properties, which may indicate some phase of this process.

In describing the antennal gland of *Homarus*, Marchal (1892) referred to the more anterior portion of the labyrinth as the *white lobe*, a term which was later accepted by Waite (1899) and Peters (1935). In *Jasus* the main lobe of the labyrinth is continuous with a dorso-ventrally flattened forward extension, which may likewise be termed the *white lobe* (figs 38, 39) because it is somewhat lighter in colour than the main lobe and may be analogous to this particular part of the labyrinth of *Homarus*. Macroscopically it appears to be less compact than the main lobe of the labyrinth, but examination of sections indicates that, while its wall may be less intricately folded, there is little histological difference between it and the main lobe. As in the latter, ramifications of the end sac run parallel to the canals of the white lobe, so that the total volume of the end sac is subequal to that of the labyrinth.

The white lobe curves upward, forward, and inward over the levator muscle of the antenna and extends almost to the cerebral ganglion. Passing downward from its anterior extremity are a number of peculiar, branched tubules which invade the lumen of the ureter and are attached to its anterior wall by connective tissue strands. These *labyrinthic tubules*, as they are herein labelled (fig. 39), are produced into small, conical processes which project freely into the lumen of the ureter, where each probably opens by a minute pore. The presence of pores is difficult to determine both in whole mounts and in sectioned material and, so far as can be ascertained, there is no direct opening from the labyrinth into the bladder. The labyrinthic tubules therefore represent the only connexion between the glandular and the storage parts of the organ, and it seems logical to suppose that their free ends are perforated.

In *Palinurus* Marchal (1892) has described an accessory gland (glande annexe) which opens by a fine canal into the ureter, but is distinct from the labyrinth; the latter, however, communicates with the bladder by a number of dorsal pores. No such accessory gland is present in *Jasus*, but a possible analogy between it and the tubules in the ureter cannot be overlooked. In this context, it is of interest to note that Marchal (1892) and Waite (1899) have shown that in *Homarus* there is also no direct passage from the labyrinth into the bladder and that the white lobe opens into the ureter by several minute pores. From this it may be inferred that the arrangement in *Jasus* closely approximates that of *Homarus* in the rather unusual relationship between the labyrinth and the ureter. It follows that, as in *Homarus*, waste products must reach the bladder by a somewhat devious route, having to proceed along the ductules of the labyrinth into the ureter and thence upward and backward into the bladder. In confirming Marchal's original observations, Waite concluded that storage of urine in the bladder could be effected by closure of the external excretory aperture. While this is a possibility, it may be significant that in *Jasus* the narrow, so-called remotor muscle of the antenna (figs 18, 38) runs obliquely across the main lobe of the labyrinth. As previously mentioned (p. 74), this muscle may merely support the labyrinth, but its insertion on the epidermis a short distance from the excretory pore and almost on a level with the lower end of the labyrinthic tubules in the ureter also suggests that it may participate either in forcing urine into the bladder or in its expulsion to the exterior.

(c) *The bladder*

The bladder or vesicle (figs 38, 39), within which the urine is stored before being voided from the body, is a large, transparent, roughly globular sac, the lower wall of which is inseparably adherent to the upper surface of the labyrinth. Its delicate wall consists of a single layer of small columnar cells which are structurally similar to those of the peripheral part of the labyrinth. On the outer surface there is a thin connective-tissue layer, which is probably highly contractile, for the bladder shrinks immediately and markedly upon immersion in fixing agents. Owing to its transparency, the full extent of the bladder is not easily discernible in ordinary dissections but, by injecting coloured latex or coloured gelatine mass either directly into it or through the excretory pore, the whole structure is thrown into relief against the neighbouring organs. It can then be seen that medially, dorsally and ventrally it fits closely into the contours of the cardiac fore-gut, while posteriorly it extends between the anterior and dorsal lobes of the digestive gland and may even invade the former. Anteriorly it projects for a short distance in front of the white lobe of the labyrinth and narrows considerably as it approaches the ureter.

(d) *The ureter*

The ureter (figs 38, 39) is the transparent, relatively broad efferent duct continuous with the bladder. It is antero-posteriorly flattened, and is so closely applied to the base of the proximal segment of the antenna that it is largely obscured by the antennal levator muscle which occupies the space between the main lobe of the labyrinth and the ureter. As it passes outward from the bladder, its lateral wall lies rather superficially below the base of the antennal peduncle; the duct then curves backward for a short distance and narrows as it proceeds to its small, crescentic opening situated anteriorly at the tip of a whitish, conical tubercle (figs 38, 39) on the ventro-lateral surface of the epistoma. Marchal (1892) and others have described the flexible membrane stretching across the tubercle as the operculum but, as Maluf (1941) has rightly observed, the term is inappropriate, for in most decapods the excretory aperture is exposed on the surface of the membrane and is not covered by it. Balss (1944), however, has summarized the operation of the so-called operculum in Brachyura, and has explained that early observers regarded the antennal glands as auditory organs.

(e) *General remarks*

The most significant difference between the antennal gland of the fresh-water crayfish, *Astacus*, and that of *Jasus* and other marine Decapoda is the presence in the former of a long, convoluted nephridial canal or white medullary tubule, which is intercalated between the greenish labyrinth and the bladder. It was suggested by Marchal (1892) that the absence of this canal in marine decapods and the functional differences between their glands and those of fresh-water species might be correlated with the salinity of the external medium. In apparent confirmation of this, it has been demonstrated by Peters (1935) that, contrasted with the urine of the marine *Homarus* which is known to be isotonic with the blood, that of *Astacus* is markedly hypotonic owing to a decrease in the chloride concentration of the urine in transit from the labyrinth to the bladder. The production of a hyposmotic urine may therefore indicate that the additional part or nephridial canal in the antennal gland of crayfishes is an adaptation to their fresh-water habitat. It has generally been considered that the canal assists in necessary osmoregulatory processes, and that the dilution of the urine is effected either by an outward secretion of water or by the resorption of chloride from the excretory products passing through its lumen. However, in recent analyses of the fluid removed from different parts of the antennal glands of fresh-water crayfishes Riegel (1965) has shown that the bladder may be even more important than the nephridial canal in diluting the urine. Some information is also available concerning the function of the antennal glands of marine species, Forster & Zia-Walroth (1941) having concluded that water is neither secreted nor resorbed in the antennal glands of *Homarus americanus*, while Burger (1955–7) has shown that, although the glands of *Homarus* are capable of resorbing glucose, they are not instrumental in the conservation of chloride, which presumably enters through the gills. The gist of existing knowledge collated by Parry (1960), Robertson (1960), and Lockwood (1962) is that, except in such fresh-water forms as crayfishes, *Asellus aquaticus* and species of *Gammarus*, and in the brackish-water *Gammarus duebeni*, the urine of Malacostraca is generally isotonic with the blood and the excretory glands play no significant part in osmoregulation. According to Robertson (1960), it has also been established that in marine decapods the main function of the antennal glands is the maintenance of the ionic balance of the body fluids. Selective excretion of Mg^{++} and SO_4^{--} by the antennal glands has been proved in a number of species, while other ions, including K^+ and Ca^{++}, are conserved.

There is still no universal agreement among physiologists regarding the method of urine formation, and opinions differ as to whether it is a product of filtration or of secretion. For different reasons, Peters (1935) and Picken (1936) decided that the processes of filtration, secretion, and resorption probably take place in the antennal glands in much the same way as they do in the vertebrate kidney. Based chiefly on histological studies of the antennal glands of *Astacus* and *Homarus*, the former investigator deduced that the primary urine is produced as an ultrafiltrate of the blood supply to the wall of the end sac, and a similar conclusion was reached by Picken on determining that the hydrostatic pressure of the blood of *Astacus* usually exceeded its colloid osmotic pressure. Some additional data supporting the filtration theory have been presented by Forster & Zia-Walroth (1941) and Burger (1955–7), whose experiments on inulin renal clearances in *Homarus americanus* demonstrate that in this animal the primary urine is probably formed by filtration. Furthermore, the unusual glycosuria reported by Burger in lobsters treated with phlorizin, a drug known to check resorption of glucose from the vertebrate kidney, may have a similar significance.

Histologically there is a resemblance between the antennal glands of *Homarus* and *Jasus*, in both of which the marked structural differences between the epithelial cells of the end sac and the labyrinth suggest functional differentiation of the parts. Whereas occasional cells of the end sac of *J. lalandii* may have granular contents and the lumen is practically empty (figs 40, 41), the convoluted channels of the labyrinth (figs 40, 42) are filled with globules. Similar vesicles or 'Sekretblasen' in the labyrinth of *Astacus* and *Homarus* were regarded by Peters (1935) as products of the wall of this part of the gland, and he implied that active resorption of essential substances from them into the blood could take place in the nephridial canal. Moreover, while Peters doubted the secretory potential of the end sac, Marchal (1892) was of the opinion that secretion by the detachment of vesicles from the cells prevails in all parts of the organ, including the bladder of some species. However, Parry (1960) has indicated that filtration is possible through the presumed semipermeable wall of the end sac, especially as there are pressure differences between its blood supply and its lumen. In dissections of anaesthetized specimens of *J. lalandii*, it was observed that the blood courses through the antennary artery under considerable pressure on its way to the antennal gland; this fact and the distribution of the renal arteries would seem to provide some evidence that primary filtration may take place through the wall of the end sac. The alternative theory that the urine is produced by secretion also has a number of supporters, whose studies have been cited by Parry (1960) and Lockwood (1962), but recent research confirms the presence of a filtration mechanism. Kirschner & Wagner (1965) have proved experimentally that the primary ultrafiltrate is formed in the end sac of fresh-water crayfishes, and Riegel (1965) has also subscribed to this view.

As yet, there is no published information on the physiology of the antennal glands of *J. lalandii* and, although they differ in certain respects from those of marine species which have been studied by other investigators, several of the histological similarities between them and the organs of *Homarus* (Peters, 1935) may have some significance. It is therefore conceivable that filtration takes place in the end sac and that some unknown substances are added to the primary urine in other parts of the gland by secretion from the blood.

2. OTHER EXCRETORY ORGANS

From information presented by Parry (1960), it is patent that analyses of the end products of protein metabolism in Crustacea are compatible with the findings in most aquatic invertebrates. The antennal glands, however, are not primarily concerned with nitrogenous excretion and, although ammonia is the principal waste product, relatively small quantities of it and also of urea are found in the urine. By contrast, the urine contains rather high percentages of amino nitrogen, but the source of the small amounts of uric acid known to be excreted has not definitely been ascertained. The explanation of some of these facts seems to be that, as a consequence of the importance of the antennal glands in the regulation of the internal ionic levels, other parts of the body have become involved in the elimination of nitrogenous wastes.

It has long been assumed that the gills and the digestive glands are essential components of the excretory system and that the former play an important role in osmoregulation and ionic balance, their surface permeability, according to Krogh (1939) and Burger (1957), allowing of an intake of water and salts to compensate for the loss of these from the antennal glands. Among other things, Burger (1957) has suggested that ammonia is removed by the gills, while Parry (1960) has indicated that analyses of the digestive glands of a number of species demonstrate the presence of relatively large quantities of uric acid. An excretory function has also been attributed to the gut, to the integument, and to special large cells, termed the *nephrocytes* or nephrophagocytes, in which excretory matter appears to accumulate and is presumably later eliminated by some means or another. Nephrocytes have been reported mainly in the epipodites, the gills and the branchio-pericardial vessels of Decapoda, and have been shown by Bock (1925) and Dornesco & Homei (1940) to be confined to the channels containing oxygenated blood in the gills of *Astacus* and *Palinurus* respectively. Numerous oval cells, measuring about 25 μ by 14 μ, have a similar distribution in the gills of *Jasus*. They are conspicuous in transverse sections (fig. 44) by their size, their staining properties, and their apparent ability to phagocytose injected India ink, and are doubtless identical with the nephrocytes of other Decapoda.

F. RESPIRATORY ORGANS

Respiration is performed by a series of 21 pairs of segmentally-arranged *gills* or *branchiae* which, according to the observations of several authors cited by Calman (1909), develop as outgrowths of the bases of the thoracic appendages. They are lodged on each side of the cephalothorax in a somewhat compressed *branchial chamber* (figs 43, 53) bounded by the thoracic epimera on the inside and enclosed by the overarching branchiostegite (figs 1, 2, 10, 53, 77) on the outside. The latter is a lateral fold of the carapace composed of an outer strongly-calcified wall and an inner, thin, transparent, cuticular lining which, for convenience, has been termed the *branchial membrane* (figs 9, 10, 77); it is distinguished by its dense, inner covering of short, brown, finger-like processes tipped with slender spines and interspersed with long, straggling, finely-barbed hairs. The lower margin of the branchiostegite is closely applied to the bases of the coxopodites of the thoracic limbs, but its slight sinuosity allows of ingress of water into the branchial chamber through the gaps between the limbs.

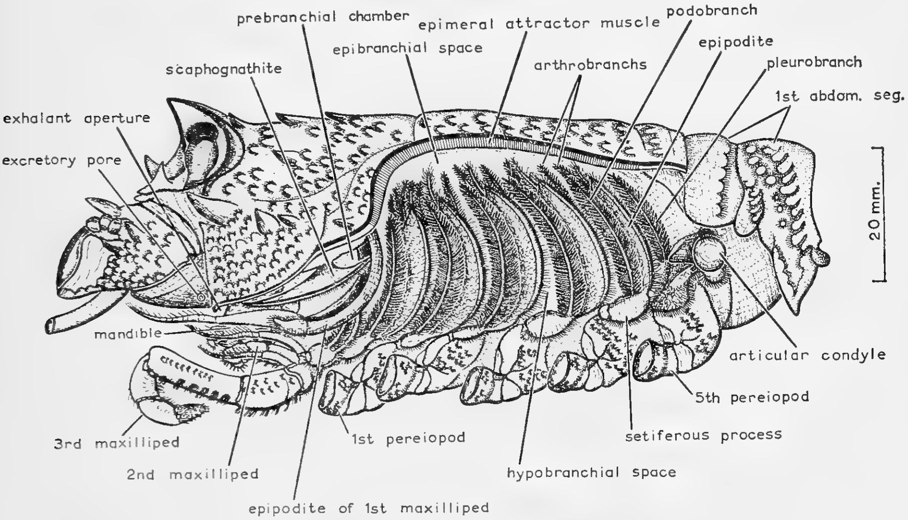


FIG. 43. Left branchial and prebranchial chambers.

The *gills* (figs 43, 53), which curve upward from the limb bases and arch slightly forward, are arranged into segmental sets from the second to the last thoracic segment. The successive groups of gills are separated by vertical *epipodites* (figs 43, 53, 55), each of which is a thin-walled, lamellate, hairy plate originating on a conspicuous, somewhat triangular setiferous process (figs 5, 43, 56) at the base of the coxopodite of its corresponding appendage. In some Decapoda the epipodites are bilobed structures, but in *Jasus*, although they are folded down the middle into inner and outer laminae in the puerulus stage, in the adult the duplication is only apparent in the reflection of the outer margin of each epipodite over the gills of the segment behind.

According to their attachment relative to the appendages and the body wall, Huxley (1881) differentiated the gills into three types (figs 43, 53, 55): the *podobranchs* arising with the epipodites on the setiferous processes, the *anterior* and *posterior arthrobranchs* associated with the arthrodial membranes, and the *pleurobranchs* situated on the epimera. Thus on each side of a typical segment (fig. 53) there is one epipodite and four gills, but the full complement is only realized in the fifth, sixth, and seventh segments (fig. 55), the anterior segments lacking pleurobranchs and sometimes other gills, while the last segment (fig. 55) has only a pair of pleurobranchs. The arrangement of the various gills on one side of the body and their corresponding appendages are tabulated in the following *branchial formula*, which applies not only to the adult but also in some measure to the puerulus stage. In this connexion, it is of interest to note Gilchrist's (1920) conclusions that in the phyllosoma larva there are characteristically one podobranch, one arthrobranch, and an anterior and a posterior pleurobranch on each side of a given segment. It is said that this arrangement is retained in the puerulus stage, but that subsequently the larval posterior pleurobranch is transposed and becomes the posterior arthrobranch of the adult. This may account for the somewhat forward position of the first three pleurobranchs in the adult (fig. 56), and perhaps also explains the fact that in some juvenile animals the last pleurobranch tends to be aligned more with the arthrobranchs than with the pleurobranchs of other segments.

Appendage	*Epipodites*	*Podobranchs*	*Anterior Arthrobranchs*	*Posterior Arthrobranchs*	*Pleurobranchs*	*Total*
1st Maxilliped	1	—	—	—	—	Ep. + 0 gills
2nd Maxilliped	1	1	—	1	—	Ep. + 2
3rd Maxilliped	1	1	1	1	—	Ep. + 3
1st Pereiopod	1	1	1	1	—	Ep. + 3
2nd Pereiopod	1	1	1	1	1	Ep. + 4
3rd Pereiopod	1	1	1	1	1	Ep. + 4
4th Pereiopod	1	1	1	1	1	Ep. + 4
5th Pereiopod	—	—	—	—	1	0 + 1
Total	7	6	5	6	4	7 Ep. + 21 gills

The above interpretation of the arrangement of the epipodites and gills agrees with Huxley's findings, except for one minor point relating to the single arthrobranch on the second thoracic segment. Huxley identified this as an anterior arthrobranch in *Astacus* and in *Palinurus*, but Bock (1925) has shown that in the former genus it is posterior in position. In most thoracic segments of *Jasus* (fig. 56) the level of attachment of the podobranch is almost midway between the anterior and posterior arthrobranchs and, while the exact position of the single gill on the narrow arthrodial membrane of the second maxilliped is somewhat elusive, the indications in adult specimens and in sections of the puerulus stage are that it is slightly behind its corresponding podobranch and may, therefore, be regarded as a posterior arthrobranch.

Structurally each gill belongs to the *trichobranchiate type* and is a plumose, pyramidal organ having a central shaft or *gill axis*, which is roughly triangular in transverse section (fig. 44) with rows of thin-walled, slender *gill filaments* (fig. 44) along the longer outer anterior and posterior margins. The narrower inner or more medial surface of the axes of the arthrobranchs and the pleurobranchs is almost smooth, being furnished only with sparsely-distributed, minute, hooked setae, but that of the podobranchs has a fairly dense covering of long, finely-barbed setae similar in appearance and length to those on the surfaces of the epipodites. The filaments decrease progressively in number and

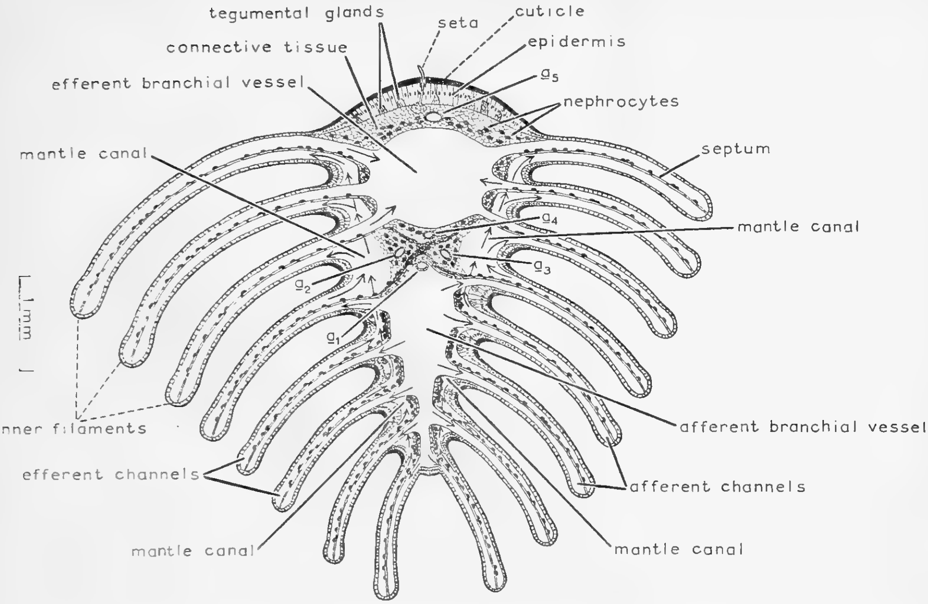


FIG. 44. Diagrammatic transverse section of last left pleurobranch of adult; a_1 to a_5, branchial arteries.

size from the base to the tip of the gill axis and, while they are bilaterally symmetrical in number and arrangement along the axis of the pleurobranchs, there are characteristically fewer filaments on one side of the axis of the arthrobranchs and the podobranchs than on the other.

Microscopic examination of transverse sections (fig. 44) reveals that the gill axis, like other parts of the body, is bounded by an epidermis consisting of a single layer of columnar cells interspersed with tegumental glands; its cuticular layer is fairly thick in the interfilamentar regions but much thinner on the filaments. The latter are horizontal evaginations of the gill axis, with the epidermis of which their delicate walls are continuous. Gaseous exchange, resulting in the oxygenation of the blood, takes place through the epidermis of the filaments, which, unlike the syncytial condition observed by Dornesco & Homei (1940) in *Palinurus*, is composed of cuboidal cells with conspicuous rounded nuclei.

Four main blood channels occur in the gill axis (fig. 44), the two median ones being an outer *afferent branchial vessel* lined with a very thin epithelium and an inner *efferent branchial vessel* which is surrounded by a relatively wide dermal layer of loose connective tissue riddled with blood lacunae. Flanking the median vessels is a pair of blood spaces corresponding to the circular vessel reported by Herrick (1911) in the gills of *Homarus* and to the Mantelkanal, first described by Bock (1925) in *Astacus* and later by Dornesco & Homei (1940) in *Palinurus*. The two *mantle canals* are separated from the afferent and efferent branchial vessels by a sheath of rather coarse fibrous connective tissue and attain their greatest width and adjoin each other between the two median vessels. Prolongations of the fibrous coat of each mantle canal extend outward towards the filaments and appear to participate in the formation of the longitudinal *septum* (fig. 44) which divides the lumen of each filament into *afferent* and *efferent channels*. Numerous conspicuous, oval cells, the *nephrocytes*, occur in the mantle canals, in the connective tissue around the efferent branchial vessel, and also along the septa of the filaments where, however, they are located only on the side of the efferent channels. Their presence is indicative of the subsidiary part played by the gills in the excretory mechanism of the body.

The course of the *respiratory current of water* through the branchial chamber is substantially similar to that of *Carcinus maenas* (Borradaile, 1922) and *Astacus astacus* (Bock, 1925), and can be demonstrated easily by introducing carmine particles in suspension in sea water into the inhalant openings between the leg bases by means of a fine pipette. To facilitate the observations, the specimen may be temporarily immobilized by immersing it in an anaesthetic agent, such as a 1 : 2000 dilution of 'Sandoz' in sea water. Within a few minutes the animal becomes quiescent, and it is then possible to perform simple experiments to prove that the carmine entering the inhalant openings eventually clouds the water exuding from the exhalant aperture. Subsequently, to demonstrate the path of water through the branchial chamber, two 'windows', about 1·5 by 1·0 cm, may be cut in the branchiostegite, one in the intersegmental region between the third and fourth pereiopods a short distance above the lower edge of the branchiostegite, and the other more dorsally at the anterior end of the branchiostegite just behind the prebranchial chamber. Carmine introduced between the third and fourth pereiopods will be seen to swirl up around the bases of the gills into what Borradaile (1922) has termed the *hypobranchial space* (fig. 43), and will later be observed through the second 'window' to flow forward in the upper or *epibranchial space* (fig. 43) on its way to the prebranchial chamber and the exhalant aperture.

It is thus apparent that the main inhalant stream of water for aerating the gill filaments enters the branchial chamber through segmental openings between the limb bases and the lower border of the branchiostegite and that the setae on these parts are a safeguard against the instrusion of foreign particles into the branchial chamber. As previously indicated (p. 17), the branchiostegite is postero-laterally secured to a projecting articular condyle or knob on the last thoracic epimeron, below which there is a triangular plate corresponding with the setiferous processes of the coxopodites in other segments. This locking device and its underlying plate preclude the entrance of water at the postero-ventral edge of the branchiostegite, but between the first abdominal segment and the overlapping carapace there is a narrow dorsal passage with an upper row of inwardly-directed setae which, judging by the course of introduced carmine particles, allows of an incurrent stream of water for the ventilation of the pleurobranch on the last thoracic segment.

The passage of water into the lower or *hypobranchial space* around the bases of the gills is doubtless facilitated by movements of the appendages, but its subsequent circulation over the gill filaments and into the *epibranchial space* at the dorsal extremities of the gills is dependent on the scooping action of the scaphognathite of the second maxilla, which is lodged in the *prebranchial chamber* (fig. 43). The latter is an exhalant passage in the cephalic region beneath the antero-lateral part of the exoskeleton, its immediate roof being the epimera of the mandibular and maxillary segments. It is separated from the branchial chamber by the arched and thickened epipodite of the first maxilliped which, with the exopodite of the same appendage, forms the trough of the prebranchial chamber. Within this chamber the scaphognathite of the second maxilla lies more or less horizontally and has freedom of movement, its strong sinuous action drawing water from the branchial chamber and driving it forward and out through the *exhalant aperture* (figs 2, 4, 43). Situated behind the excretory pore, the exhalant aperture is defined by a slight dorso-lateral deflection of the roof of the prebranchial chamber and the overlapping edge of the head exoskeleton, while on its medial border lie the tuft of setae on the antero-lateral margin of the mandible and a row of short setae in the antero-medial corner of the prebranchial chamber. When the excurrent stream of water leaves the exhalant aperture, it flushes obliquely forward over the epistoma, carrying with it the products from the antennal gland.

That the gills are not the only respiratory surfaces is suggested by the rich blood supply to the epipodites and the branchial membrane lining the branchiostegite, which are sufficiently thin-walled to permit of gaseous exchange between their contained ramified blood vessels and the inhalant current of water. In addition to their respiratory function, active chloride absorption has been attributed to the gills of some freshwater Crustacea by a number of physiologists, among whom Ewer & Hattingh (1952) have also indicated that the inner surface of the branchiostegite, as well as the gills, of the fresh-water prawn, *Caridina nilotica*, has potential chloride-absorbing regions.

G. BLOOD VASCULAR SYSTEM (Figs 44, 46–56, 74)

While the main arteries may be traced in freshly-killed or in preserved specimens, the vessels are delicate and collapsible and the ramifications of their finer branches are not easily followed. Injection of various coloured media may also be rather unsatisfactory, one of the disadvantages being that the heart ostia are often open in dead animals, and leakage of the injection fluid from the heart inhibits its flow into the vessels. In the present observations, the best results were obtained by introducing Higgins black indian ink, diluted with equal parts of distilled water, into an animal which was partially anaesthetized after immersion for twenty to thirty minutes in two gallons of sea water containing nine grams of sodium phenobarbitone. After securing the animal to a dissecting board, a small hole, approximately equal in size to the diameter of a fine capillary tube, was drilled through the middle of the cardiac region of the carapace, either into the pericardial cavity or into the heart. The capillary tube, attached by a length of rubber tubing to a raised glass thistle funnel containing the diluted India ink, was then inserted into the hole in the carapace and the ink was allowed to flow into the vascular system by a slow and regular drip-feed process. As the ink dripped from the capillary tube, it was carried by the rhythmical pumping of the heart to all parts of the vascular system, including the haemocoelic sinuses, the afferent branchial vessels, and the gill filaments. The operation was completed in from ten to fifteen minutes, by which time about 5 to 6 cc of the ink had been injected and the animal was moribund. On removing the capillary tube, the hole in the carapace was plugged with plasticine and the animal was placed in 10% formalin for a few days. It was then possible, not only to trace the dilated and clearly-defined arteries to various parts of the body, but also, as a result of the deposition of carbon particles, to gain a good impression of the extent of the haemocoelic sinuses.

As in typical decapod Crustacea, the oxygenated blood is pumped from a short, compact, muscular *heart* lying in the *pericardial cavity* into a number of *arteries*, which usually branch extensively and terminate in fine vessels in the tissues and organs. Another characteristic is the absence of direct capillary connexions between the arterial and the venous parts of the circulation and, as indicated by Maynard (1960), it is generally assumed that the deoxygenated blood passing from the tissues traverses interstitial (lymphatic) lacunae before being collected into *sinuses* which therefore, strictly speaking, contain haemolymph. In the present account the sinuses are simply regarded as irregular venous channels; they are more or less continuous throughout the body, and the wide perivisceral spaces constitute the body cavity or *haemocoel*.

The general concept is that in most Decapoda the deoxygenated blood from all parts of the haemocoel eventually drains into a *sternal sinus* in the thorax and is then directed into *afferent branchial vessels* on the outer side of the gill axes and thus conducted to the gill filaments where oxygenation takes place. On leaving the gill filaments, the oxygenated blood passes into *efferent branchial vessels* which lie on the inner side of the gill axes and communicate with a series of *branchio-pericardial vessels*. The latter are located along the inner walls of the thoracic epimera and discharge dorsally into the pericardial cavity. The blood then enters the heart through three pairs of openings, the *ostia*, and, on contraction of the cardiac muscles, is driven into the arterial system.

Dissolved in the blood plasma is a copper-containing respiratory pigment *haemocyanin*, which has a bluish tint when oxygenated. Wolvekamp & Waterman, (1960) have given an account of the problems relating to respiration in Crustacea, including the factors influencing oxygen consumption, gaseous exchange between the external medium and the respiratory surfaces, and oxygen transport by the blood. Various studies of the biochemistry of haemocyanin and other pigments have been reviewed by Goodwin (1960), and he and Wolvekamp & Waterman have indicated that in Arthropoda haemocyanin has only been found in chelicerates and in decapod and stomatopod Crustacea.

1. PERICARDIAL CAVITY AND HEART

(a) *The pericardial cavity* (Figs 53, 56)

The heart (figs 9, 10, 31, 53, 78) lies in the middle of an irregularly rectangular space, the *pericardial cavity*, which occupies the mid-dorsal posterior half of the cephalothorax and is exposed on removal of the cardiac region of the carapace (fig. 9). The pericardial cavity is roofed over by the dorsal body wall, while ventrally there is a thin *pericardial septum* (fig. 53) which forms a broad, somewhat convex, horizontal sheet extending above the posterior lobe of the digestive gland and the reproductive organs and is attached laterally to the epimeral plates. Anteriorly the septum slopes upward behind the dorsal lobe of the digestive gland to meet the body wall, while the posterior boundary of the cavity is formed by the union of the septum with the anterior margin of the first abdominal segment. The septum is a transparent, elastic membrane containing delicate, lateral *alary muscles* which pass inward from the epimera as a series of contiguous, parallel bands; they do not extend across the middle third of the septum, and frequently appear to be stronger posterior to the heart. Although the heart is completely separated from the general perivisceral haemocoel, the pericardial wall is perforated anteriorly and posteriorly by the main arteries leaving the heart and ventro-laterally by the entrance of the branchio-pericardial vessels. In addition, the paired lateral and deeper thoraco-abdominal muscles invade the pericardial cavity (figs 9, 10, 45, 53) and lie one above the other on each side of the heart.

(b) *The pericardial pouches* (Figs 9, 45)

Posteriorly the pericardial cavity is prolonged into a wide dorsal space which is covered by the inturned posterior margin of the carapace and the thin intertergal arthrodial membrane between the cephalothorax and the abdomen, while the pericardial septum forms its floor. In the vicinity of the articular condyle for the carapace, it expands somewhat into a lateral pocket, and a slightly paired effect is produced. The two halves thus seem comparable to the *pericardial pouches* which have been described in Brachyura by Pearson (1908), Drach (1939), and Bliss (1956, 1963), but they appear to be relatively smaller and to contain less connective tissue. The whole structure seems to be a modification of the anterior half of the thoraco-abdominal intertergal region and has a basket-like appearance owing to the presence of fairly obvious, inner transverse muscles and thinner, outer longitudinal muscles.

The transverse muscles form a sheet of more or less parallel fibres, those of the two sides meeting at a median raphe; but as they differ in length, their lateral attachments take the form of a curved line on the wall of the pouch, with some of the anterior fibres extending between the posterior edge of the epimeral plate and the inner ridge of the carapace. On each side of the mid-line the longitudinal fibres are attached to the dorsal body wall at the junction of the inturned margin of the carapace and the thoraco-abdominal intertergal

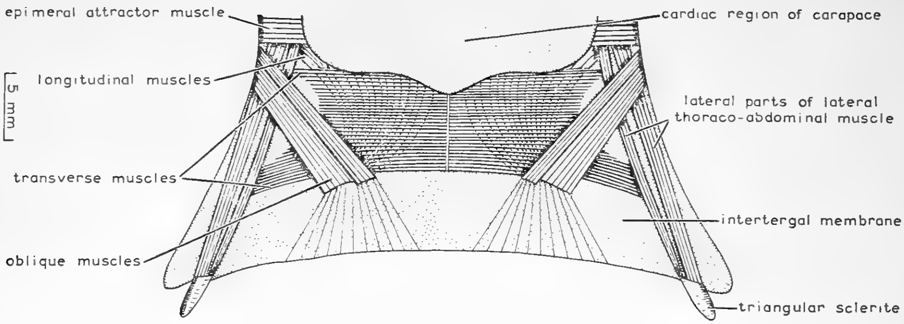


FIG. 45. Diagrammatic inner view of muscles associated with the pericardial pouches.

membrane, and some may even originate in the postero-dorsal corner of the branchial chamber. They curve medially and are then usually inflected posteriorly to converge on a narrow, slightly thickened insertion on the line of flexure of the intertergal membrane. Associated with the longitudinal fibres, and probably also with some very delicate fibres in the posterior half of the intertergal membrane, are two parallel bundles of oblique fibres (fig. 45). These arise on the epimeron behind the epimeral attractor muscle and below the lateral portions of the lateral thoraco-abdominal muscle. Passing in a postero-medial direction under the medial section of the latter muscle, they are inserted at the base of the longitudinal muscles. They are probably concerned with the infolding of the membrane, while the transverse and longitudinal fibres may be responsible for alternate constriction and shortening of the intertergal membrane and the pouches.

Pericardial pouches have been reported in a number of decapod Crustacea, but for many years their function has been uncertain. In 1939, however, Drach drew attention to the fact that, although the new lining of the gut in marine Brachyura is responsible for water absorption, the pericardial pouches act as storage organs for the absorbed water, and the elasticity of their walls is effective in controlling the hydrostatic pressure within the body during the critical period of ecdysis. Bliss (1956, 1963) has also proved experimentally that in the land crab, *Gecarcinus lateralis*, while they may be the normal focus of intake and retention of water during the intermoult, they become greatly enlarged by increased absorption before ecdysis. The position of the pericardial pouches in other Decapoda also supports the view that they are closely associated with this process, for, as Travis (1954) has remarked in *Panulirus argus*, one of the most striking changes observed in moulting specimens of *J. lalandii* before the old carapace became detached was the gradual distortion of the body between the thorax and the abdomen owing to the distension of the thoraco-abdominal intertergal membrane. Once the latter had been ruptured, the old carapace slid forward rapidly and the soft-bodied animal emerged dorsally between the cephalothorax and the abdomen of the old exoskeleton.

(c) *The heart* (Figs 46–48, 50)

The heart is elongate with sloping anterior margins and a rounded posterior extremity; it is a comparatively large, whitish, spongy organ, measuring about 20 mm long by 8 to 9 mm broad in medium-sized animals. As in other Decapoda, it is provided with three pairs of slit-like openings, the *ostia* (figs 31, 46–49, 53), through which the blood collected in the pericardial cavity enters the heart. The ostia are antero-dorsal, postero-lateral, and ventral in position and, while the dorsal ostia are directly obliquely forward and outward, the lateral ostia are more or less vertical and the ventral ostia are transverse. Each ostium is bordered by fairly wide, thin-walled lips, and closure of the opening is effected by contraction of a band of muscles along the free edge of each lip. The muscle bands of the two lips meet at the corners of the opening, and one overlaps the other before the muscle fibres pass into the wall of the heart. Inwardly projecting ostial valves, which have been reported in some Malacostraca, were not observed.

The heart is suspended in the pericardial cavity by groups of delicate elastic threads which are associated with the expansion of the heart and the influx of blood during diastole. The fine strands constituting any one group usually arise in a common, short, narrow ligament secured to some particular part of the pericardial wall, but spread out and tend to interlace on their way to the heart. They are comparable to the *alae cordis* of *Cancer* (Pearson, 1908) and the *suspensory ligaments* of *Astacus* (Baumann, 1921), and comprise anterior and posterior dorsal strands and six sets of fan-shaped lateral bands. As in *Astacus*, the *anterior ligaments* (figs 46, 47) are small, tough strips attached dorsally to the integument and inserted on either side of the root of the ophthalmic artery. Posteriorly the heart is suspended mid-dorsally to the body wall at the anterior margin of the pericardial pouch by a tuft of short fibres which, although they seem to be paired at their origin, represent the median *posterior ligament* (figs 46, 47) of other forms.

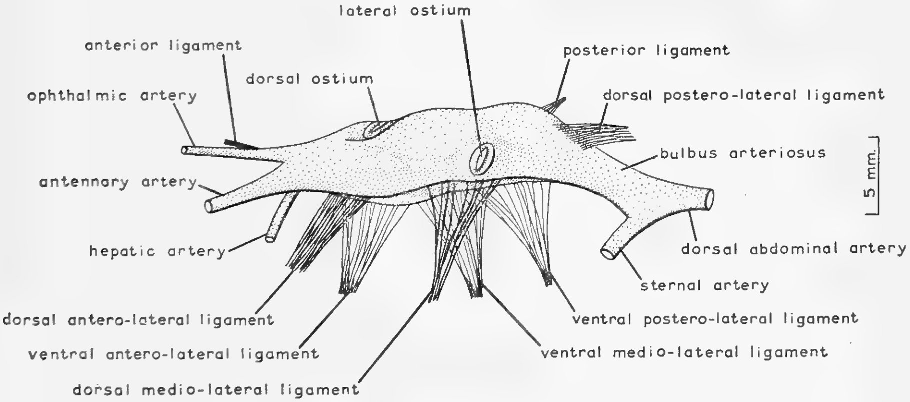


FIG. 46. Side view of heart.

Three of the six lateral suspensory ligaments (figs 46–48) are inserted dorsally and the other three ventrally along the lateral edges of the heart. The *dorsal* and *ventral antero-lateral* and *postero-lateral ligaments* are similar to those described by Pearson (1908) and Baumann (1921), but between them are additional bands which have been termed the *dorsal* and *ventral medio-lateral suspensory ligaments*. The dorsal antero-lateral and dorsal postero-lateral ligaments are more compact than the others and, while the former is attached antero-laterally to the pericardial septum behind the dorsal lobe of the digestive

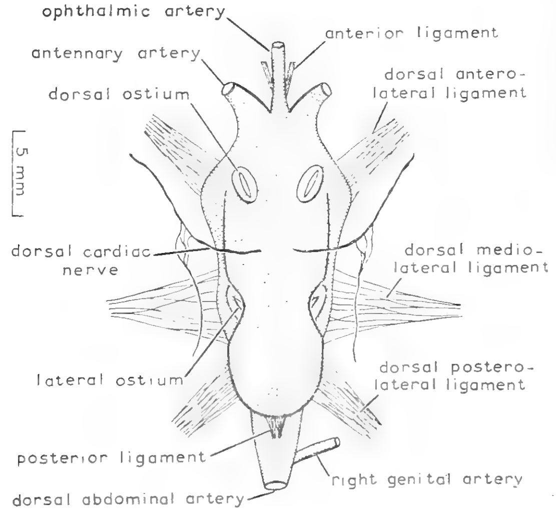


FIG. 47. Dorsal view of heart.

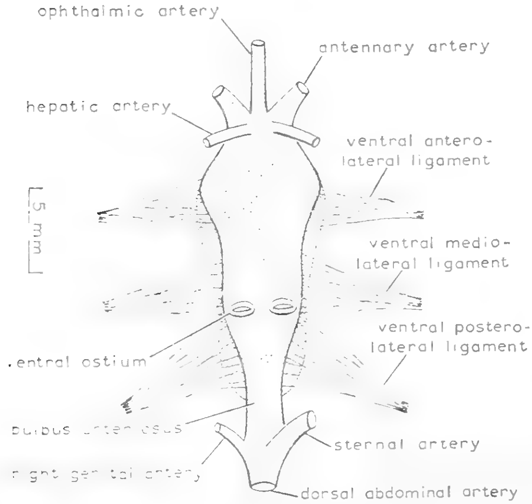


FIG. 48. Ventral view of heart.

gland, the dorsal postero-lateral ligament originates close to the antero-lateral margin of the pericardial pouch (fig. 9). The more fragile dorsal medio-lateral ligament arises on the epimeron above and approximately midway between the anterior and the middle branchio-pericardial orifices and passes horizontally over the deeper thoraco-abdominal muscle. The three ventro-lateral ligaments underlie the dorso-lateral bands and have strong attachments at intervals in the midst of the alary muscles of the pericardial septum.

In addition to the above, there are several short, mid-dorsal threads extending between the roof of the pericardial cavity and the wall of the heart, and associated with the sides of the bulbus arteriosus are a number of fibres probably comparable to the paired posterior ala cordis of *Cancer* (Pearson, 1908) and the ligamentia ventralia indicated by Baumann (1921) in *Astacus.*

(d) *Inner structure of the heart*

The lumen of the heart is covered by a relatively thin dorsal wall, composed of a spongy network of rather fine muscles. Ventrally there are sets of stronger cardiac muscles (fig. 49) which branch and interlace in the lumen and curve upward into the lateral and dorsal walls. The arrangement seems to be more complex than in the heart of *Astacus,* in which Baumann (1921) distinguished a main longitudinal musculus obliquus cordis and a group of trans-

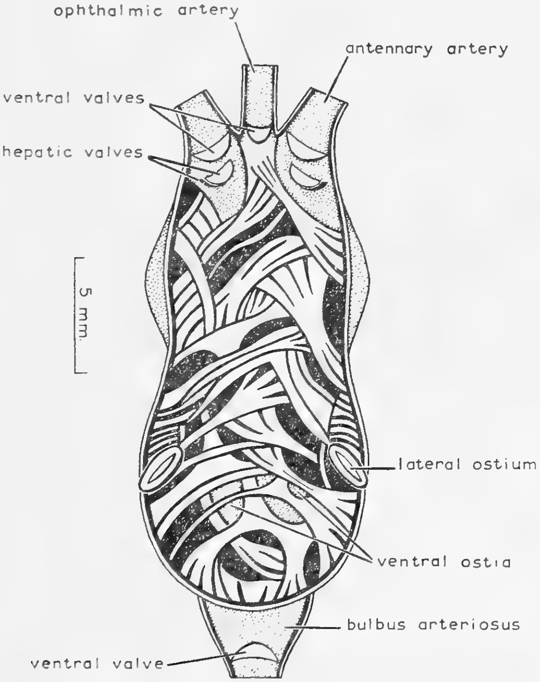


Fig. 49. Impression of cardiac muscles, after removal of dorsal wall of heart.

verse musculi frontales. In the heart of *Jasus* there is no continuous longitudinal muscle, but several separate bundles are slanted antero-posteriorly, and all the strands are so organized that none traverses the perimeters of the ostia.

The anterior muscles, which may be analogous to the musculi frontales of *Astacus*, arise between the hepatic arteries and form the boundaries of niches for these vessels and also for the ophthalmic and antennary arteries and the dorsal ostia. In the middle third of the heart the muscle strands are more or less obliquely transverse before and behind the level of the lateral ostia and demarcate recesses for these and the ventral ostia. The muscles in the posterior third are longitudinally arched and define a comparatively deep ventral space leading into the bulbus arterious. All the recesses occasioned by gaps between the muscles communicate widely with the central lumen during diastole, and it seems likely that the disposition of the muscles and their contraction at systole ensures a balanced distribution of blood to the various arteries.

2. ARTERIAL SYSTEM

From the anterior end of the heart there arise five arteries: a median *ophthalmic* (cephalic of Pearson, 1908; Aorta mediana of Baumann, 1921; carotid artery of Brody & Perkins, 1930), a pair of *antennary* arteries (lateral arteries of Pearson; Arteriae laterales cephalicae of Baumann), and a pair of ventro-lateral *hepatic* arteries. Posteriorly there is a slight *bulbus arteriosus* in which the *dorsal abdominal artery* (posterior aorta of Pearson; Arteria dorsalis pleica of Baumann) and the *sternal artery* (descending artery of Pearson and Baumann) originate. Guarding the exit of each of the five anterior arteries is a dorsal and a ventral, partly muscular, semilunar valve, and a similar pair of valves occurs at the distal end of the bulbus arteriosus immediately in front of the origin of the sternal and the dorsal abdominal arteries (fig. 49).

(a) *Ophthalmic artery* (Figs 10, 31, 46–51, 58, 64, 78)

This median vessel passes directly forward from the heart in the mid-dorsal line and, after running between the right and left mandibular posterior adductor muscles, it continues over the dorsal surface of the fore-gut, where it lies immediately beneath the dorsal body wall. Anteriorly it proceeds between the paired anterior gastric and the posterior basal eye muscles and dilates into a sort of accessory heart. This local enlargement (figs 50, 64) has been described by Baumann (1921) as the *cor frontale* and as the dilatation of the carotid artery by Brody & Perkins (1930). In *Jasus* it is suspended to the wall of the head close to the insertions of the posterior basal eye muscles by a pair of fibrous strips, and it is likely that compression of the cor frontale by these muscles drives the blood into the more anterior vessels.

Passing forward from the cor frontale, the now appreciably narrower ophthalmic artery curves abruptly downward and enters the median cylinder of the fused eyestalks, where it divaricates into a pair of conspicuous *optic arteries* (figs 50, 71, 74). Each of these is directed horizontally into the eyestalk

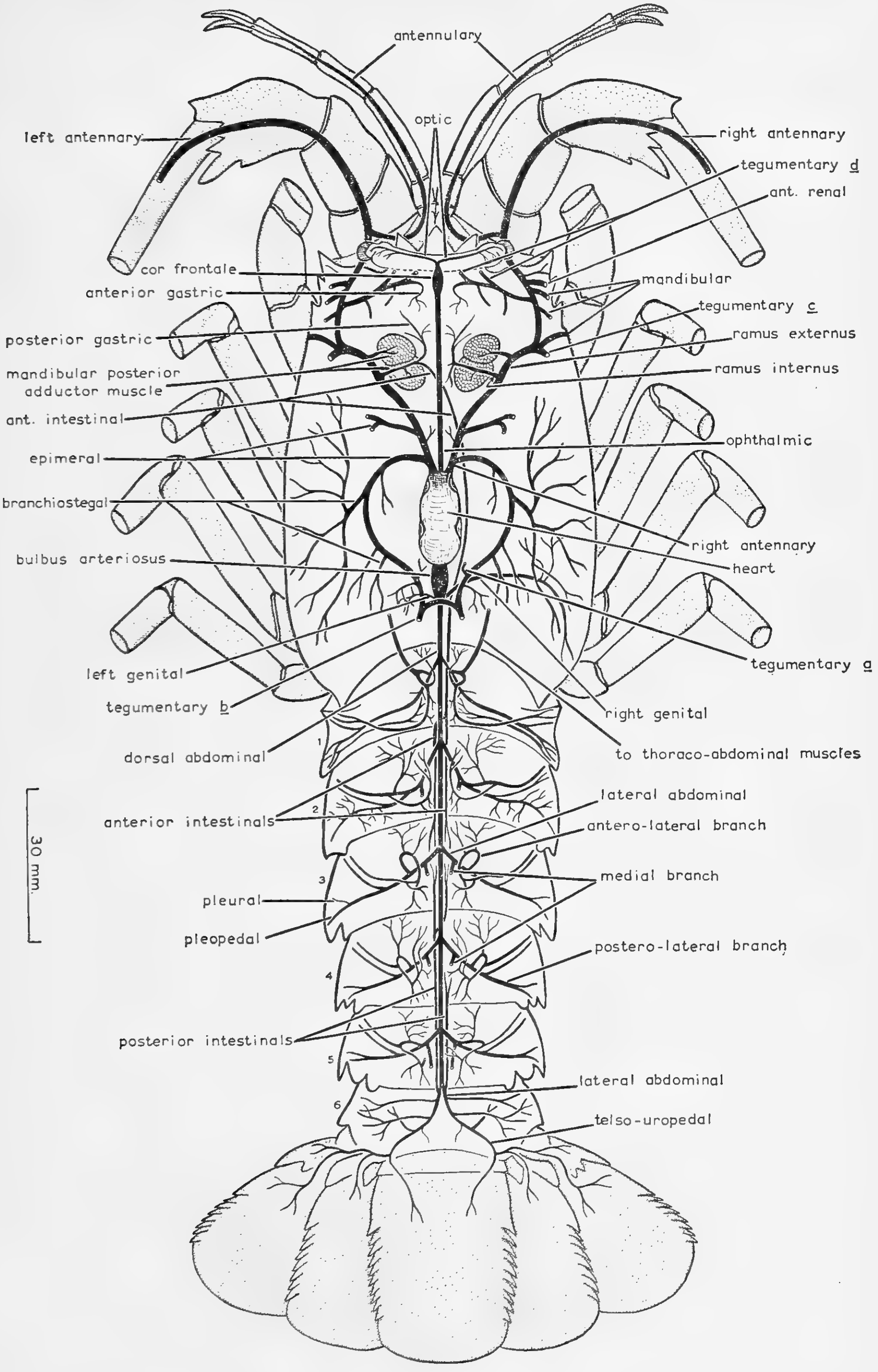


Fig. 50. Dorsal view of arterial system.

and, running anterior and parallel to the optic nerve, it enters the optic cup within which it branches to the optic ganglia. (Some details of the ramifications of the optic artery are given later (pp. 194–196) in the description of the compound eyes.) In *Jasus* there is no evidence of the continuation of the median ophthalmic artery in front of the optic arteries to form minor antennulary arteries, such as have been traced in *Astacus* by Baumann (1921), but a stout *cerebral artery*, which ramifies profusely in the brain, is given off ventrally from the cor frontale.

(b) *Antennary arteries* (figs 10, 31, 38, 39, 46–51, 78)

Arising antero-laterally from the heart on each side of the median ophthalmic artery there is a conspicuous *antennary artery*, which courses forward and outward, dividing repeatedly to irrigate many parts of the cephalothorax. It may be regarded as having three major branches, the *epimeral*, the *ramus internus*, and the *ramus externus*.

The *epimeral artery* (fig. 50) is a substantial vessel originating dorsally close to the root of the antennary artery. It has been so called because it passes laterally below the medial bundle of the lateral thoraco-abdominal muscle and proceeds under the branchio-cardiac groove to the epimeral attractor muscle. It not only supplies the latter, but also gives off several lateral branches which ramify extensively in the branchial lining of the branchiostegite and these have, therefore, been termed the *branchiostegal arteries* (fig. 50). This profuse vascularity of the branchiostegal membrane and Calman's (1909) statement that in Decapoda the blood from a minor circulation in the branchiostegites is returned to the pericardium, suggest that the inner lining of the branchiostegite has a possible inherent respiratory function. In injected adult specimens of *Jasus* and in transverse sections of the puerulus stage the portal of entry of the stream returning from the branchial membrane to the pericardial cavity is difficult to detect with certainty, but its most likely position is at the postero-lateral corner of the pericardial cavity near its junction with the pericardial pouch.

Posteriorly the main epimeral artery curves medially, giving off a rather delicate medial *tegumentary artery* (tegumentary *a*, fig. 50) to the hypodermis in the hinder part of the cardiac region of the cephalothorax before anastomosing with the epimeral artery of the opposite side towards the posterior limit of the pericardial cavity. From this transverse anastomosis there arises a pair of fairly stout *tegumentary arteries* (tegumentary *b*, fig. 50) which pass vertically upward to the muscles of the pericardial pouch and the integument behind the pericardial cavity.

Ramus internus. While proceeding forward parallel and anterior to the curvature of the cervical groove, the main antennary trunk gives rise to a delicate medio-dorsal *tegumentary artery* and one or more comparatively strong *epimeral arteries* to the anterior part of the epimeral attractor muscle. It then becomes divisible into two main branches opposite the posterior adductor muscle of the mandible; these are similar to the *ramus internus* and the *ramus* *externus* defined by Baumann (1921) in *Astacus*.

The *ramus internus* (fig. 50) passes off medially from the main stem and traverses the posterior bundle of the mandibular posterior adductor muscle, to which a number of small twigs are given off. It then constitutes the *posterior gastric artery* (fig. 50) which divides into an intricate network of vessels to the muscles of the pyloric fore-gut and the posterior part of the cardiac region of the fore-gut. The indications are that the left posterior gastric artery is usually more widespread than the one on the right side, its posterior offshoot continuing towards the mid-dorsal line of the pyloric fore-gut where it bifurcates into right and left branches. Both branches supply the mid-gut and the beginning of the hind-gut in the cephalothorax, but the right branch may extend along the hind-gut as an *anterior intestinal artery* (figs 50, 51) which subdivides to supply the wall of the intestine approximately as far as the third abdominal segment.

Ramus externus. The residual part of the antennary artery is the ramus externus (fig. 50) which courses laterally through the cephalothorax, giving off several arteries to neighbouring tissues including the hypodermis (tegumentary *c*, fig. 50), and eventually terminates in distal branches to the antenna, the antennule, and the eye muscles. It is thus more extensive than the ramus internus, and comprises the following main vessels.

The *anterior gastric artery* (figs 50, 51) is less conspicuous than the posterior gastric branch of the ramus internus and is the terminal part of a fairly wide vessel which passes off medially from the ramus externus and runs between the hypodermis and the antennal promotor muscle, both of which it supplies. Continuing medially towards the procephalic process, it separates into several small tegumentary arteries (tegumentary *d*, fig. 50) in the rostral region and a larger vessel that extends across the anterior end of the anterior gastric muscle and then curves ventrally towards the cardiac fore-gut.

Mandibular and oesophageal arteries. The blood supply to the muscles of the mandible is derived from at least three different sources. Close to the separation of the ramus externus from the ramus internus, a short artery enters directly into the anterior bundle of the mandibular posterior adductor muscle (fig. 50). The minor abductor and the anterior and posterior lateral adductor muscles are supplied by vessels which spring from the ramus externus proximal to the renal arteries. The remaining mandibular muscles are served by a large artery which is a prominent lateral branch of the ramus externus. It is indicated in figure 50 opposite the level of the first pereiopod, whence it bends lateroventrally between the anterior and the dorsal lobes of the digestive gland and extends below the former into the concavity of the mandible to reach the anterior adductor and the major abductor muscles. This distribution of blood to the mandibular muscles is obviously different from that observed by Baumann (1921) in *Astacus*, in which the mandibular artery is a branch of the subneural artery.

An examination of serial sections of the puerulus stage demonstrates that a delicate *oesophageal artery* continues forward in front of the branches to the inner mandibular muscles and conveys blood to the oesophagus and the labrum. This arrangement is probably normal, for Baumann (1921) has shown that in *Astacus* an oesophageal artery separates from the anterior end of the mandibular branch of the subneural artery and forms a peri-oesophageal ring.

Renal arteries. At least two fairly wide vessels may be traced from the ramus externus to the antennal gland. They have been called the posterior and the anterior renal arteries and respectively appear to be comparable with the saccular and the anterior renal arteries described by Marchal (1892) and Baumann (1921) in other decapods. The *posterior renal artery*, which has been omitted in figure 50 but is represented in figure 39, is a short stout vessel that arises ventrally from the ramus externus. It penetrates the main lobe of the labyrinth and becomes associated more particularly with the central cavity of the end sac (fig. 40). The *anterior renal artery* (figs 39, 50) originates more dorsally on the ramus externus and its branches ramify in the white lobe of the labyrinth but, like those of the posterior renal artery, they invade the spaces between the epithelial walls of the end sac and the labyrinth.

Dissections of the antennal gland (figs 38, 39) reveal the presence of at least one branching *vesicular artery* to the wall of the bladder and another which passes to the ureter and also supplies the antennal remotor muscle. In several species of Decapoda Marchal (1892) observed that part of the antennal gland was irrigated from the subneural artery by a branch which he termed the posterior renal artery. Baumann (1921) also described a similar artery in *Astacus*, but no such remote source of arterial blood to the antennal gland was detected in *J. lalandii.*

The *antennary artery* proper (fig. 50) separates laterally from the anterior end of the ramus externus. It is a moderately wide vessel which courses through the antennal peduncle more or less medial to the antennary nerve; it supplies the various muscles in each peduncular segment and ends in the flagellum.

Beyond the origin of the antennary artery proper, the terminal portion of the ramus externus travels horizontally inward, and towards the mid-line it produces a rather thick *antennulary artery* (fig. 50). This bends acutely forward to enter the antennulary peduncle, through which it travels lateral to the antennulary nerve and eventually bifurcates into the two flagella.

Oculomotor artery. Baumann's (1921) observation, that in *Astacus* the antennulary and oculomotor arteries are branches of a common stem, is substantiated in serial sections of the puerulus stage of *J. lalandii.* It is apparent that the two vessels represent the somewhat disproportionate terminal bifurcation of the ramus externus, the slender oculomotor artery diverging just as the more conspicuous antennulary vessel curves into the base of the antennulary peduncle. The right and left oculomotor arteries turn rather abruptly upward close to each other in front of the brain and between the promotor muscles of the two antennules, to which a number of twigs seem to be given off. Each artery then curves outward and courses laterally backward above the brain, running for a short distance along the side of the apical muscle before entering the eyestalk lateral to the optic nerve or pedunculus lobi optici (fig. 58). Its route through the eyestalk is not easily followed in injected specimens, but serial sections of the adult eye indicate that it consists essentially of two main branches: one supplies the adductor and medial retractor eye muscles and the other the remaining eye muscles and, in addition, both terminate in fine vessels in the subretinal connective tissue. It is thus evident that, as in *Astacus* (Baumann, 1921), there are two independent supplies of blood to the eye, one from the median ophthalmic artery via the optic artery to the optic ganglia, and the other to the eye muscles from the oculomotor branch of the antennary artery.

On the whole, the picture presented by the extensive ramifications of the antennary artery is fundamentally similar to that of *Astacus astacus* (Baumann, 1921) and *Palaemonetes vulgaris* (Brody & Perkins, 1930). In these two species, however, there is a fairly obvious supply from the antennary artery to the gonads, but in *Jasus* this seems to be of minor importance. Only a very short and inconspicuous *anterior genital artery* (fig. 51) passes off ventrally from the root of the antennary trunk and is supplemental to an equally small genital branch from the proximal part of the hepatic artery (fig. 51).

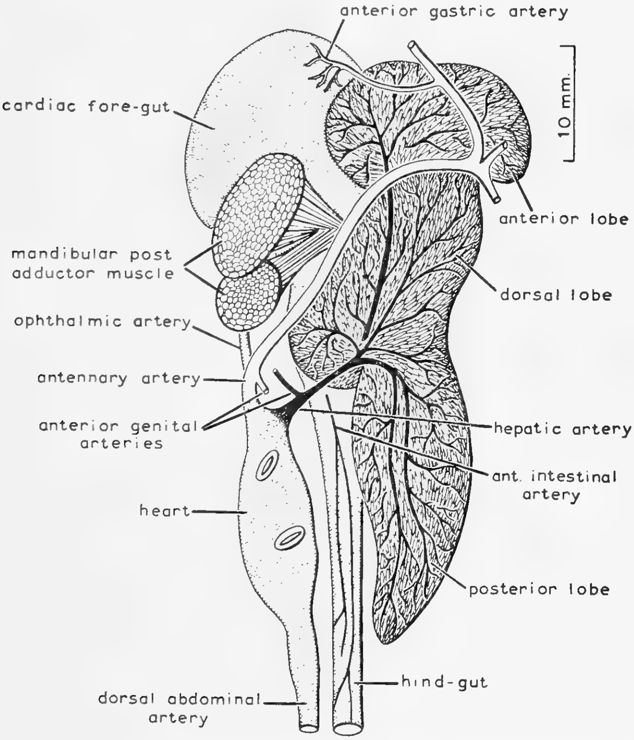


FIG. 51. Side view of dissected right digestive gland, showing ramifications of hepatic artery.

(c) *Hepatic arteries* (Figs 37, 46, 48, 51)

This pair of blood vessels arises ventrally from anterior the end of the heart almost directly below the antennary arteries and can only be seen satisfactorily in a lateral dissection and preferably in an injected specimen.

On leaving the heart, they proceed obliquely downward and outward, passing between the paired gonads immediately behind their transverse connecting bridge and frequently becoming obscured by the enlarged ovaries in mature females. On its course, each gives off a fine *anterior genital artery* (fig. 51) to the beginning of the posterior half of the gonad before it travels more ventrally to penetrate into the digestive gland approximately at the junction of the dorsal and posterior lobes and close to the entrance of the hepatic duct into the mid-gut (fig. 37). Shortly after entering the digestive gland, the hepatic artery divides into three large branches, one to each of the lobes of the gland, within which a complex network of vessels is formed.

(d) *Dorsal abdominal artery* (Figs 10, 31, 46–48, 50, 51, 54, 77, 78)

Beginning at the posterior extremity of the bulbus arteriosus at the hinder end of the heart and outside the pericardial cavity, the dorsal abdominal artery passes mid-dorsally through the posterior region of the cephalothorax, where one pair of arteries, the *genital*, is given off. It continues down the length of the abdomen above the hind-gut, and produces regular segmental *lateral abdominal arteries* which supply most of the abdominal muscles and the abdominal appendages.

Genital arteries. Some previous mention has been made of subsidiary genital vessels from the antennary and the hepatic arteries, but the main supply to the gonads is derived from a pair of *genital arteries* (fig. 50) which leave the dorsal abdominal artery immediately behind the bulbus arteriosus. As in *Astacus* (Baumann, 1921), the two of the pair are variable in size and distribution, the right genital artery (figs 47, 48, 50) being almost consistently larger than the one on the left side. Both genital arteries pass outward, branching repeatedly to supply the posterior half of the gonads and the gonoducts. The right genital artery, however, continues laterally, coursing dorsally over anterior oblique muscle 1 and sending tributaries, not only to this muscle, but also to posterior oblique 1, to oblique transverse 1, and to the lateral part of the anterior thoracic muscle.

On the left side, where the more delicate genital artery appears to terminate in the reproductive organs, it was observed in some specimens that the supply to the left thoracic musculature was derived from a stout branch arising from the sternal artery midway between the heart and the sternal canal (fig. 31). This muscular artery also occurs as a branch of the sternal artery in the puerulus stage, the muscles of the right side being irrigated by a more conspicuous artery which originates separately behind the bulbus arteriosus at the beginning of the dorsal abdominal artery and probably represents the future right genital artery of the adult.

Lateral abdominal arteries (fig. 50). In each abdominal segment the dorsal abdominal artery gives off a pair of broad, lateral vessels which penetrate between the dorsal extensor and the more ventral flexor muscles, sending branches to the muscles and even to the pleopods. The distribution of the vessels is by no means symmetrical on both sides, nor is it identical in successive segments, but in general three main branches are apparent. A *medial branch*, which passes downward to supply the central and the anterior oblique muscles, usually arises towards the proximal end of the lateral abdominal artery. An *antero-lateral branch* becomes defined by the bifurcation of the lateral abdominal artery beyond the medial branch. This vessel provides the main supply to the superficial and deeper extensor muscles by an intricate system of ramifications. A relatively wide and extensive *postero-lateral branch* represents the outermost prolongation of the lateral abdominal artery. After passing between and irrigating the auxiliary and the anterior oblique muscles, it proceeds laterally to the pleural region, where it divides into at least two main arteries. One, the *pleural*, runs chiefly to the larger proximal muscles of the pleopod, while the other, herein termed the *pleopedal* (fig. 50), enters the protopodite of the pleopod and breaks up into several vessels, some of which extend into the lamellate exopodite and endopodite. This somewhat peculiar and remote origin of the supply of arterial blood to the ventral pleopods from the dorsal abdominal artery appears to be fairly characteristic of decapod Crustacea, for it has also been described for *Homarus* (Herrick, 1911), *Astacus* (Baumann, 1921), and *Palaemonetes* (Brody & Perkins, 1930).

The arrangement of vessels in the first abdominal segment departs slightly from that in other segments in that there are no pleopods and the postero-lateral branch of the lateral abdominal artery ends in the pleuron. This, however, is consistent with the findings in other Decapoda in which, even when, as in *Astacus* (Baumann, 1921), appendages are present on this segment, the lateral abdominal artery passes only to the pleuron, and the first pair of abdominal appendages is supplied from the subneural artery and not from the dorsal abdominal vessel as are the other pleopods.

The antero-lateral branch in the first abdominal segment produces a somewhat prominent antero-dorsal artery, which extends forward into the cephalothorax and divides into sundry vessels to the lateral and deeper thoraco-abdominal muscles. Furthermore, in some specimens a delicate branch was observed to arise close to the root of each first lateral abdominal artery and was traced into the cephalothorax below the pericardial septum to the posterior part of the gonad.

As in other genera described by Herrick (1911), Baumann (1921), and Brody & Perkins (1930), on entering the sixth abdominal segment the dorsal abdominal artery bifurcates into a pair of conspicuous lateral trunks, each of which almost immediately gives off a branch which travels over the surface of the anterior oblique muscle and supplies the large auxiliary muscle. The two trunks then gradually diverge on either side of the intestine, each passing outward towards the antero-lateral margin of the telson under the anterior oblique muscle, to which and also to the ventral flexor muscle of the telson tributaries pass off. The postero-lateral extent of the trunk, which may be termed the *telso-uropedal artery* (fig. 50), after dividing to serve the anterior and posterior flexors of the telson and the telso-uropedal muscles, continues into the protopodite of the uropod and eventually reaches both the exopodite and the endopodite of this appendage.

According to Baumann (1921), numerous intestinal arteries branch from the dorsal abdominal and also from the segmental lateral abdominal arteries in *Astacus*, but in *Jasus* there is no regular segmental supply to the hind-gut. Instead, there may be either a median intestinal artery from the posterior bifurcation of the dorsal abdominal artery or, more commonly, a pair of fairly obvious *posterior intestinal arteries* (fig. 50) originates ventrally on the last lateral abdominal arteries. The paired arteries extend forward, closely adherent to the dorso-lateral wall of the intestine, the one on the left side usually travelling as far as the third segment, while the right one may be shorter and end in the fourth segment. These vessels provide arterial blood to the caudal part of the intestine, the proximal portion of which is served by the anterior intestinal arteries (p. 143) derived from one of the posterior gastric arteries.

(e) *Subneural arteries* (Fig. 52)

A mid-ventral system, which is situated below the ventral nerve cord and is of special importance in distributing arterial blood to the ventral nerve cord and the thoracic appendages, is formed by divarication of the lower end of the very wide *sternal artery*. The latter (figs 31, 46, 48) is directed vertically downward from the bulbus arteriosus at the posterior end of the heart and runs either to the left or to the right of the intestine. Some investigators have indicated that the sternal artery is originally paired, and the variability of its position relative to the intestine in the adult is doubtless caused by the irregular suppression of one or the other of the two vessels. The sternal artery passes between the mesophragms of the endophragmal skeleton and, entering the sternal canal (fig. 31), it penetrates the ventral nerve cord between the connectives joining the third and fourth thoracic ganglia. Having thus attained a subneural position, it immediately divides into anterior and posterior branches, which are usually respectively termed the *ventral thoracic* and the *ventral abdominal arteries*, and are best seen in injected specimens that have been dissected mid-ventrally between the appendages (fig. 52).

The anterior subneural or *ventral thoracic artery* (figs 31, 52, 53) is subequal in diameter to the sternal artery as it proceeds forward giving off stout, paired vessels to the third, the second, and the first pereiopods, and the third maxillipeds (fig. 52). Anterior to the latter, the median artery, which has become progressively narrower, bifurcates; each fork sends offshoots into the second and the first maxillipeds and then curves laterally to irrigate the second and the first maxillae.

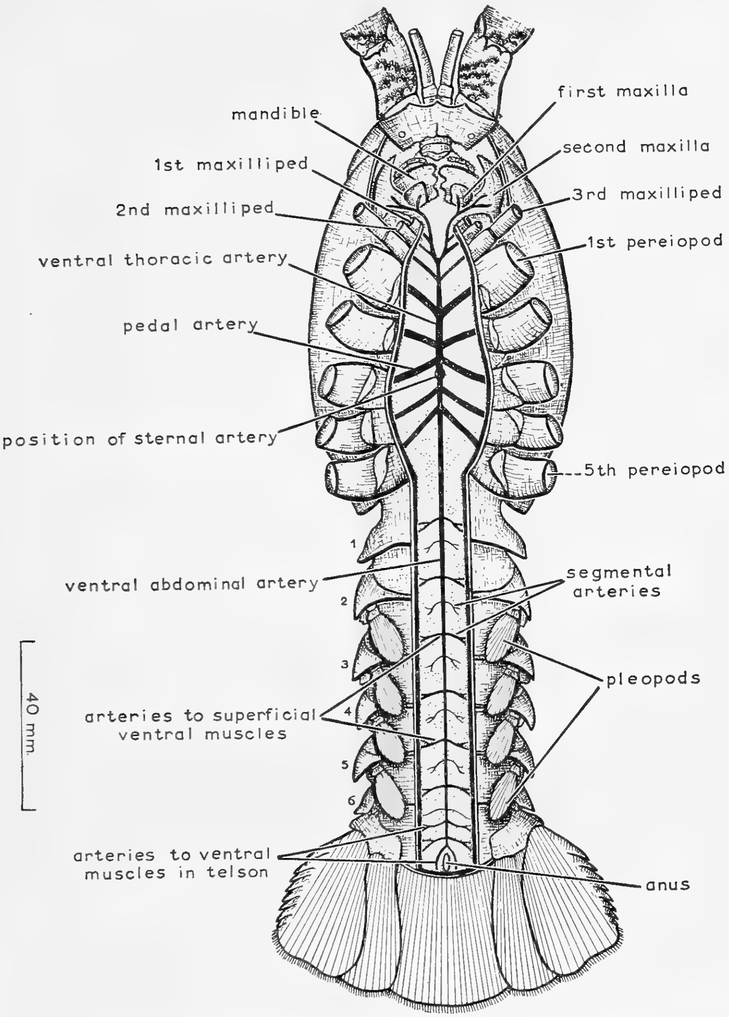


FIG. 52. Ventral view of subneural arteries in male specimen.

Unlike *Astacus* (Baumann, 1921) and *Palaemonetes* (Brody & Perkins, 1930), the ventral thoracic artery does not continue forward into the mandible, nor apparently does it reach the oesophagus: as indicated on page 143, these parts derive their blood supply from the mandibular branch of the antennary artery. Moreover, the point of bifurcation of the anterior end of the ventral thoracic artery seems to be variable for, according to Brody & Perkins (1930), it takes place in *Palaemonetes* in front of the first pereiopods. On the other hand, Baumann (1921) has shown that in *Astacus* the subneural artery is a continuous median vessel from which the first maxilliped and the two maxillae on each side receive blood from divisions of a common lateral branch, while more anteriorly the main artery terminates in the mandibular muscles and in the wall of the oesophagus.

In addition to supplying the anterior thoracic appendages, Baumann (1921) demonstrated that in *Astacus*, close to its origin from the descending (sternal) artery, the rostral part of the subneural artery sends a pair of vessels to the anterior thoracic muscles. Similar vessels also occur in *Jasus*, but usually two additional pairs are present in front of these, and all of them extend upward and spread into the anterior thoracic muscles.

The posterior subneural or *ventral abdominal artery* (figs 31, 52, 54) supplies the fourth and fifth pereiopods and then passes mid-ventrally along the abdomen. Commonly in each segment it produces two pairs of rather weak vessels to the superficial ventral muscles: the more conspicuous pair underlies the dorso-lateral nerves to the main abdominal muscles, and the subsidiary pair occurs more anteriorly, approximately in the middle of the segment. Towards the posterior extremity of the abdomen, the median vessel gradually becomes more attenuated, and in front of the anus several branches are given off to the flexor muscles of the telson and to the anal compressor and the anal dilatator muscles. Anterior to these there may be an anastomosis with the last pair of lateral abdominal arteries of the dorsal abdominal system, the arrangement being reminiscent of the peri-intestinal ring described by Baumann (1921) in *Astacus*.

The whole of the ventral nerve cord is richly supplied with oxygenated blood by short vessels arising irregularly along the course of both the ventral thoracic and the ventral abdominal arteries, the branches to the thoracic ganglia (fig. 53) being particularly noticeable.

3. VENOUS SINUSES

It is apparent in injected adult specimens and in sections of the puerulus stage that the haemal sinuses are provided with delicate limiting membranes and that they form a system of wide, interconnected spaces surrounding the viscera, including the arteries and nerves passing to various parts of the body.

In the head region a spacious sinus, which encompasses the brain (fig. 58), the circum-oesophageal connectives, the antennal glands, the beginning of the fore-gut, and the anterior lobe of the digestive gland, collects blood anteriorly from the eyes, the antennules and the antennae, while the venous spaces of the labrum, the mandibles, and the first maxillae open into it ventrally.

More posteriorly, the cephalic apodeme of the endophragmal skeleton marks the transition from the head to the thoracic region of the body and the division of the haemocoel into dorsal and ventral compartments. Thus, throughout most of the thorax a *sternal sinus* (fig. 53) becomes defined around the ventral nerve cord and the subneural artery in the sternal canal, and at its anterior end it receives deoxygenated blood from the second maxillae. Connected with the sternal sinus through interstices in the endophragmal skeleton, but separated from it at intervals by the transverse mesophragms, is the *dorsal* *sinus*, which envelops the fore-gut and is laterally continuous with the hepatic sinus around the dorsal lobes of the digestive gland and also with the venous spaces in the branchiostegites and the anterior part of the genital sinus. In the cardiac region of the thorax (fig. 53) the large dorsal sinus lies below the pericardial septum and surrounds the beginning of the hind-gut, the posterior lobes of the digestive gland, and the gonads.

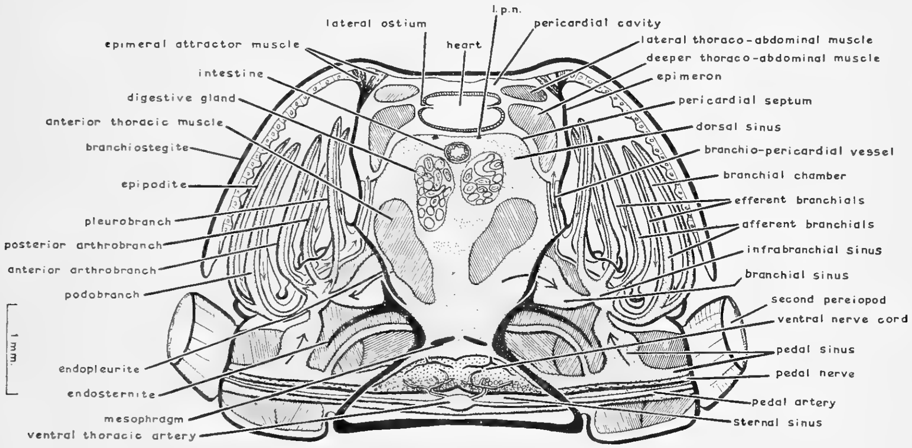


FIG. 53. Puerulus stage: diagrammatic transverse section through fifth thoracic segment. To give clearer definition to the arrangement of the gills, the gill filaments have been omitted; *l.p.n.*, longitudinal ventral pericardial nerve, size exaggerated.

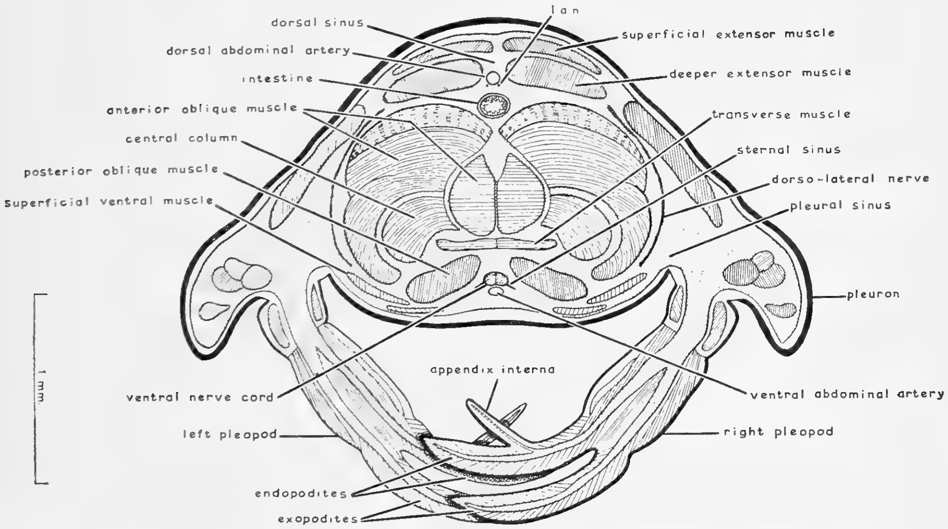


FIG. 54. Puerulus stage: diagrammatic transverse section through third abdominal segment; *l.a.n.*, somewhat enlarged longitudinal arterial nerve.

These two main thoracic sinuses are directly continuous with similar blood spaces in the abdomen, in each segment of which (fig. 54) the median *dorsal sinus* lies above the anterior oblique muscles and contains the dorsal abdominal artery and the intestine, while the *sternal sinus*, situated beneath the oblique muscles, encloses the ventral nerve cord and the ventral abdominal artery. In addition, each abdominal segment has a pair of *pleural sinuses* (fig. 54) which drain the deoxygenated blood from the paired appendages in the second to the sixth segment, but the blood from the telson enters the end of the dorsal abdominal sinus. The four abdominal sinuses are linked together by channels running between the large abdominal muscles, from which blood is also collected.

4. BRANCHIAL CIRCULATION

The deoxygenated blood in the haemocoel must eventually be conveyed to the respiratory organs for oxygenation, and Huxley's dictum (1881:69) that in *Astacus* 'all the blood in the body sooner or later makes its way . . . into the *sternal sinus*' . . . from which . . . 'passages lead to the gills', seems to have been accepted as the standard for all Decapoda. It is considered, however, that in *Jasus* the circuit to the gills differs somewhat from this concept of events in the crayfish, and that it bears some resemblance to the circulation in *Cancer*, in which Pearson (1908) described a series of *branchial sinuses* for the transport of blood through the pleural muscle chambers of the appendages *en route* to the gills.

The thoracic sternal sinus of *Jasus* (fig. 53) is considerably smaller than the dorsal sinus, which is in line with the pleural muscle chambers, but the two sinuses communicate freely through gaps in the endophragmal skeleton. An examination of serial sections of the puerulus stage suggests that the greatest volume of blood is directed towards the gills, not from the sternal sinus, but from the dorsal sinus by relatively wide and distinct *branchial sinuses* (fig. 53) located in the pleural muscle chambers of the limb bases. At the same time, vessels passing from the sternal sinus traverse the sternal muscle chambers and communicate more particularly with the *pedal sinuses* (figs 53, 55) which return deoxygenated blood from the appendages. Paired branchial sinuses are apparent in all thoracic segments, except the first, and on each side of the body they and the pedal sinuses become associated with a longitudinal *infrabranchial sinus* (figs 53, 55) which runs along the bases of the gills from the second to the last thoracic segment and seems to end in the articular condyle for the carapace. In the absence of a branchial sinus in the first thoracic segment, the blood from the first maxilliped and the dorsal and ventral sinuses passes directly into the anterior end of the infrabranchial sinus. The paired pedal sinuses in the last thoracic segment not only join the right and left infrabranchial sinuses, but some of the pedal blood may also enter the stream flowing forward from the sternal and pleural sinuses in the intersegmental region between the abdomen and thorax. The reason for this appears to be that the sternal canal does not extend to the end of the thorax, and thus in the floor of the last thoracic segment there is a wide confluence of ventral abdominal and thoracic blood, including some passing through the sternal muscle chambers of the last pair of pereiopods.

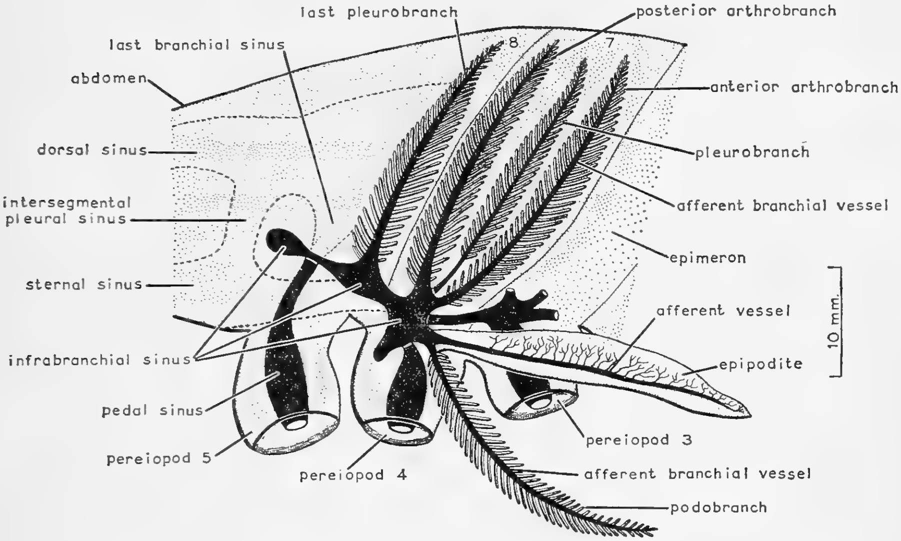


FIG. 55. Side view of right posterior gills; the epipodite and podobranch of the seventh thoracic segment have been displaced, and the course of the afferent branchial vessels is shown.

From each *infrabranchial sinus* the deoxygenated blood proceeds into a series of 21 *afferent branchial vessels* (figs 44, 53, 55, 56) running along the outer part of the axes of the serially-arranged gills in the second to the eighth thoracic segments. Each epipodite (fig. 55) is also furnished with a vessel which arises as a branch of the afferent branchial to the corresponding podobranch, and in serial sections of the puerulus stage it is also evident that an afferent vessel passes from the anterior end of the infrabranchial sinus into the epipodite of the first maxilliped.

By serial sections of the gills and observations of injected specimens, it can be shown that offshoots from the afferent branchial vessel traverse the lateral mantle canals and, radiating into the gill filaments, convey deoxygenated blood into the outer *afferent channels* in the filaments (fig. 44). The wall of each filament functions as a respiratory membrane and, after oxygenation, the blood enters the *efferent channel* (fig. 44) which lies on the inner side of the filament and is separated from the afferent channel by a longitudinal connective-tissue septum. The actual transition from the afferent to the efferent channel is problematic. Bock (1925) concluded that in *Astacus* it could only be established through blood lacunae at the apex of the filament but, according to Dornesco & Homei (1940), it may occur in *Palinurus* along the length of the filament through irregular spaces formed between the epidermis and the median septum. The feasibility of the latter suggestion is supported by inspection of the gills of *Jasus*, in which injected India ink successfully delineated the whole course of the afferent blood stream: carbon particles, which fill the axial afferent branchial vessel and the filamentar afferent channels, fail to penetrate into the filamentar efferent channels, but irregular traces are evident in lateral lacunae beneath the epidermis of the filament. It is also of some significance that in all the gills the afferent channels are given off only to the *outer filaments* adjacent to the afferent branchial vessels and that the *inner filaments* (fig. 44), which are opposite the efferent branchial vessel, receive no blood directly from the afferent branchial vessel. Characteristically, there are fewer inner than outer filaments and the two are sharply contrasted in injected specimens by the absence of injection fluid in the inner filaments. Thus, for instance, in sections across the widest part of the pleurobranch (fig. 44) there are usually three pairs of inner filaments and about fourteen pairs of outer filaments, although the number of the latter has been reduced by about one third in the given simplified diagram.

Assuming that the lateral lacunae mark the junction between the afferent and efferent streams and that in them gaseous exchange takes place, the blood oxygenated in the outer filaments will drain into and proceed along the efferent channels. Before it eventually reaches the *efferent branchial vessels* (fig. 44) on the inner side of the gill axis, however, it describes a somewhat tortuous course through the gill axis and the remaining inner gill filaments. In this connexion, the two *mantle canals* (fig. 44) running along the sides of the afferent and efferent branchial vessels are of supreme importance. Into them the efferent channels from the *outer filaments* discharge directly, and the blood is then transported to the *inner filaments* which have passages analogous to the afferent and efferent channels of the outer filaments. The blood directed from the mantle canals into the afferent channels of the inner filaments traverses the superficial lacunae and enters the corresponding efferent channels, which in turn open widely into the *efferent branchial vessel.* Since, however, the blood has presumably already been oxygenated in the outer filaments, it follows that, while circulating through the inner filaments, it must be subjected to a further process of oxygenation before it enters the efferent branchial vessel. These observations confirm the conclusions of Bock (1925) and Dornesco & Homei (1940) that the blood is twice oxygenated on its course from the afferent to the efferent branchial vessel. Dornesco & Homei, however, have described a further complication in the branchial circulation of *Palinurus*, in which a third category of one or more pairs of filaments is intercalated between the outer and the inner filaments. Such filaments, which are not apparent in *Jasus*, are said to have two longitudinal septa dividing the lumen into three channels, the outermost of which receives the deoxygenated blood from the afferent branchial vessel, while the middle and the inner passages accommodate the oxygenated blood and respectively conduct it into the mantle canal and the efferent branchial vessel.

In addition to the main vessels, five narrower, but distinct, blood channels (a_1 to a_5, fig. 44) are evident in sections of the gill axes and are similar to the *branchial arteries* indicated by Dornesco & Homei (1940) in the gills of *Palinurus*.

Two of the three unpaired vessels, a_4 and a_5, are doubtless associated with the blood lacunae in the loose connective tissue around the efferent branchial vessel, but they also give off relatively stout lateral branches which seem to pass into the septa of the inner filaments. From the paired vessels, a_2 and a_3, which are located in the midst of the loose connective tissue in the wider parts of the mantle canals, branches travel along the gill axis to the septa of the outer filaments. The remaining artery, a_1, is adjacent to the inner wall of the afferent branchial vessel but, apart from delicate tributaries to the latter, it appears to have no obvious connexion with the gill axis.

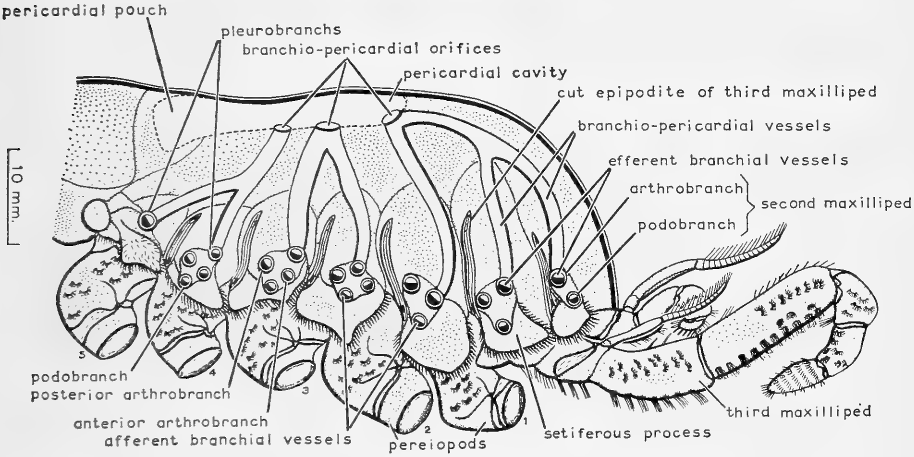
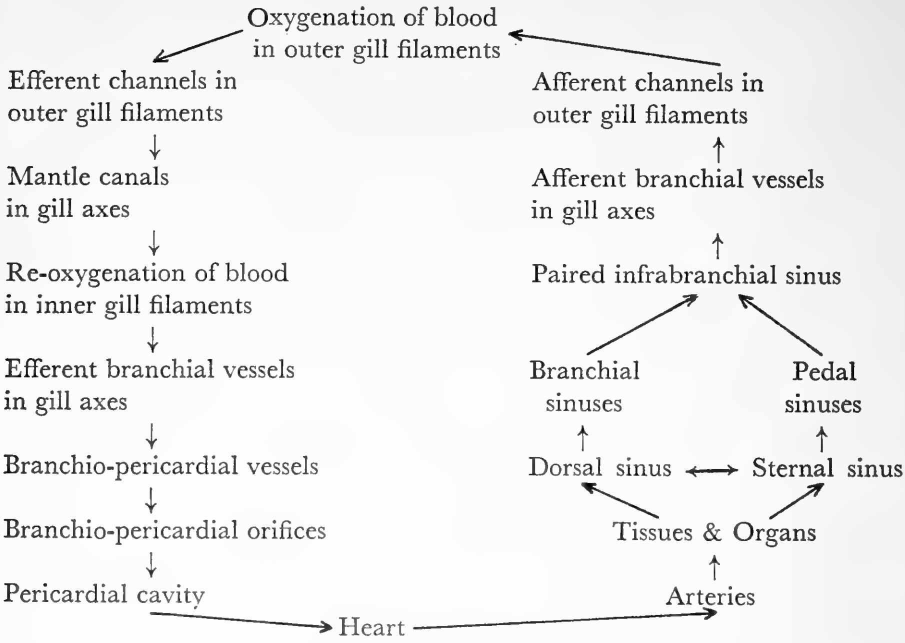


FIG. 56. Diagram of right branchial chamber with the gills removed and the course of the branchio-pericardial vessels exposed.

In each segment the efferent branchial vessels of the gills and the epipodite communicate with a *branchio-pericardial vessel* (figs 53, 56) which travels along the inside of the thoracic epimeron and conveys the oxygenated blood to the pericardial cavity. All told, there are effectively seven branchio-pericardial vessels on each side of the thorax but, as they join in pairs before reaching the pericardial cavity, only three wide *branchio-pericardial orifices* (fig. 56) occur laterally in the pericardial septum. By viewing the pericardial cavity from above, these may be easily seen, even in uninjected specimens; they are located in the angles between the epimera and the attachments of certain bundles of the thoracic muscular system (fig. 11) and are practically in line with the first three pereiopods. The oxygenated blood entering through the branchio-pericardial orifices fills the pericardial cavity and is sucked into the heart lumen through the ostia at each diastolic expansion of the heart; when the cardiac muscles contract at systole, it is pumped via the arterial system to all parts of the body.

The complete circulation of the blood may be expressed in the following synoptic diagram:



One of the main differences between the above interpretation of the blood circulation and that described by Huxley (1881) for the crayfish is the recognition of branchial sinuses for the reception of blood from the dorsal thoracic sinus of the haemocoel. However, by reference to Huxley's familiar and frequently reproduced diagram, it may be surmised that branchial sinuses similar to those of *Jasus* probably also occur in *Astacus* in the lateral spaces between the median sternal sinus and the leg bases.

H. Nervous System

As the greater portion of this system is ventral in position, its full exposure from the dorsal aspect involves careful removal of most of the contents of the body cavity and the median part of the endophragmal skeleton. Although in gross dissections it may be advisable to excise the large thoracic and abdominal muscles, it should be noted that several important nerves either innervate them or pass between them to other organs.

In its entirety it is divisible into two subsections, the central nervous system and the sympathetic nervous system.

The *central nervous system* comprises an antero-dorsal brain and a ventral nerve cord consisting of a chain of segmental ganglia running mid-ventrally down the length of the body and giving off lateral peripheral nerves to the muscles and occasionally to other organs in each segment.

The delicate *sympathetic* or *stomatogastric nervous system* is associated with the brain, but functions chiefly in the innervation of the fore-gut and a few neighbouring structures.

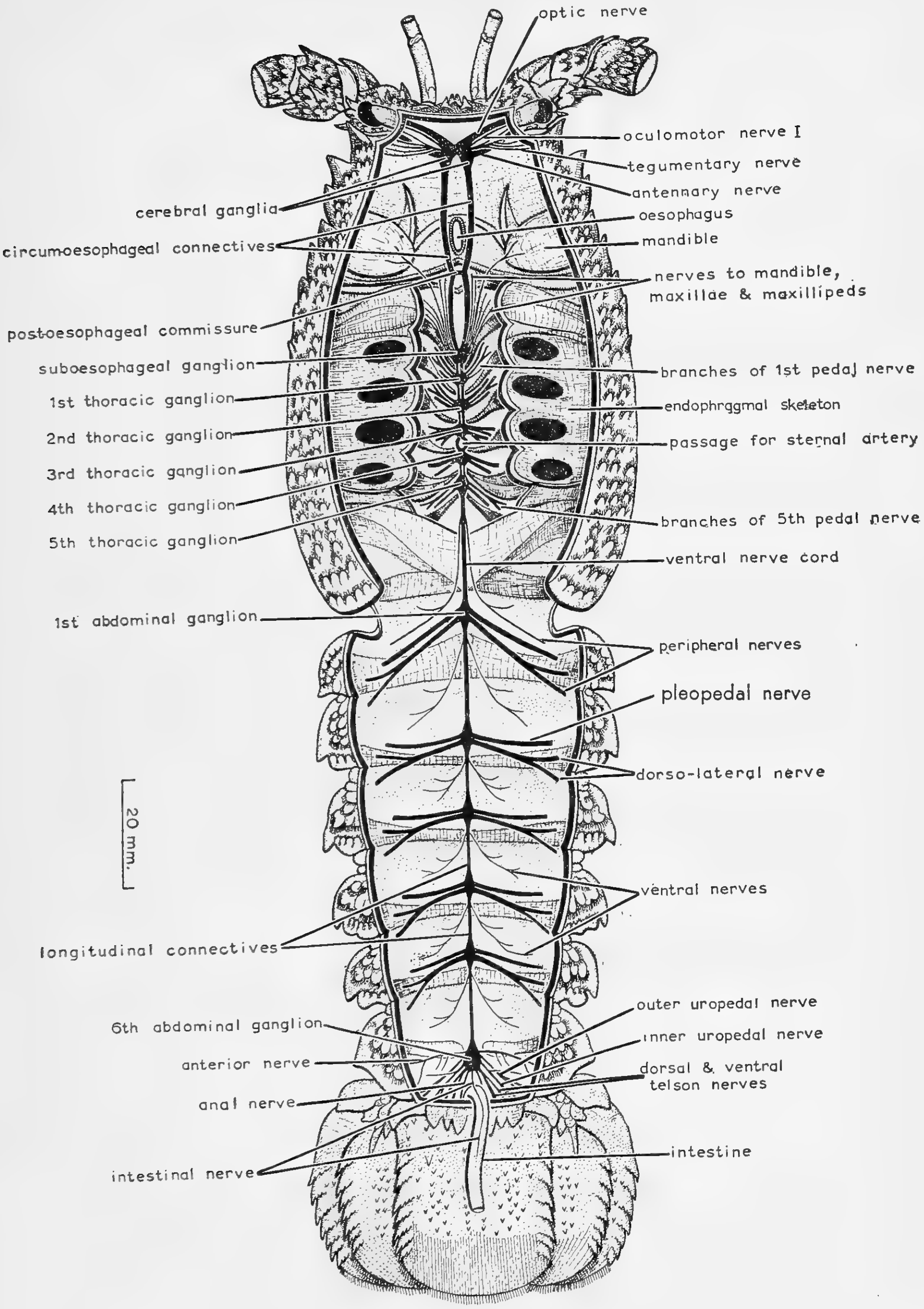


FIG. 57. Dorsal view of central nervous system.

1. CENTRAL NERVOUS SYSTEM (Fig. 57)

Probably the easiest method of tracing this is to expose the abdominal part of the ventral nerve cord first by displacing the hind-gut and the abdominal extensor and flexor muscles. It will then be possible to follow the cord forward through the cephalothorax by opening the sternal canal and completing the dissection by displaying the parts in the frontal region.

The *brain* is situated antero-dorsally in the cephalothorax in front of the cardiac fore-gut, below the rostrum and between the eyes, while the *ventral nerve cord* is composed of a series of thoracic ganglia, lodged in the sternal canal beneath the mesophragms of the endophragmal skeleton, and of six abdominal ganglia lying mid-ventrally close to the sterna.

(a) *Cerebral ganglia* (Figs 31, 57, 58, 61, 64)

The brain represents a fusion of three pairs of cerebral ganglia, the limits of which are hardly perceptible in ordinary macroscopic dissections. Transverse sections (fig. 58), however, disclose the arrangement of various groups of cells, intricate fibre tracts, and masses of fibrous tissue or neuropiles, and are essential to the determination of the origins of various peripheral nerves.

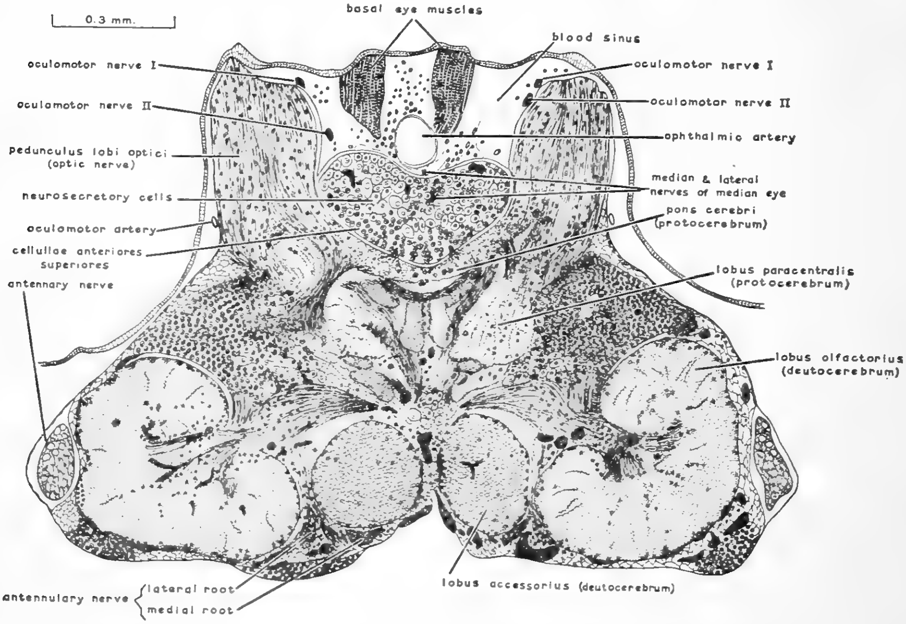


FIG. 58. Puerulus stage: transverse section of brain; provisional terminology after Hanström (1947).

Omitting details of the complex histology of the brain, it may be observed that, as is characteristic of Malacostraca, it consists of three main regions comparable to its pairs of fused ganglia. The anterior *protocerebrum* (figs 58, 61) innervates the apical muscles, the compound eyes, and the eye muscles; also connected with it are three short, median, frontal nerves to the median or nauplius eye (figs 61, 70), and in some species an unpaired superior ventricular nerve to the stomatogastric system has been reported. The *deutocerebrum* (fig. 58) is more ventral, and from it the nerves to the antennules and the statocysts pass forward and downward. The posterior region of the brain, the *tritocerebrum* (fig. 61), gives off the tegumentary and the antennary nerves, and continues posteriorly as two conspicuous circum-oesophageal connectives which link the brain with the suboesophageal ganglion at the anterior end of the ventral nerve cord. The tritocerebrum is also associated with the stomatogastric system by a median inferior ventricular nerve.

(b) *Cerebral nerves*

In addition to the nerves of the median eye (fig. 70), the following paired nerves may be traced on each side of the brain.

A delicate *apical nerve* (fig. 61) runs forward from the frontal edge of the protocerebrum to the apical muscle situated in the middle cylinder of the compound eyes. The two of the pair are frequently linked by a transverse anastomosis above the median eye, which is thus practically embraced by them. Proximally they are adjacent to the lateral nerves of the median eye (fig. 70), with which they seem to have either common or contiguous centres in the brain.

The *optic nerve* (figs 31, 57–59, 61, 71, 74) or *pedunculus lobi optici* (Hanström, 1947) is a very conspicuous trunk originating dorso-laterally in the protocerebrum. It passes obliquely upward and forward to the eyestalk where it enlarges into four optic ganglia, some particulars of which are supplied in the description of the compound eyes (p. 187).

There is no proof that, as in *Astacus* (Keim, 1915), the anterior and posterior basal eye muscles are innervated from the oculomotor nerves. Instead, the anterior muscles are clearly served by a pair of delicate nerves (fig. 61) passing upward from the protocerebrum between the two optic nerves, while the posterior basal eye muscles seem to be associated with the sympathetic nervous system. Consequently, as the pulsation of the accessory heart or cor frontale is probably influenced by the contraction of the basal eye muscles, the innervation of the latter suggests that the mechanism is partly controlled by the brain.

In each eyestalk the eye muscles are innervated by two *oculomotor nerves* which originate independently of each other in the protocerebrum. Their subdivisions are comparable with the three branches of the single oculomotor nerve of *Astacus* described by Keim (1915), and more directly with those of the discrete oculomotor nerves I and II discovered by Welsh (1941) while investigating the physiology of the sinus gland of *Cambarus bartonii*.

The thicker nerve, *oculomotor I* (figs 57–59, 61, 71) arises from the brain dorso-lateral to the optic nerve; within the eyestalk it passes above the attractor eye muscle and divides at the base of the optic cup into two stout branches

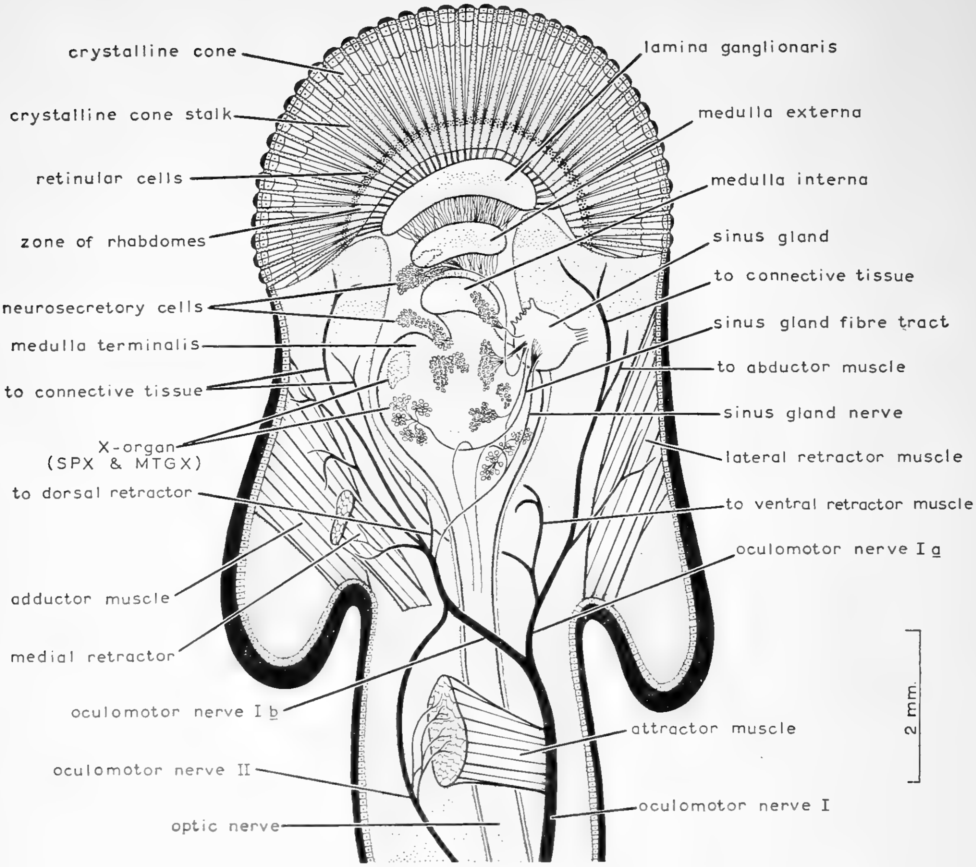


FIG. 59. Diagrammatic impression of nerves of right eye of adult, based on serial sections and dissections. The approximate positions of the sinus gland and neurosecretory cells are indicated.

(fig. 59). The sub-branches of these are distributed to the eye muscles in the optic cup and are often linked by delicate collateral plexuses. *Oculomotor I a* supplies the lateral retractor and the abductor eye muscles and extends distally to the subretinal connective tissue in the dorso-lateral region of the optic cup. It has a further relatively strong medial branch, which dips ventrally to innervate the ventral retractor eye muscle and gives rise to a long offshoot that travels below the distal part of the optic nerve and proceeds to the ventro-medial subretinal connective tissue.

The second branch, *oculomotor I b*, is equally widespread and, after innervating the medial retractor, the dorsal retractor, and the adductor eye muscles, it continues distally to the dorso-medial subretinal connective tissue. One of its most interesting subdivisions is the *sinus gland nerve* (fig. 59), which passes forward and penetrates the neurilemma at the base of the medulla terminalis. In sections of the eye it is possible to trace its deeply stained basophilic fibres through the medulla terminalis; at least three of them enter the sinus gland, while another strong fibre passes medially towards a plexus around the main optic tract and approaches the fibre tract that links the X-organ (MTGX) with the sinus gland.

Oculomotor nerve II (figs 58, 59, 61, 71) is somewhat finer than the first nerve and originates from the brain antero-medially to the optic nerve, to the dorsal surface of which it appears to be partly adherent when examined in sections of the eye, but in dissections the two are easily separated. Shortly after entering the medial half of the eyestalk above the optic nerve, it gives off at least two anastomosing branches which ramify in the attractor eye muscle. It then curves forward into the basal region of the optic cup where it unites with oculomotor I *b* before the latter branches to the sinus gland and the more medial eye muscles. In supplying the attractor eye muscle, it resembles the first branch of the single oculomotor nerve distinguished by Keim (1915), but varies from it in its origin and in having no connexion with the basal eye muscles.

These findings substantiate Welsh's (1941) disclosure of two distinct oculomotor nerves and his speculation as to the presence of a nerve to the sinus gland, but differ slightly from his observations in that the sinus gland nerve (fig. 59) is derived mainly from a branch of oculomotor I and not directly from the second oculomotor nerve as in *Cambarus bartonii*. As, however, the two oculomotor nerves anastomose in *Jasus*, it is feasible that fibres from both of them contribute to the formation of the sinus gland nerve.

A careful study of serial sections of the puerulus stage shows that, as in other Decapoda (Balss, 1941; Hanström, 1947), the *antennulary nerve* has medial and lateral roots (fig. 58) and resolves into branches supplying the statocyst, the sensory hairs of the antennulary flagella, and the antennulary muscles. Therefore, unlike the arrangement in *Astacus* (Panning, 1924) and *Homarus* (Cohen, 1955), the fairly substantial *statocyst nerve* (fig. 60) appears as a branch of the main antennulary nerve and initially represents its medial root. It is traceable to the neuropilum antennulare mediale (Balss, 1941) or the lobus parolfactorius (Hanström, 1947), and travels in a ventral direction together with the fibres of the main antennulary nerve. Before reaching the antennulary peduncle, it divides into several branches, some supplying the tactile hairs on the proximal segment of the antennule and others terminating in delicate fibres in the walls of the statocyst. A slight variation in the number of branches to the statocyst may prevail, four having been observed in one specimen, but, more commonly, there are only two branches which seem comparable to the nervi acustici internus and externus of *Astacus* (Panning, 1924), although these were described as having separate origins in the brain. In sections there are also indications that the sensory hairs of the statocyst are innervated by single neurones.

Arising more laterally from the deutocerebrum, in regions termed the neuropilum antennulare laterale and lobus olfactorius by Balss (1941), are the

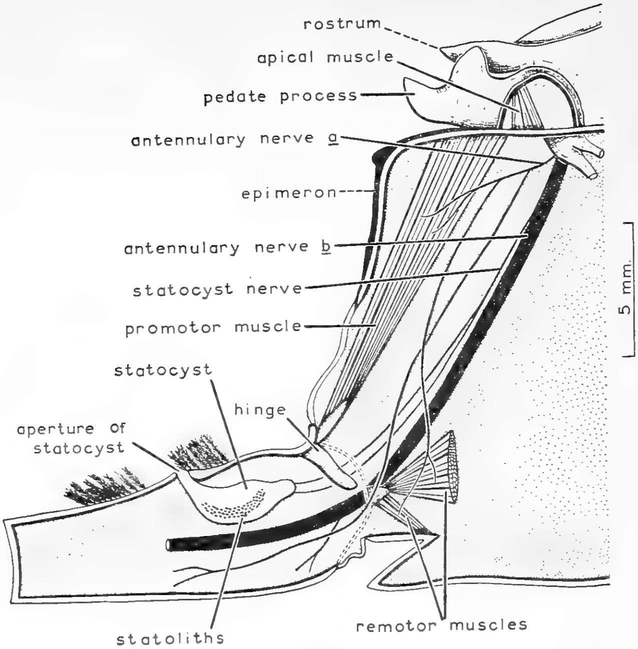


FIG. 60. Lateral dissection of base of left antennule to show disposition of antennulary and statocyst nerves. The left antenna and left compound eye have been excised, and the left apical muscle is seen in the middle cylinder of the fused eyestalks.

inner and outer fibres of the conspicuous lateral root of the *antennulary nerve* (fig 58), from which two well-defined branches later separate. Apparently originating in the outer fibres, a comparatively thin *antennulary nerve a* (fig. 60) provides the main supply to the proximal antennulary muscles; it is directed forward to the promotor muscle, but also gives off other branches which extend downward to the remotor and abductor muscles. Emerging from the brain slightly postero-ventral to the first branch, the inner and outer fibres continue as a thick *antennulary nerve b* (fig. 60) which slopes downward through the frontal region of the head and, curving below the dorsal hinge of the antennule, enters the peduncle and travels more or less medially, supplying the various muscles in the three segments. Sections show that throughout their course the inner and outer fibres of antennulary nerve *b* retain their individuality and separate distally, the inner fibres passing to the inner flagellum, while the outer fibres terminate in the setae and the aesthetascs of the outer flagellum.

The conspicuous *tegumentary nerve* (figs 57, 61) arises dorsally in the tritocerebrum and splits into several branches, the subdivisions of which fan out to the antero-lateral cephalic hypodermis.

On displacing the tegumentary nerve, the more ventral *antennary nerve* (figs 31, 57, 58, 61) is revealed as a prominent element composed of a number

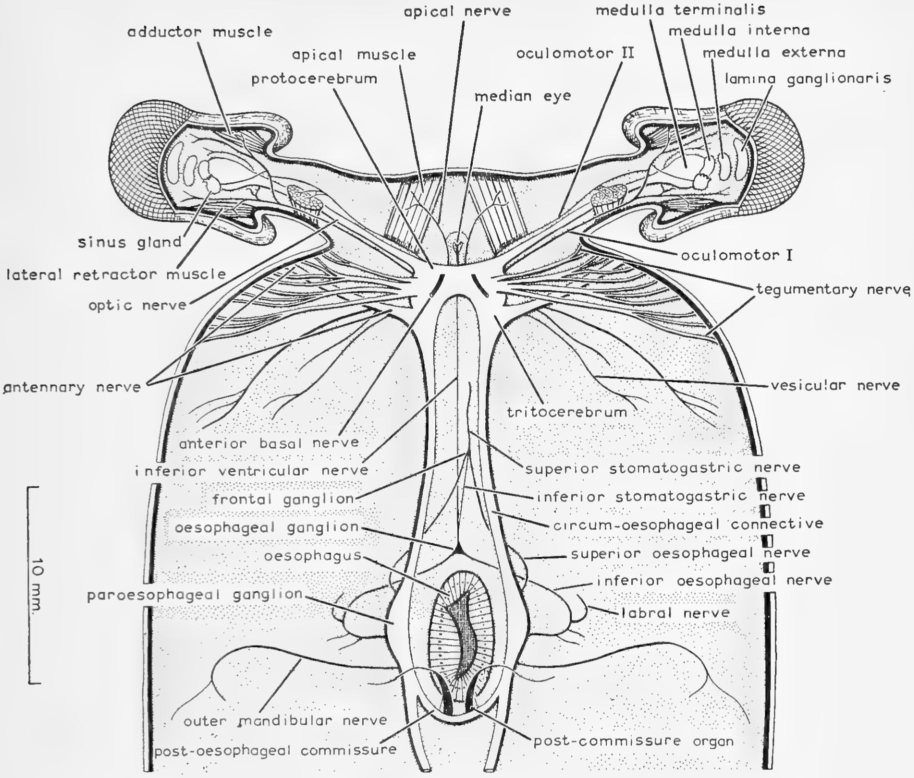


FIG. 61. Dorsal view of cephalic portion of central nervous system and part of stomatogastric nervous system.

of thick fibres springing ventro-laterally from the tritocerebrum. Proximally it supplies the antennal remotor, depressor, levator, and promotor muscles, and then proceeds medially through the peduncle, branching from time to time to the muscles in the three segments.

The innervation of the bladder of the antennal gland is effected by a delicate nerve (fig. 61) which arises from the root of the antennary nerve in proximity to the branches to the antennal remotor and depressor muscles. It is analogous to the *vesicular nerve* of *Astacus* which, however, was traced by Keim (1915) from the tegumentary nerve. It is admitted that several branches of the latter nerve run close to the wall of the bladder and, although they terminate more laterally in the hypodermis, there may be very fine connexions between some of them and the wall of the bladder. Further proof that the tegumentary nerve is not the source of the supply to the bladder has been provided by Maluf (1941), whose observations indicate that in *Procambarus clarkii* it is served by two sets of fibres derived from the root of the antennary nerve. Chaudonneret (1956) has also briefly mentioned that in *Orconectes limosus* (*Cambarus affinis*) the bladder is innervated by a branch of the antennary nerve, and perhaps further investigations will establish that this is the rule in most Reptantia. One difference between *Jasus* and the few other decapods so far examined by other investigators is that in a number of dissections a branch of the vesicular nerve was traced to the labyrinth of the antennal gland and suggests a possible supply to this part of the organ.

(c) *Ventral nerve cord*

The long and relatively thick pair of *circum-oesophageal connectives* (figs 57, 61, 62, 64) slope downward from the posterior end of the tritocerebrum below the cardiac fore-gut, and at the side of the oesophagus each has a fairly obvious swelling, the *commissural* or *paroesophageal ganglion* (figs 31, 61, 64) which is an important centre of the stomatogastric system. Behind the oesophagus and practically beneath the cephalic apodeme of the endophragmal skeleton, the two circum-oesophageal connectives are bridged by a short, narrow, transverse *post-oesophageal commissure* (figs 57, 61), from which a pair of small, so-called *post-commissure organs* (fig. 61) arises. The connectives then continue into the sternal canal, where they merge into an elongate *suboesophageal ganglion* which marks the beginning of the *ventral nerve cord.*

(i) The *suboesophageal ganglion* (Figs 57, 62, 64)

This represents the fusion of at least six pairs of ganglia and gives rise ventro-laterally to the paired nerves of the mandibles, the first and second

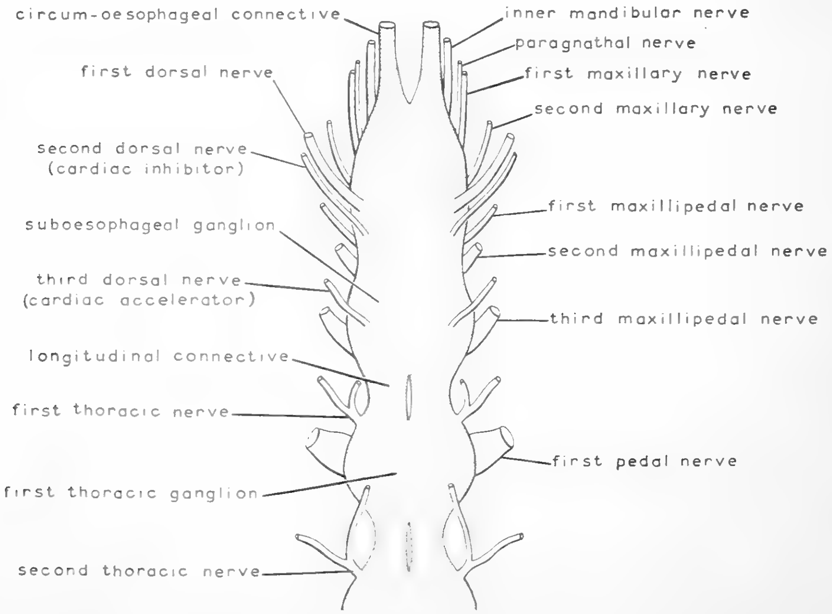


FIG. 62. Rough sketch of dorsal view of anterior part of ventral nerve cord to illustrate origins of paired nerves.

maxillae, and the three maxillipeds. Three additional pairs of dorsal nerves also originate at intervals along the length of the suboesophageal ganglion and belong to the neuromeres of certain of the appendicular nerves.

The overall arrangement is consistent with that observed in *Astacus* by Keim (1915) and Stoll (1925) and in *Orconectes limosus* by Chaudonneret (1956). Stoll also reported the presence of a median oesophageal nerve and a distinct pair of paragnathal nerves and, although the former has been confirmed by Chaudonneret, it does not seem to exist in *Jasus*, in which a slender median blood vessel occurs in a similar position between the bases of the two circum-oesophageal connectives. Keim and Stoll further claimed that the labyrinth of the antennal gland of *Astacus* was innervated by a nervus glandulae viridis, but this was not observed either in *Procambarus clarkii* by Maluf (1941) or in *Orconectes limosus* by Chaudonneret (1956) and could not be detected in *Jasus*. Chaudonneret has rightly drawn attention to certain obvious misinterpretations in Stoll's identification of the nerves, and his suggestion that Keim has mistaken the real paragnathal nerve and Stoll the inner mandibular nerve as the supply to the labyrinth partly clarifies the confusion concerning the distribution of the anterior nerves from the suboesophageal ganglion.

The mandibular muscles are innervated by distinct inner and outer nerves which at first sight appear to stem from different levels of the nervous system, but in serial sections are seen to originate in the same neuromere. The *outer mandibular nerve* (figs 61, 64) separates from the circum-oesophageal connective shortly behind the paroesophageal ganglion; it passes behind the ventral pyloric dilator muscle and then sweeps outward and forward in front of the anterior mandibular apodeme before curving backward to the mandibular lateral adductor muscles. Commenting on the unusual position of this nerve in *Astacus*, Keim (1915) suggested that histological investigations might reveal that it is centred in the suboesophageal ganglion, and this has been verified by Chaudonneret (1956) in dissections and sectioned material of *Orconectes limosus*. In sections of the puerulus stage of *Jasus* it can also be seen to originate in the suboesophageal ganglion, but it is bound up with and inseparable from the circum-oesophageal connective until it leaves the latter anteriorly near the paroesophageal ganglion. The remaining mandibular muscles are served by a comparatively stout *inner mandibular nerve* (figs 62, 64) which arises more obviously from the anterior end of the suboesophageal ganglion. It consists initially of subequal medial and lateral branches which course forward close to the ventro-lateral surface of the circum-oesophageal connective. After giving off a nerve to the lower end of the oesophagus, the medial branch bends abruptly into the cavity of the mandible and divides to the mandibular anterior adductor muscle and the flexor muscles of the palp. The rather more dorsal and slightly thinner lateral branch is distributed to the mandibular posterior adductor and the major and minor abductor muscles, much as in *Astacus* (Keim, 1915).

The paired *paragnathal nerve* has been the subject of discussion by Chaudonneret (1956), who has argued in favour of the recognition of a premandibular somite homologous to the superlingual region of Insecta. He has asserted that the paragnathal nerve of *Orconectes limosus* arises medial and therefore anterior to the inner mandibular nerve, but this is not substantiated by observations of the arrangement in *Jasus*. Contrary to expectations based on his conclusions and also on Keim's (1915) remark that the lower lip of *Astacus* is innervated by a branch of the inner mandibular nerve, the latter nerve in *Jasus* was found to be unrelated to the supply to the metastoma and paragnaths. In fact, the *paragnathal nerve* (fig. 62) has its origin in the suboesophageal ganglion close to the root of the first maxillary nerve. It is directed forward adherent to the first maxillary nerve and, separating medially from the branch to the abductor muscle of the first maxilla, it travels inward below the inner mandibular nerve and subdivides to the tissues and the muscles of the metastoma and the homolateral paragnath. Making allowance for Stoll's (1925) erroneous identification of the first maxillary nerve as the inner mandibular nerve, the position of the paragnathal nerve of *Astacus* is suggestive of that of *Jasus*, except that in the latter it is medial and not lateral to the first maxillary nerve. Consequently, it may be inferred that the paragnathal nerve in some forms, at least, is not so far removed from the first maxillary nerve as Chaudonneret (1956) has assumed, and there seems little justification for accepting his hypothesis that the paragnaths represent vestigial appendages of a premandibular segment.

The nerves to the *two maxillae* and the *three maxillipeds* arise in sequence ventro-laterally from the suboesophageal ganglion (fig. 62) usually by single roots, but most of them divide almost immediately into two main branches which travel forward to the coxopodite of the appendage. The large root of the third maxillipedal nerve originates some distance behind that of the second maxillipedal nerve in a somewhat distinct posterior section of the suboesophageal ganglion. This may account for the fact that the thoracic part of the ventral nerve cord of *Astacus* is sometimes described as a combination of the suboesophageal and six thoracic ganglia, the first of the latter being set aside for the sole purpose of supplying the third maxillipeds.

The three pairs of *dorsal nerves* apparently correspond to the first, second, and fourth described in fresh-water crayfishes by Keim (1915), Stoll (1925), and Chaudonneret (1956), and the reason for the suppression in *Jasus* of the counterpart of the third dorsal nerve of other forms is obscure. It is obvious, however, from Keim's remarks that the fourth dorsal nerve of *Astacus* is relatively insignificant and does not participate in the innervation of the dorsal muscles, while Chaudonneret has stated that the origin of the third dorsal nerve from the neuromere of the second maxilliped is less distinct in *Orconectes* than in *Astacus*.

The dorsal nerves are of special importance for, not only do they supply certain thoracic muscles, but the second and the third also contain fibres which, in combination with neurosecretions, regulate the frequency of the heart beat and serve respectively as the *cardiac inhibitor* and the *cardiac accelerator nerve*.

While these and other delicate nerves may be traced in preserved specimens or in serial sections, they are best displayed by adopting the vital staining technique recommended by Alexandrowicz (1932) and successfully used by other physiologists. For this purpose, immature specimens with a cephalothoracic length of approximately 4·4 cm were anaesthetized and, as suggested by Maynard (1953*a*), the ventral nerve cord was severed and the antennae and the legs were removed to expedite bleeding. After exposure of the heart by excision of the dorsal part of the carapace, the specimens were immersed in sea water containing methylene blue, made up in the proportion of 15 to 20 drops of an 0·5% solution of the stain in distilled water to 100 cc of sea water. Observations during two to four hourly periods showed the gradual pigmentation of the larger nerves and the presence of a nerve plexus associated with the heart.

The paired *first dorsal nerve* (figs 62, 64) is pre-eminently strong and issues dorsally from the suboesophageal ganglion slightly behind the second maxillary nerve. It passes upward and forward into the body cavity from the sternal canal in front of the fused paraphragms of the first and second maxillipeds. After supplying the posterior dorso-ventral muscle, it travels backward below the digestive gland and sends branches to the anterior part of the epimeral attractor muscle and the hypodermis.

The *second dorsal nerves* and the accompanying cardiac inhibitor fibres (figs 62, 64) are a pair of delicate strands which arise almost level with the origins of the first maxillipedal nerves and emerge from the sternal canal behind the cephalic apodeme. Each extends forward for some distance close to the more conspicuous first dorsal nerve and then courses upward and backward between the medial and lateral parts of the anterior thoracic muscle. Entering the pericardical cavity, it runs along the medial side of the deeper thoraco-abdominal muscle, loops around the dorsal antero-lateral ligament of the heart, innervates the epimeral attractor muscle, and also anastomoses with the accelerator nerve to form the lateral pericardial plexus.

The *third dorsal nerve*, with which the cardiac accelerator fibres are associated (figs 62, 64), is also slender, but slightly more substantial than the second dorsal nerve. From its source in the suboesophageal ganglion approximately dorsal to the root of the third maxillipedal nerve, it passes upward and forward supplying the first thoracic superficial ventral muscle and then curves backward beneath the outer face of the lateral part of the anterior thoracic muscle. It enters the pericardial cavity below the dorsal antero-lateral ligament of the heart and the cardiac inhibitor nerve and, after uniting with the latter in the lateral pericardial plexus, it continues posteriorly between the lateral and deeper thoraco-abdominal muscles, sending branches to them and to the epimeral attractor muscle.

On each side a *lateral pericardial plexus* (fig. 64), established by the union of the cardiac inhibitor and cardiac accelerator nerves, is located above the deeper thoraco-abdominal muscle. It represents a part of the *pericardial organ* discovered by Alexandrowicz (1953), and fine branches deriving from it constitute the anterior and posterior ligamental plexuses which are associated more particularly with the dorsal antero-lateral and the dorsal postero-lateral cardiac ligaments. Of perhaps even greater significance is the combination of the inhibitor and accelerator fibres into a distinct *dorsal cardiac nerve* (figs 47, 64) which extends from the lateral plexus and penetrates the dorso-lateral wall of the heart almost midway between the dorsal and lateral ostia. Within the heart the right and left dorsal cardiac nerves meet in a mid-dorsal series of neurones which function as the neurogenic pacemaker of the heart and have been described as the local nervous system by Alexandrowicz (1932) and as the cardiac ganglion by Maynard (1953*a*, 1960). In certain unpublished observations of the heart of adult specimens of *J. lalandii* made in 1959 by Mr. M. J. Penrith, and in the present study of both the puerulus stage and mature animals it is evident that the *cardiac ganglion* (diagrammatically indicated in figure 64) takes the form of a longitudinal trunk on the inner side of the dorsal wall of the heart. As in other marine Decapoda (Alexandrowicz, 1932; Maynard, 1953*a*), it consists of five closely-approximated anterior neurones and four smaller more widely spaced posterior neurones, and distinct processes, given off anteriorly, posteriorly, and laterally, can be traced into the myocardium. In summarizing recent conclusions concerning the function of the cardiac ganglion, Florey (1960) and Maynard (1960) have indicated that the large anterior cells are the follower or motor neurones and activate the myocardium; the smaller posterior neurones are the pacemakers which are capable of influencing the motor neurones. Analysing the different results of electrical stimulation of the accelerator and inhibitor nerves of the lobster and crayfishes, Florey (1960) has suggested that the possible release of excitatory and inhibitory chemical transmitter substances may account for the fact that, while acceleration provokes prolonged after-effects and practically no adaptation, stimulation of the inhibitor nerves has the opposite result.

Although the physiology of the dorsal nerves of *Jasus* has not been investigated, the present morphological findings are compatible with the more critical experimental studies by Alexandrowicz (1932), Wiersma & Novitski (1942), Smith (1947), and Maynard (1953*a*, 1953*b*) on the cardiac regulator nerves of other decapods. A similar structural pattern prevails in all the species thus far examined, and the main difference seems to relate to the fact that, while some forms, such as *Cancer irroratus* (Smith, 1947), *Panulirus argus* (Maynard, 1953*a*), and possibly *Homarus* (Maynard, 1953*b*), possess two pairs of cardiac accelerator nerves, *J. lalandii* agrees with *Procambarus clarkii* (Wiersma & Novitski, 1942) in having only one pair of accelerator nerves.

(ii) *Thoracic ganglia*

In accordance with the accounts of the nervous system of *Astacus* published by Huxley (1881), Keim (1915), and Stoll (1925), the ventral nerve cord behind the suboesophageal ganglion comprises five thoracic and six abdominal ganglia arranged serially from the fourth thoracic to the last abdominal segment. All the ganglia are double, but each pair is fused into a single mass by an inconspicuous transverse commissure, and the consecutive ganglia are united intersegmentally by a pair of longitudinal connectives. Normally the thoracic connectives are short, broad and adjacent, but those between the third and fourth ganglia are more widely separated than usual for the passage of the descending sternal artery. The fourth and fifth thoracic ganglia are approximated and joined by very short connectives, while the last thoracic and the first abdominal ganglia are linked by very long connectives that emerge from the sternal canal and pass dorsally over the superficial ventral thoraco-abdominal muscles into the abdomen.

Each thoracic ganglion gives off a pair of stout *pedal nerves* (figs 57, 62) which proceed laterally into the muscle chambers of their corresponding pereiopods and branch to the musculature in the coxopodite and the segments of the endopodite.

Immediately in front of each ganglion in the fourth to the eighth thoracic segments a pair of more delicate *thoracic nerves* (figs 62, 64) originates dorsolaterally at the end of the inter-ganglionic connectives; the first pair (fig. 62) occurs near the posterior limit of the connectives between the suboesophageal ganglion and the first thoracic ganglion and innervates the muscles in the fourth segment. As a rule, each thoracic nerve divides almost immediately within the sternal canal into medial and lateral branches; the former supplies the thoracic superficial ventral muscle and the medial part of the anterior thoracic muscle, while the lateral branch proceeds to the lateral section of the anterior thoracic muscle, the deeper and lateral thoraco-abdominal muscles, and the epimeral attractor muscle. The thoracic nerves are also responsible for the innervation of the reproductive organs, the paired *genital nerve* arising as a branch of the third thoracic nerve in the female and of the fifth thoracic nerve in the male. Towards the posterior end of the thorax some minor differences are apparent in the distribution of the thoracic nerves. Thus, as there are no epimeral attractor muscle fibres opposite the last two thoracic segments, the corresponding nerves are lacking; and, in addition to its typical branches, the last thoracic nerve contributes to the innervation of the paired first anterior oblique muscle and may also supply the superficial ventral thoraco-abdominal muscle.

Apart from slight differences in their enumeration, the thoracic nerves of *Jasus* are essentially similar to those of *Astacus* (Keim, 1915; Stoll, 1925). Stoll, however, has concluded that in the crayfish the first three thoracic nerves are bound to their corresponding pedal nerves; he has also distinguished an additional pair of commissural nerves arising from the longitudinal connectives, but these are suggestive of the thoracic nerves of *Jasus*.

Mention must also be made of further interesting and important ramifications of the thoracic nerves. It has been demonstrated by Alexandrowicz (1932) that in a variety of Decapoda they give rise to a system of *nervi segmentales cordis* which innervate the antennary, the hepatic, and the posterior cardio-arterial valves and the alary muscles of the pericardial septum and are independent of the lateral pericardial plexuses associated with the dorsal nerves from the suboesophageal ganglion. The arrangement in *Jasus* resembles that observed by Alexandrowicz in *Homarus*, *Scyllarus*, and the Brachyura. Delicate segmental nerves, passing inward from the last four pairs of thoracic nerves, combine to form a pair of faint longitudinal strands (*l.p.n.*, fig. 53) on the under surface of the middle third of the pericardial septum medial to the paired gonads. The two longitudinal threads are interconnected by several transverse anastomoses and branch anteriorly to the valves of the paired antennary and hepatic arteries. Posteriorly, after supplying the valves of the bulbus arteriosus and the sternal and genital arteries, the two strands are continuous with a similar system applied to the dorsal abdominal artery. As in the thorax, fine nerves, termed the *nervi segmentales aortae* by Alexandrowicz, separate from the abdominal nerves and usually run in a medial direction parallel to the paired lateral abdominal arteries. The valves at the origins of the latter vessels receive fine branches from these segmental nerves and, in addition, there are delicate longitudinal connectives (*l.a.n.*, fig. 54) on the surface of the dorsal abdominal artery. In discussing the significance of these elements, Alexandrowicz indicated that the cardiac muscles are functionally antagonistic to those of the cardio-arterial valves and the alary muscles of the pericardial septum. Consequently, he suggested that the delicate system of segmental nerves probably acts as a regulatory mechanism that governs the contraction of the muscles of the valves and the pericardial septum during the diastolic period when the heart is distended and filling with blood.

(iii) *Abdominal ganglia*

The six abdominal ganglia, although proportionally smaller than those in the thorax, are clearly recognizable antero-dorsal to the sternal ridges of their respective segments as elongate-oval swellings with intervening longitudinal connectives. In each of the first five abdominal segments three main pairs of peripheral nerves pass outward and backward from the nerve cord. Two broad pairs originate one behind the other in the ganglion, and the third, more delicate pair issues from the longitudinal connectives a short distance beyond the ganglion. The first paired nerve, which has been termed the *pleopedal nerve* (fig. 57), is ventral in position and travels across the segment close to the sternum; except in the first segment, where it terminates in the pleuron, it supplies the muscles of the pleopod. The branches of the second, slightly more posterior *dorso-lateral nerve* (figs 54, 57) are distributed chiefly to the abdominal flexor muscles, but there is also a comparatively strong offshoot (fig. 54) which curves dorso-laterally over the anterior oblique muscle and proceeds to the superficial and deeper extensor muscles. Arising somewhat dorso-laterally from the longitudinal connectives, the third of the series (fig. 57) are comparable with the *ventral nerves* of *Astacus* defined by Keim (1915) and Stoll (1925). Each arches backward between the ventral portions of the anterior and the posterior oblique muscles and, in addition to innervating these, also sends a branch to the abdominal superficial ventral muscle.

On the whole, the following paired nerves, which radiate from the *sixth abdominal ganglion* into the uropods and telson of *Jasus*, are essentially similar to those of *Astacus* (Keim, 1915; Stoll, 1925). In a ventral dissection (fig. 63) most of them seem to be more superficial than those of *Astacus*, and some of the variations in the distribution of their branches in the two forms may result more from differences of interpretation than from any marked specific modifications.

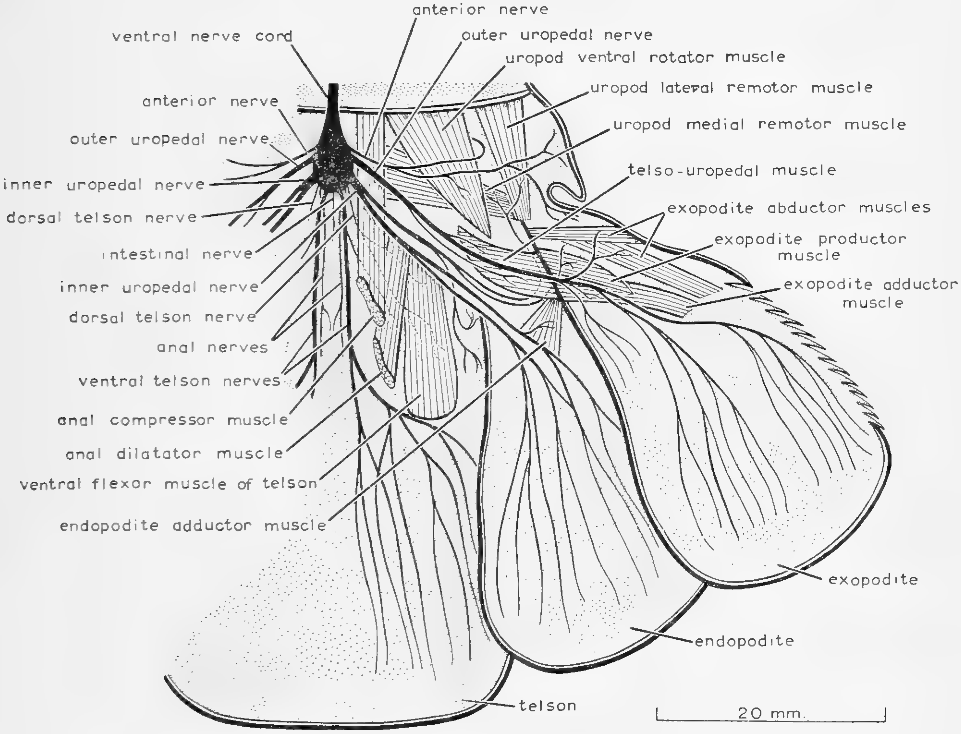


FIG. 63. Diagrammatic ventral view of sixth abdominal ganglion and nerves to parts of left uropod and left half of telson.

The relatively thin *anterior nerve* arises ventro-laterally and passes out almost horizontally close to the sternum. After giving off a delicate supply to the superficial ventral muscle of the sixth abdominal segment, it divides into two branches, one of which innervates the ventral rotator muscle of the uropod, round the lateral margin of which it then proceeds upward to the dorsal rotator muscle of the uropod. The other branch extends below the lateral remotor muscle of the uropod and ends in the hypodermis of the sixth pleuron and the lateral region of the protopodite of the uropod.

In Keim's (1915) account of *Astacus* the next two nerves were described as the nervus uropedalis and the nervus telsonos ventralis but, as the latter nerve is hardly associated with the telson in *Jasus*, it seems more appropriate to designate the two nerves in question as the outer and inner uropedals, and to reserve the name ventral telson nerve for one which occurs more posteriorly in the telson.

The conspicuous *outer uropedal nerve*, which is comparable with the uropedal nerve of *Astacus*, originates close to the root of the anterior nerve and courses obliquely outward, innervating the telso-uropedal muscles on its way to the exopodite of the uropod. Within the latter, it supplies the abductor and adductor muscles, and continues as a strong nerve from which a number of branches pass into the lamella and underlie the rows of dorsal spines.

The *inner uropedal* is the most posterior of the latero-ventral nerves from the sixth abdominal ganglion, and is subequal in thickness to the outer uropedal nerve but is more widespread. Near its origin it divides into two main branches which are directed postero-laterally over the ventral surface of the anal compressor and the anal dilatator muscles, presumably without supplying them. The thinner anterior branch subdivides into three: one offshoot travels forward dorsal to the telso-uropedal muscles and enters the lateral and medial remotor muscles of the uropod near their insertions; another curves into the proximal part of the exopodite and apparently terminates in the productor and reductor muscles; while the posterior sub-branch innervates the tissues in the proximal lateral corner of the telson. This branch is absent from the ventral telsonos nerve of *Astacus*, doubtless because Keim (1915) observed that the remotor muscles of the uropod were served by the uropedal nerve. In passing to the endopodite of the uropod and innervating its adductor muscle and broad lamella, the stouter posterior branch of the inner uropedal nerve of *Jasus* broadly conforms to Keim's (1915) description of the ventral telsonos nerve of *Astacus*, but differs in having no obvious connexions with the telso-uropedal, the anal compressor, and the anal dilatator muscles.

As in *Astacus* (Keim, 1915; Stoll, 1925), the *dorsal telson nerve* issues postero-dorsally. It is rather flat and passes above the anal compressor and anal dilatator muscles, dividing into three branches which supply the flexor muscles of the telson.

The term *ventral telson nerve* has been applied to a strong nerve that originates directly below the dorsal nerve of the telson and is represented by Keim (1915) as an extension of the nervus telsonos dorsalis in *Astacus*. In *Jasus*, however, it appears as a discrete element which travels backward medial to the anal compressor muscle and ramifies in the telson. About halfway along its course it gives off a fairly obvious, flat, lateral branch which probably innervates the anal compressor and anal dilatator muscles. The nerve supply to these muscles is difficult to determine with certainty in *Jasus*. There are occasional indications that they may receive fine fibres from the main telso-uropedal and inner uropedal nerves, but these are so indistinct and inconstant that it is assumed that the most likely source is from the ventral telson nerve.

The slender, but well-defined, *anal nerve* passes downward between the dorsal and ventral telson nerves, and in some specimens may be adherent to the latter. It innervates certain vertical muscle fibres stretching between the dorsal wall of the telson and the terminal portion of the hind-gut, and frequently the paired anal nerves are linked by a transverse anastomosis on the ventral wall of the anal region of the intestine.

In addition to the above paired nerves, there is a delicate, median *intestinal nerve* which extends from the postero-dorsal end of the sixth abdominal ganglion directly to the ventral wall of the preanal part of the hind-gut. There it divides into a short *posterior intestinal nerve* to the anal region and a long *anterior intestinal nerve* that generally proceeds undivided along the mid-ventral wall of the hind-gut. The innervation of this region is variable, however, and in some dissections the anterior intestinal nerve was observed to separate into two lateral intestinal branches, similar to those in Keim's (1915) account of *Astacus*.

2. STOMATOGASTRIC OR SYMPATHETIC NERVOUS SYSTEM

Careful dissections of preserved specimens or of animals with the nerves stained *in vivo* with dilute methylene blue in sea water, as well as the verification of some details in serial sections, are required to trace the ramifications of this system. It is linked to the brain by a median nerve and consists of several interconnected ganglionic centres from which delicate nerves diverge to the fore-gut and some neighbouring organs. The overall plan resembles that of the crab (Pearson, 1908), the American lobster (Herrick, 1911), and more particularly that of *Astacus*, the details of which as presented by Keim (1915) have proved a useful basis for the following summarized conclusions regarding the arrangement in *Jasus*.

The main centres are a pair of ganglionic swellings, termed the paroesophageal ganglia by Pearson (1908), the commissural ganglia by Herrick (1911), Keim (1915) and some modern physiologists, and the Connectivalganglien by Balss (1944). The first term seems appropriate because, as the name introduced by Balss implies, the ganglia are not related to any true commissures, but are easily observed (figs 31, 61, 64) as enlargements on the course of the circum-oesophageal connectives a short distance in front of the post-oesophageal commissure. They are also adjacent to the postero-lateral wall of the oesophagus which receives a pair of delicate nerves, either from the ganglia or from the connectives immediately posterior to them.

Emerging from each *paroesophageal ganglion* are two main nerves. The *inferior oesophageal nerve* (figs 61, 64) arises postero-ventrally and curves forward below the lateral oesophageal dilator muscle to meet the corresponding nerve of the other side anterior to the oesophagus in a small, but nevertheless discernible, *oesophageal ganglion* (figs 31, 61, 64). The inferior oesophageal nerve commonly gives off two delicate branches to the oesophageal muscles, as well as a stout *labral nerve* (fig. 61), and the latter invariably has an anastomosis with the oesophageal ganglion. Chaudonneret's (1956) observation that the

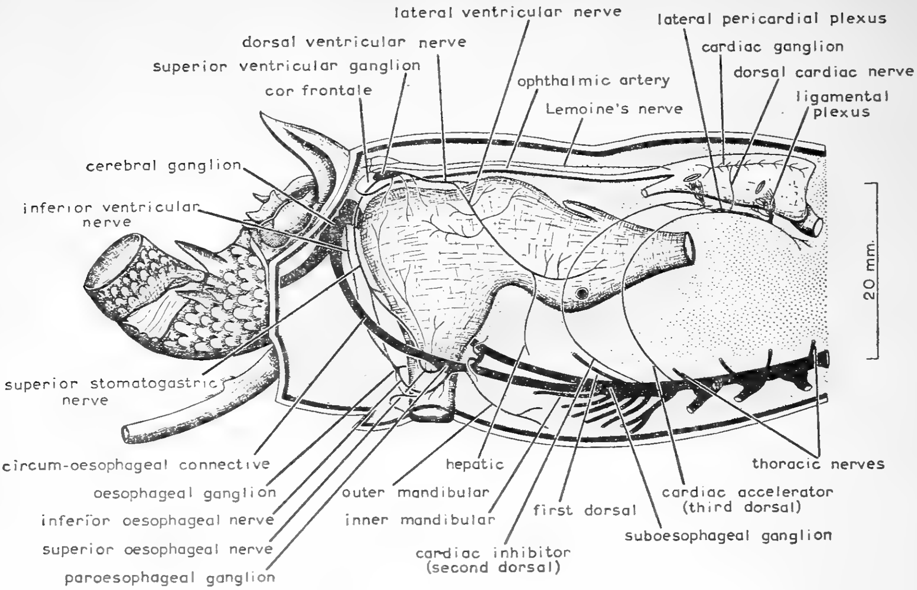


Fig. 64. Semi-diagrammatic side view of stomatogastric and cardiac nerves. The thoraco-abdominal and anterior thoracic muscles have been omitted and this may give a somewhat misleading impression of the course of the nerves.

labyrinth of the antennal gland of *Orconectes limosus* is innervated from the inferior oesophageal nerve is not realized in *Jasus* and can hardly be expected owing to the intervention of the antennal depressor muscles between the nerve in question and the gland. The most likely supply to the labyrinth so far detected in *Jasus* is derived from a branch of the vesicular nerve, which appears to enter the main lobe of the labyrinth in association with the anterior renal artery. This conclusion, however, is contrary to opinions regarding other Decapoda, in which the labyrinth is either considered to be innervated from some other source or to have no nerve supply and, in discussing the latter arrangement in *Procambarus clarkii*, Maluf (1941) was convinced that the secretory activity of the antennal gland was not governed by the nervous system.

The *superior oesophageal nerve* (figs 61, 64) leaves the paroesophageal ganglion anteriorly, and near its origin usually gives rise to two slender branches which subdivide into a plexus on the antero-lateral wall of the cardiac fore-gut. The main nerve continues forward dorsal to the inferior oesophageal nerve and unites with its pair of the opposite side in front of the cardiac fore-gut.

As in other decapods, a long, fairly thick, median *inferior ventricular nerve* (figs 61, 64) issues from the tritocerebrum between the two circum-oesophageal connectives. It is directed postero-ventrally through the tendon of the basal muscles of the eye and joins the upper end of the oesophageal ganglion.

According to Keim (1915), the paired inferior and superior oesophageal nerves, as well as the median inferior ventricular and inferior stomatogastric nerves of *Astacus*, are all centred in the oesophageal ganglion, but in *Jasus* the right and left superior oesophageal nerves converge some distance above the oesophageal ganglion. From their point of union, another nerve passes downward and joins the oesophageal ganglion in immature specimens, but tends to connect with the inferior ventricular nerve in mature animals. This arrangement may prove to be fairly general, for Chaudonneret (1956) has observed a similar disposition of the inferior and superior oesophageal nerves in *Orconectes limosus*, and has commented on its being one of the differences between his findings in the American crayfish and previous accounts of the decapod sympathetic nervous system. It is nevertheless possible that the stomatogastric system varies in different species of Macrura, and the only means of correlating the circumstances in *Jasus* with those of *Astacus* (Keim, 1915) is to suggest that the slight ganglionic swelling at the union of the pair of superior oesophageal nerves represents a somewhat ventrally situated *frontal ganglion* (fig. 61).

If this interpretation is correct, then the vertical anastomosis between this frontal ganglion and the oesophageal ganglion or the inferior ventricular nerve, as the case may be, is comparable to the median *inferior stomatogastric nerve* (fig. 61), although it is considerably shorter than that of *Astacus*.

Pursuing this line of thought, it is also reasonable to suppose that the lower position of the frontal ganglion in *Jasus* has resulted in a lengthening of the median *superior stomatogastric nerve* (figs 61, 64) which extends upward from the frontal ganglion along the anterior wall of the cardiac fore-gut. Thus, as in *Astacus*, the inferior and superior stomatogastric nerves are respectively below and above the frontal ganglion but, owing to the difference in position of the latter in the two animals, there is an inverse ratio in the lengths of the two nerves.

The superior stomatogastric nerve links the ventral part of the system to a conspicuous, spindle-shaped *superior ventricular ganglion* (fig. 64) which is located within the cor frontale at the anterior end of the median ophthalmic artery. Three pairs of nerves are commonly distributed to the anterior muscles of the fore-gut, partly from the superior ventricular ganglion and partly from the nerve continuous with it posteriorly.

In Keim's (1915) account of *Astacus*, the frontal ganglion enters into relationship with the brain by way of a *superior ventricular nerve*, but in *Jasus* no such connexion was observed. In fact, it is questionable if this delicate median nerve exists in *Jasus*, and it has therefore been omitted in figures 61 and 64. All the other nerves of the sympathetic system are distinct, but this one, which should extend upward from the protocerebrum to the superior stomatogastric nerve, has eluded positive identification. In all dissections, two bundles of delicate striated fibres, which could easily be mistaken for nerves, were seen to be located between the pair of nerves to the anterior basal eye muscle and to pass upward from the margin of the protocerebrum apparently to the optic arteries. Between these bundles there were occasional evidences of one or two very tenuous nerve fibres, but it is doubtful if they are related to the stomatogastric nervous system. The presence of a superior ventricular nerve in Decapoda has been generally accepted (Balss, 1944; Hanström, 1947), but Balss has indicated that it was not observed by Mocquard (1882) and Police (1908).

Continuous with the posterior extremity of the superior ventricular ganglion there is a median *dorsal ventricular nerve* (fig. 64) which leaves the lumen of the ophthalmic artery ventrally and travels over the mid-dorsal surface of the cardiac fore-gut, subsequently bifurcating into a pair of lateral ventricular nerves. Each *lateral ventricular nerve* (fig. 64) is directed postero-ventrally over the fore-gut and innervates the posterior gastric muscles as it passes between them and the anterior bundle of the mandibular posterior adductor muscle. It also gives off fine anterior twigs to the lateral wall of the cardiac fore-gut, a stronger posterior branch which curves beneath the posterior gastric muscles to reach the muscles of the pyloric fore-gut, and a more ventral *hepatic nerve* (fig. 64) to the digestive gland.

Keim (1915) has discussed some of the earlier uncertainties and discrepancies concerning the origin of the median nervus cardiacus or Lemoine's nerve as it is sometimes called, and has established that in *Astacus* it is derived from the superior stomatogastric nerve. Although *Lemoine's nerve* in *Jasus* (fig. 64) is fairly easy to detect as a delicate thread running dorsal to the median ophthalmic artery, its course above the cor frontale is more obscure and evidently differs from that of *Astacus*. It seems to have a paired origin in the superior ventricular ganglion, the two roots passing forward and upward round the ligaments suspending the cor frontale to the wall of the head. At this level, which is dorsal to the cor frontale and anterior to its contained superior ventricular ganglion, the two nerves are interconnected by a transverse anastomosis at either end of which is a minute ganglion that probably innervates the posterior basal eye muscle. Behind the anastomosis the two nerves converge to the left of the cor frontale and form the long median Lemoine's nerve, from which a fine plexus is given off almost immediately to the postero-dorsal wall of the cor frontale. The median nerve maintains its position to the left of the ophthalmic artery for some distance, but on approaching the heart it becomes mid-dorsal. It then passes between the anterior cardiac ligaments and proceeds to the cardio-arterial valves at the base of the ophthalmic artery.

The function of Lemoine's nerve has been investigated by a number of physiologists, among whom Wiersma & Novitski (1942) have demonstrated that it has no effect on the heart beat, and this seems to support the view that it does not extend into the myocardium. Assuming that it terminates in the valves of the ophthalmic artery, it is presumably similar in function to the nerves of other cardio-arterial valves and controls rhythmic contraction of the valves alternating with that of the cardiac muscles.

I. Sense Organs

The more obvious sense organs, such as the eyes and the statocysts, have been well described in various Crustacea, and recently considerable attention has been given to delicate, less conspicuous, but none the less essential, sensory mechanisms. Detailed studies of the proprioceptors in the limb joints of Reptantia have been made by a number of physiologists, including Burke (1954), Alexandrowicz (1958), Wiersma (1959), Whitear (1962), and Bush (1962, 1965), and a concise account of the structure and function of these and other similar receptors has been given by Cohen & Dijkgraaf (1961). It has been shown that the limb proprioceptor organs are located in elastic strands, most of which stretch between a muscle tendon in one limb segment and the integument at the proximal edge of the next limb segment. The proprioceptors are associated with bipolar sensory neurones, and the fibres in each organ have been observed to respond to the direction of movement and the position of the joint.

Many of the diverse setae distributed over the body and the appendages are tactile in function, but certain of the antennulary hairs are probably chemoreceptive. Investigations by Lindberg (1955) on the behaviour of *Panulirus interruptus* and some observations made during the present study of *J. lalandii* indicate that the antennules are highly sensitive to prevailing environmental conditions and that they are particularly active during locomotion and foraging. Electrophysiological experiments performed by Laverack (1962*a*, 1962*b*, 1963) and Mellon (1963) have demonstrated that minute hairs located in numerous shallow pits on the body surface of *Homarus* and *Procambarus* may be differentiated into hair-peg organs which function as water current receptors, and hair-fan organs which act as pressure receptors.

From a number of published accounts, it is apparent that sound production is fairly general in decapod Crustacea, but it seems to be of little importance in the few members of Parker's (1884) Palinuridae Silentes. As indicated by George & Grindley (1964), however, Dr. Heydorn has reported that in nature *J. lalandii* emits audible noises. These sounds are thought to be produced by the gnashing of the mandibles, and a similar acoustic mechanism has been cited by Dijkgraaf (1955) for *Maja squinado* and related forms. The antennal stridulatory organs of the Palinuridae Stridentes have been well documented by Parker (1878), Dijkgraaf (1955), Lindberg (1955), Moulton (1957), Hazlett & Winn (1962*a*, 1962*b*), and George & Grindley (1964). Two types of sound were distinguished in *Panulirus argus* by Moulton (1957), who suggested that each was related to a different behavioural pattern: a 'conversational' tone or 'slow rattle' was heard when the animals were undisturbed, but, when they were alarmed, a defensive 'rasp' was produced.

It appears from Lindberg's (1955) and Moulton's (1957) observations that the sounds produced by *Panulirus* have practically no effect on possible predators. They may be signals that can be recognized by other members of the same species but, so far, little is known about the sense organs responsible for their detection. Experimenting with several species of Decapoda, Prentiss (1901) demonstrated that, whereas excision of both statocysts resulted only in a slight weakening of the reactions to artificial sound vibrations, removal of the antennules and the antennae markedly reduced sensitivity to stimulation; this was particularly noticeable in a species of *Hippolyte* (*Virbius*) in which statocysts are normally absent. He therefore inferred that decapod crustaceans lack true auditory organs and that their responses to sound waves are merely tactile reflexes. Dijkgraaf (1955) also found that ablation of both statocysts of *Palinurus elephas* had no marked effect on reactions to experimental stimulation, while Burke (1954) has suggested that the protopodite-dactylus proprioceptor of the pereiopods of *Carcinus maenas* may be partly a vibrator receptor. It has been concluded by Cohen (1955) and Cohen & Dijkgraaf (1961) that, although there is experimental evidence of the presence in the statocysts of some receptors which only respond to vibrations passing through the solid substratum, hearing in the widely accepted sense has not been proved in Crustacea.

1. SENSORY SETAE

The different kinds of decapod cuticular hairs and bristles and their possible functions have been reviewed and illustrated by Balss (1944). Therefore, only a few general remarks are given here as an introduction to a more detailed inspection of the antennulary setae which include important categories of cuticular sense organs.

(a) *Tactile and olfactory setae*

Despite considerable morphological variation, the setae on the body surface and the appendages may, according to Prentiss (1901), be differentiated structurally and presumably functionally into two main types, namely, tactile elements or mechanoreceptors and olfactory hairs or chemoreceptors.

Characteristically, the *tactile setae* have a long, tapering, feathered shaft attached by a basal spherical bulb or ampulla that allows of great mobility. The conclusion reached by Farre (1843) and Prentiss (1901) that each tactile seta is innervated by a single nerve fibre has received some confirmation from more recent investigators, but there is experimental proof that certain short hairs on the carapace of *Procambarus clarkii* (Mellon, 1963) and on the chelae and carapace of *Homarus gammarus* (Laverack, 1963) are mechanoreceptors, each of which is supplied by a pair of sensory neurones.

Olfactory setae are commonly shorter than the tactile setae, from which they also differ in lacking an obvious ampulla, in being non-plumose, and in their innervation by several nerve elements. Experiments performed by Holmes & Homuth (1910) have shown that in the crayfish olfactory receptors are present on the antennae, the mouth-parts, and the extremities of the chelipeds, but that the greatest response to chemical stimulation is displayed by the outer flagellum of the antennule. A gustatory sense has frequently been attributed to the olfactory setae on the mouth-parts of some species, but Barber (1961) has indicated that, while this appears to be substantiated by behavioural experiments, it is difficult to determine if the subtle discrimination between smell and taste exists in Crustacea.

In *J. lalandii* numerous, short, plumose setae occur on the general body surface, and also in a row along the upper margin of the raised antennal flagellum and on the flagella of the exopodites of the three pairs of maxillipeds, while the slender hairs on the epipodites are barbed, rather than plumed. Some of the setae on the endopodite of the first maxilla are likewise plumed, and, although most of the parts of the second maxilla are fringed with plumose hairs, the longer setae projecting from the posterior extremity of the scaphognathite into the anterior region of the branchial chamber are non-plumose and may be chemoreceptive.

(b) *Antennulary setae*

In describing the appendages, it was noted that the antennulary flagella of *Jasus* are short and slightly dimorphous, the outer flagellum being somewhat smaller and broader and more or less fitting into the lateral concavity of the inner flagellum. Both are furnished with plumose and non-plumose setae which conform to the above general definitions of tactile and olfactory receptors. Most of the setae are arranged in regular transverse rows coinciding with the broadest annulations which number approximately 28 on the inner flagellum and 33 on the outer flagellum.

The *inner flagellum* is compressed and, while its medial convex and lateral concave surfaces are bare, it carries relatively short dorsal and longer ventral marginal setae, the majority of which are plumed and have a basal ampulla provided with a minute pointed spur. Predominantly, but not consistently, the plumose setae in each annulus are arranged in a row of four near each dorso-lateral and ventro-lateral edge, but occasionally there may be a supplementary group of two (fig. 65) or three setae proximal to the main set. In addition, two or three small, unplumed bristles occur along the dorsal margin, and the ventral

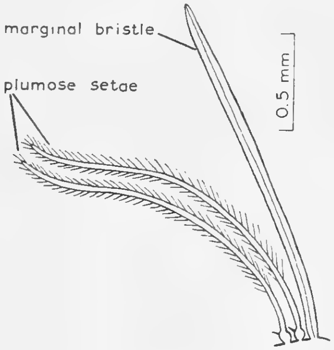


FIG. 65. Ventral setae of inner flagellum of antennule.

setae are bordered by a conspicuous projecting bristle and usually a short, plumose seta: all the long ventral plumose and non-plumose setae are so directed that they embrace the setae of the outer flagellum.

The dorsal surface of the *outer flagellum* is smooth and convex, the setae being located ventrally and comprising three structural kinds in each annulus (fig. 66). The greater area of the ventral surface supports rows of long, delicate, non-plumose, colourless hairs, which are faintly annulated distally, measure about 1·2 mm long, and are comparable to the *aesthetascs* of other Crustacea. There are fewer aesthetascs proximally and distally, but in most of the middle annuli there are two rows, in each of which 20 to 30 aesthetascs were counted. Lateral to the aesthetascs is a long, stiff, pointed bristle, approximately 1·4 mm in length, and one or two short plumose setae, about 400 to 500 μ long, which are probably respectively similar to the large guard and the smaller companion hairs of *Panulirus argus*, described by Laverack (1964) and Laverack & Ardill (1965). On the medial edge of each annulus a relatively long, unplumed bristle, with its tapering point slightly curved outward over the aesthetascs, also resembles a guard hair.

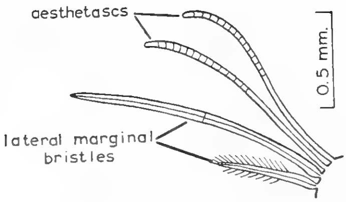


FIG. 66. Setae of outer flagellum of antennule.

By analogy with the sundry functions attributed to the antennulary setae of other Decapoda, it may be assumed that in *Jasus* the plumose setae respond to tactile stimulation, while the others, and particularly the aesthetascs, are probably chemosensitive. Calman (1909) has remarked that in many Crustacea the aesthetascs are better developed in the males and assist in the detection of the females, while Marcus (1911) found that the males of certain blind, deep-sea Galatheidae had a higher olfactory quotient than the females and correlated this with the loss of eyes. Presumably, as indicated by Forster (1951) in *Palaemon* (*Leander*) *serratus*, sight plays a minor role in the mating behaviour, and only a recently moulted female with ripe gonads will provide the necessary chemical stimulation attractive to the male. It is also of interest that Barber (1961) has not included the Decapoda in the list of Crustacea in which this quantitative sexual dimorphism of the aesthetascs has been observed. A cursory examination of a few South African palinurids reveals no marked sexual differences of aesthetascs in *Projasus parkeri* (George & Grindley) or in *Panulirus homarus* (L.) [*P. bürgeri* (de Haan)], but it is possible that they may be rather more numerous, longer, and finer in the males than in the females of *Palinurus gilchristi* Stebb. and *J. lalandii*. For instance, in the latter species there may be approximately 25 per row in the female and 30 per row in the male, but it is doubtful if this numerical difference has any functional significance.

Krijgsman & Krijgsman (1954) concluded that the antennulary flagella of *J. lalandii* are 'osmoreceptive', in that they are capable of registering experimental changes in the salinity of the water, while, according to Cohen & Dijkgraaf (1961), there is evidence that the antennules of *Carcinus maenas* are sensitive to water currents, and, if the antennules of *Jasus* are likewise sensitive to water-borne vibrations, it seems likely that the plumose setae would react to such stimuli. The exact site of 'osmoreception' is unknown, but Laverack (1964) has indicated the difficulties of defining the loci of individual receptors. It has also been demonstrated by Laverack (1964) and Laverack & Ardill (1965) that the outer flagellum of *Panulirus argus* is chiefly concerned with chemoreception and that each aesthetasc is supplied by as many as 350 neurones, while the guard hairs and the companion hairs are probably doubly innervated.

2. STATOCYSTS

The paired balancing organ or statocyst, which has been examined in various decapod Crustacea by Farre (1843), Prentiss (1901), Panning (1924), Lang & Yonge (1935), Cohen (1955), Dijkgraaf (1955, 1956) and others, is

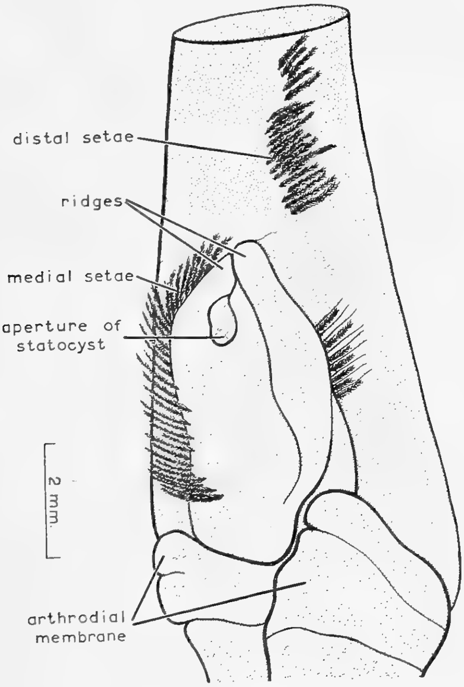


FIG. 67. Dorsal view of base of right antennule.

located in the proximal segment of each antennule. In *Jasus* its position is marked by a paler, dorsal area bounded by definite ridges and, as in other Macrura, it is an open vesicle. The small external aperture (figs 60, 67) occurs in a depression between the medial and lateral ridges, and the short, slightly oblique entrance is overlapped by the dorsal wall of the antennule. Associated with the statocyst are three sets of conspicuous, external setae (fig. 67): latero-distal to the aperture there is a row of approximately 22 relatively long, plumed setae; along the lateral ridge is a group of about 16, more or less alternating long, stiff, unplumed bristles and shorter plumose setae; and the medial border of the statocyst area is fringed with two or more rows of numerous, fairly long, feathered setae, the anterior and posterior pinnules of which are often unequal in length.

The *statocyst* (figs 60, 68) is a thin-walled, transparent, fluid-filled, oval sac, measuring about 4·1 mm long by 1·75 mm wide in medium-sized specimens, and having a rounded anterior margin and a more pointed posterior extremity. It projects inward and downward at an angle slightly inclined to the horizontal plane and, being dorso-ventrally flattened, its longer, curved, lateral and shorter medial margins are pronounced. Its walls, which may conveniently be described as dorsal and ventral, are lined with about 500 delicate, plumose hairs which are directed into the lumen and belong to the category of tactile sensory elements.

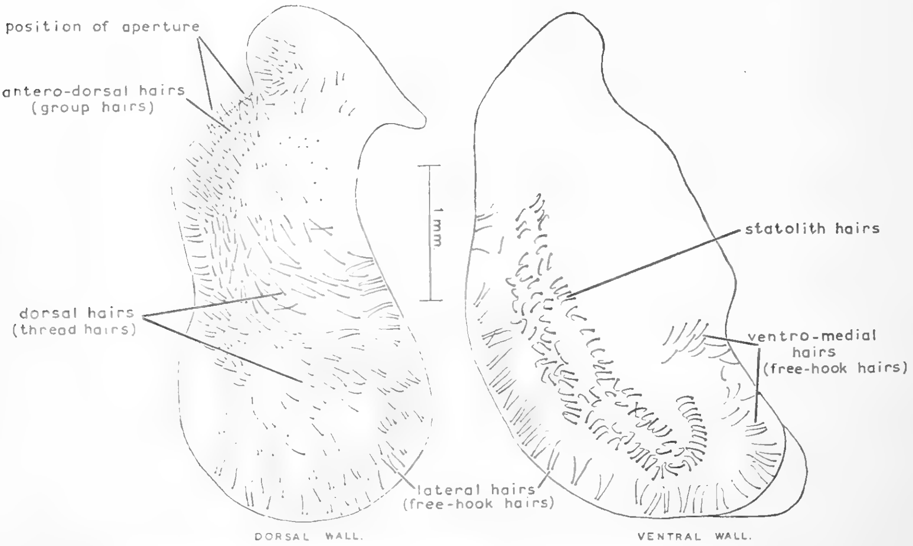


FIG. 68. Inner views of walls of bisected left statocyst from which the statoliths have been removed.

Although the arrangement of the statocyst hairs hardly corresponds with any of the patterns so far reported in other species, four structural types, comparable with those of *Carcinus maenas* (Prentiss, 1901; Dijkgraaf, 1956), *Maja* *verrucosa* (Dijkgraaf, 1956), and *Homarus americanus* (Cohen & Dijkgraaf, 1961), may be differentiated.

The middle of the ventral wall of the statocyst is slightly convex and raised into a somewhat crescentic area, termed the sensory cushion by Prentiss (1901). This is furnished with two main and an additional third scanty row of rather small and relatively stout *statolith* or *hook hairs* (figs 68, 69), the plumose tip of each of which is characteristically bent at an acute angle on the proximal part of the shaft. Resting on the statolith hairs are numerous small sand grains or *statoliths* (fig. 60) which are bound together by a mucous adhesive, said by Prentiss (1901), Lang & Yonge (1935), and Cohen & Dijkgraaf (1961) to be secreted by special glands situated beneath the walls of the statocyst. Experiments described by Cohen (1955), Dijkgraaf (1956), and Cohen & Dijkgraaf (1961) demonstrate that the statolith hairs react to movements of the statoliths resulting from the force of gravity; they are considered to serve as position receptors, whose response is mainly to displacement about the transverse axis, but also partly to postural changes about the longitudinal axis.

FIG. 69. Sensory hairs of statocyst.

Thread hairs (figs 68, 69), which are long and slender with a tapering plumed tip, are distributed over the dorsal wall. Similar hairs in other decapods are stimulated, not by positional changes, but by movements of the fluid contents of the statocyst; they have been defined by Dijkgraaf (1956) and Cohen & Dijkgraaf (1961) as rotation receptors which are sensitive to movements about vertical and horizontal axes.

The longest hairs (figs 68, 69) within the statocyst occur usually in pairs along the lateral and medial margins of both walls, and each is distinguished by a fine, tapering, slightly curved, plumose tip. They are probably comparable with the *free-hook hairs* mentioned by Dijkgraaf (1956) and Cohen & Dijkgraaf (1961), who have suggested that they may assist in governing the rotatory reflexes initiated by the responses of the thread hairs to stimulation.

The *group hairs* described by Prentiss (1901) in proximity to the statocyst aperture of *Carcinus maenas* differ from the other kinds of hairs in being short. coarse, and unplumed. This definition does not apply to any of the statocyst hairs of *J. lalandii*, but in a position corresponding to that of the group hairs of *Carcinus maenas* there is an obvious antero-dorsal field (fig. 68) with numerous comparatively stout, medium-sized hairs, each of which (fig. 69) is jointed, heavily fringed at the tip, and directed towards the aperture. In the statocyst of other species Farre (1843) and Panning (1924) have also indicated that there is a triangular field of sensory hairs guarding the aperture. Although their function has not yet been determined, Prentiss (1901) suggested that the group hairs of *Carcinus* might be modified tactile hairs that had been invaginated during the formation of the statocyst.

3. EYES

The main visual organs of adult decapod Crustacea are a pair of stalked, lateral, compound eyes, but in some species a small unpaired or median eye, which is characteristic of malacostracan larvae, may be retained in the adult.

(a) *Median eye*

According to Gilchrist (1913*b*), a median eye-spot, as well as lateral compound eyes, occurs in the recently-hatched naupliosoma larva of *J. lalandii*, and Von Bonde (1936) has indicated that it is a feature of an even younger prenaupliosoma stage but that 'it disappears and is lost' (p. 18) after the 3·8 mm stage of the phyllosoma larva. However, in the course of the present study close inspection of the phyllosoma and puerulus stages proves that the small median eye is still visible through the transparent exoskeleton; moreover, it also persists in the adult. It projects mid-dorsally from the brain immediately below the fused eyestalks of the compound eyes and, on exposure of the anterior part of the nervous system of juvenile and more mature specimens (fig. 61), it is easily detected by its mass of reddish pigment. In sections of the puerulus stage (fig. 70) the bulk of the pigment is seen to be arranged in two crescentic layers along the medial borders of a pair of obvious, closely-apposed lateral cups composed of sensory cells with relatively large nuclei; ventral to these

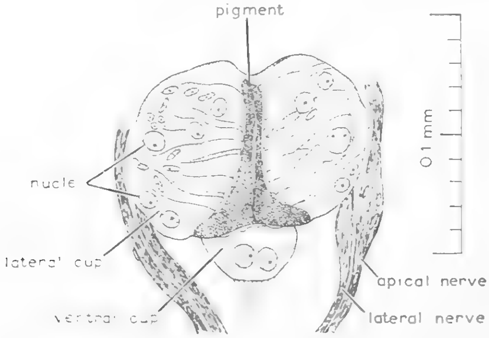


FIG. 70. Semi-diagrammatic vertical section of median eye of puerulus stage. The lateral nerves and lower parts of apical nerves were added from a section 30 μ behind that passing through the three cups of the eye.

there is a smaller median cup occupied by three large cells. The three portions of the median eye are innervated independently by very short, fairly broad nerves that converge at the frontal margin of the protocerebrum midway between the apical nerves to which the lateral nerves are adjacent. The several nerves can be seen mid-dorsally in the cellulae anteriores superiores (fig. 58), but presumably have deeper centres in proximity to the pons cerebri. The whole structure lies between the median ophthalmic artery and the brain about 130 μ in front of the section drawn in figure 58. It has apparent distal connexions with the mid-dorsal epidermis, the cells of which are modified and considerably elongated; the lateral extensions encircle the ophthalmic artery, but another one appears to pass directly upward through the middle of the artery.

The median or nauplius eye has been carefully investigated in a variety of adult Decapoda by Elofsson (1963), who has concluded that broadly speaking it is a combination of the nauplius eye *sensu stricto* and the dorsal frontal organ. The latter is represented by a pair of large postero-lateral cups, and the lateral nerves are formed by the axons of its cells. The perfect nauplius eye s.s., as described by Elofsson in some Natantia, consists of the ventral cup and two antero-lateral cups above the dorsal frontal organ, each of which contains three sensory cells. Elofsson has also indicated that, as the axons of the three nerves leave the proximal ends of the sensory cells and pass through the pigment, the eye is of the everse type. A similar arrangement holds good for *Jasus*, in which the median fibres extend vertically downward while the fibres forming the lateral nerves curve outward from the inner frontal ends of the cells in the posterior two-thirds of the lateral cups and usually enter the brain some distance in front of the median nerve. Although the antero-lateral cups of the nauplius eye s.s. and the dorsal frontal organ are not clearly differentiated in the eye of *Jasus*, it is assumed that the whole of the lateral cup represents an intimate association of the two parts. A paired ventral frontal organ, extending between the brain and the epidermis, is manifest in many of the species studied by Elofsson, but no definite conclusions have been reached as to its identity in *Jasus*.

No observations of the median eye of Palinuridae were made by Elofsson (1963) but, owing to its prevalence in other adult Reptantia, he suggested that it might be present in Palinura and Astacura. From his account and illustrations it is evident, however, that the median eye of *Jasus* bears a closer resemblance to that of some of the Natantia than to any of the Reptantia he has examined. He has disclosed that a median eye is exceptional in adult Brachyura and that, while in other Reptantia it is reduced and located either on or under the epineurium, in various Natantia it projects above the brain, much as has been observed in *Jasus*. Elofsson has mentioned that it is a photosensitive organ but, so far as is known, the function of the median eye of marine Decapoda has not been fully investigated. However, Baylor & Smith (1957) have demonstrated that in the fresh-water branchiopods, *Daphnia magna* and *Eubranchipus*, it is correlated with some of the movements observed during vertical migration, a positive geotaxis and a negative phototaxis being induced under ultra-violet and violet light stimulation. The reversal of this behaviour may apply to the planktonic naupliosoma and young phyllosoma larvae of *J. lalandii*, which Gilchrist (1913*a*) found to be strongly attracted to the source of bright illumination, while older larvae persistently avoided light.

(b) *Compound eyes*

From examinations of serial sections it is apparent that the microscopic details of the paired eyes of the adult and the puerulus stage are comparable to those of other Decapoda. Those of the puerulus stage, however, are more nearly related to the traditional model, and have therefore been selected as the basis of the following remarks.

In describing the musculature (p. 65), it was indicated that the eyes are

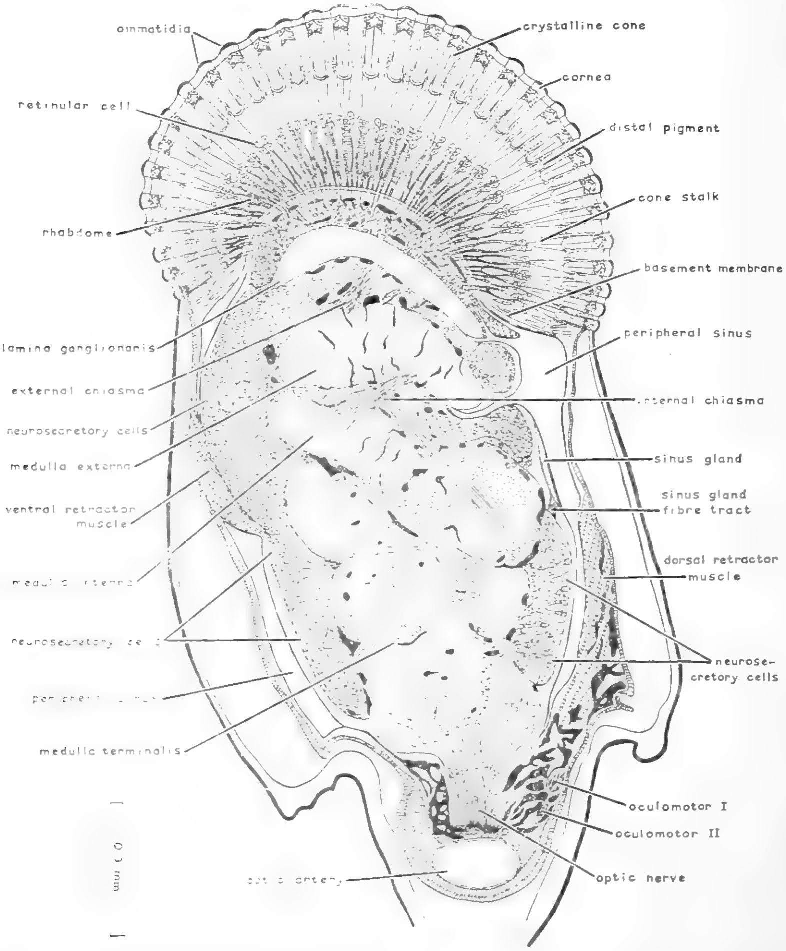


FIG. 71. Puerulus stage: longitudinal section of compound eye; only half the number of ommatidia are represented.

normally perpendicular to the long axis of the body and that each is located in a spheroidal cup supported by a movable two-segmented stalk or peduncle. The numerous visual elements are similar, cylindrical, radiating structures, the *ommatidia*, which are closely aggregated in a deeply-pigmented, somewhat reniform area. A transparent *cornea* covers the surface of the eye and is demarcated into regular rows of minute, contiguous, square *facets*, each representing the periphery of an underlying ommatidium.

Apart from the eye muscles and blood vessels, the optic cup is largely occupied by the *lobus opticus* which consists of four ganglia (figs 59, 61, 71, 74), termed the *lamina ganglionaris*, the *medulla externa*, the *medulla interna*, and the *medulla terminalis*. The latter is the largest mass and is connected to the brain by the *pedunculus lobi optici* or *optic nerve* (figs 31, 57–59, 61, 71, 74). According to Hanström (1939), the first three are primary optic ganglia, while the medulla terminalis represents a portion of the protocerebrum which, together with the optic centres, has migrated into the peduncle. The three medullae consist of layers of neuropiles surrounded by neurones, but the lamina ganglionaris is distinguished by the fact that it seems to be composed of parallel structures, the *neurommatidia* (fig. 72 *A*), each of which is considered by Hanström (1947) and other observers to be formed by the axons of several primary optic fibres coming from the ommatidia. The three distal ganglia are linked by the *external* and *internal chiasmata* (fig. 71), but there is no distinct chiasma between the medulla interna and the medulla terminalis, and these two regions are broadly united and merge almost imperceptibly into each other.

(i) *The ommatidia*

The component parts of the ommatidia of other Crustacea have been so fully described by authors such as Huxley (1881), Parker (1890, 1891), Exner (1891), Pearson (1908), Demoll (1917), Debaisieux (1944), Ramadan (1952), Mayrat (1956), Kampa (1963), and Kampa, Abbott & Boden (1963), that a brief outline of the elements of a single ommatidium observed in longitudinal and transverse sections of the eye of the puerulus stage will suffice.

The *cornea* (figs 71, 72 *A*) is a convex, transparent, exoskeletal layer, composed of numerous, delicate, horizontal laminae and visible externally as a square facet.

The rather flat *corneagen cells* (fig. 72 *A*), of which there are two per ommatidium, secrete the cornea and are considered to be epidermal in origin.

The *crystalline cone cells* underlie the corneagen cells, and in transverse sections (fig. 72 *B*) it is evident that there are four in each ommatidium.

The *crystalline cone* (figs 71, 72 *A*), which is secreted by the cone cells, is a hyaline, refringent body which is rectangular and quadripartite in transverse section (fig. 72 *C*). It is more or less pyramidal in outline, with its broad base adjacent to the cone cells and its apex directed inward to become associated with a more delicate, long, tapering *crystalline cone stalk* (figs 71, 72 *A*). The latter is also squarish and quadripartite in cross section.

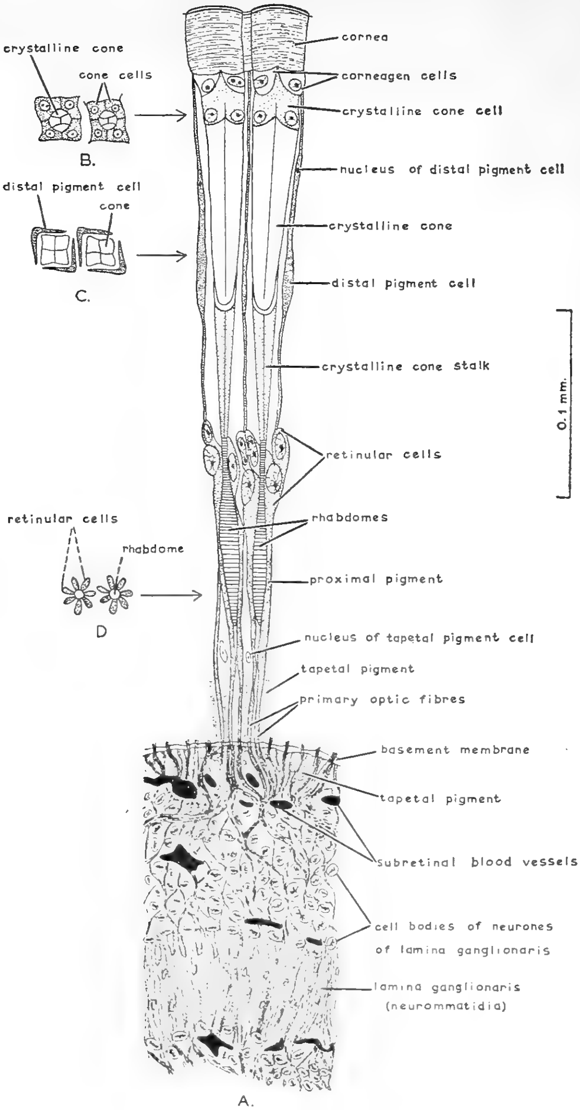


FIG. 72. Puerulus stage: *A*, longitudinal section of two ommatidia; *B*, transverse section of cone cells; *C*, transverse section of cones; *D*, transverse section of rhabdomes.

The *retinula* is composed of seven, similar, elongate retinular cells (figs 71, 72 *A*, *D*) arranged around an axial rod, the rhabdome. The retinular cells extend from the level of the proximal end of the cone stalk to the basement membrane (figs 71, 72 *A*) which is a convex connective-tissue network separating the eye proper from the optic cup. The somewhat bulbous distal end of each retinular cell accommodates a conspicuous nucleus, behind which the cell narrows appreciably and is prolonged as a primary optic fibre. The primary optic fibres (fig. 72 *A*) pierce the basement membrane and, becoming associated in bundles, are said to synapse with the neurones of the lamina ganglionaris. In addition to the seven main retinular cells, there is a less obvious, eccentric eighth or accessory retinular cell, which is chiefly recognizable by its distinct oval nucleus.

The *rhabdome* (figs 71, 72 *A*, 72 *D*), which is a refractive fusiform body, is in direct contact with the proximal end of the cone stalk, and is now considered to be the main photoreceptor of the ommatidium. In longitudinal sections it seems to consist of about 30 to 40 superimposed transverse plates which give it a peculiar stratified appearance. A study of the ultrastructure of the rhabdome of *Homarus* by Rutherford & Horridge (1965) has revealed that each plate or layer of the rhabdome consists of closely fitted tubules or microvilli, which are so arranged that the tubules of adjacent layers are at right angles to one another. According to Parker (1891), Kampa (1963), and Kampa, Abbott & Boden (1963), the rhabdome is usually composed of four rhabdomeres, three of which have been shown by Parker (1891) to be located opposite six of the retinular cells, while the fourth is bordered by the seventh retinular cell.

As in other Decapoda, the *retinal pigment* is distributed in three groups of cells which have been described as the distal, the proximal, and the reflecting or tapetal pigment cells by Welsh (1930) and subsequent investigators. On the outside of each crystalline cone are two right-angled distal pigment cells (fig. 72 *A*) which contain brownish pigment. In transverse sections (fig. 72 *C*) it is apparent that the cells are placed diagonally opposite each other and are in such close proximity to those of neighbouring ommatidia that they form a frame of screening pigment around the individual cones. Approximately at the middle level of the cone, each cell has a small, but distinct, nucleus, while distally and proximally the cell is reduced to delicate processes which extend respectively to the cornea and to the retinular cells. The dark brown proximal pigment (fig. 72 *A*), which is located in the seven functional retinular cells, forms a sheath around the rhabdome and is continued into the primary optic fibres. The reflecting or tapetal pigment (fig. 72 *A*) occurs in irregular cells which occupy the proximal parts of the interommatidial spaces. Each is characterized by a small, distinct, oval nucleus (fig. 72 *A*) near the level of the proximal end of the rhabdome and, in certain circumstances, the dense granular contents and also the proximal pigment may pass through the basement membrane. In this connexion, Mayrat (1956) has concluded that the normal position of the tapetal cells is probably at the distal end of the ocular peduncle, and he and other investigators have emphasized the fact that the pigment is white in reflected light, but yellowish-brown in transmitted light.

(ii) *General remarks*

Excellent accounts of the function of the various elements of the crustacean compound eye have been given by Exner (1891), Demoll (1917), Kleinholz

(1961), and Waterman (1961) and, although no critical experimental tests have been performed on the eyes of *Jasus*, some of the results obtained in other species are pertinent to the present observations. From his comprehensive study of the compound eyes of a variety of arthropods, Exner (1891) concluded that it was possible to recognize two main functional types, the *apposition* and the *superposition eye*, the former being characteristic of diurnal, littoral, and terrestrial animals and the latter of nocturnal, deep-sea, and subterranean forms. Identifying the cornea and the crystalline cone as the dioptric apparatus of the ommatidium, and expounding the principles of lens cylinders, he and later Demoll (1917) have shown that, whereas in the apposition eye the axial length of the lens cylinder is about equal to its focal distance and the resultant image is inverted, in the superposition eye the axial length of the cylinder is double that of its focal length so that inversion of the image takes place about the middle of the cylinder and there is a further reversion more proximally. Among important structural differences between the two types noted by these authors are the long, slender rhabdomes in contact with the cones in the apposition eye, compared to which the rhabdomes of the superposition eye are short and fusiform and remote from the cones. Furthermore, the physical adaptation of the apposition eye to high intensities of light is manifest in the sheath of distal and proximal pigments along the length of the ommatidium, which is thus effectively isolated from neighbouring units. Diffusion of light from one unit to another is prevented, and the stimulation of any one rhabdome is effected only by light rays passing down the main axis of its particular ommatidium. The result has been assumed to be the formation of separate minute images which, like the contiguous pieces of a mosaic, combine to produce a complete impression of the object in the visual field, but Waterman (1961) has suggested that this theory may not be strictly applicable to all apposition eyes. On the other hand, in the superposition eye, which functions in light of low intensity, the retinal pigments are normally retracted from the cones and rhabdomes and, consequently, oblique light rays entering a number of adjacent ommatidia are refracted by the several cones and are capable of stimulating a single rhabdome. In this way the superposition eye makes full use of available light rays, but visual acuity may be inferior to that of the apposition eye. Based on Exner's (1891) deductions, it has generally been supposed that the images formed by this type of eye overlap one another, but this does not appear to have been confirmed in recent observations of superposition eyes (Waterman, 1961). The tapetal pigment, which occurs near the basement membrane in most superposition eyes, probably contributes to the reflection of light towards the rhabdomes, particularly when the proximal pigment is withdrawn.

It has been indicated by Kleinholz (1961) that chemical analyses of the retinal pigments demonstrate that the proximal and distal pigments are melanins in some species but ommochromes in others, while the tapetal pigment, which was formerly thought to be guanin, is now known to contain five compounds, identified as pteridines and purines. Two additional items of general interest mentioned by Waterman (1961) are, firstly, the presence of the photosensitive pigment rhodopsin, presumably in the rhabdomes of *Homarus americanus*, *Nephrops norvegicus*, and *Meganyctiphanes norvegica*, and, secondly, the fact that light sensitivity is not restricted to the eyes, but is also evinced by the sixth abdominal ganglion of some Macrura.

Exner's (1891) observations have also established that, whereas the retinal pigments of most apposition eyes are usually fixed in position and vision is limited to daylight, in superposition eyes all three sets of pigment are freely movable and their distribution is an important factor in adapting the eyes to both nocturnal and diurnal vision. More recent support for this concept has been provided by Debaisieux (1944) and other investigators who, after exposing experimental animals to periods of bright illumination or total darkness, have found that in light-adapted eyes the distal and proximal pigments migrate around the cones and rhabdomes, providing them with a complete mantle, similar to that in a typical apposition eye. In dark-adapted eyes, however, the pigments move away from the rhabdome and the condition is comparable to that of a normal superposition eye.

In connexion with some of the foregoing remarks, it may be noted that the specimens of the puerulus stage of *Jasus* used in the present study were collected by Dr. A. E. F. Heydorn at night, but had been attracted to the nets by the beam of a powerful searchlight. They were fixed immediately in a well-illuminated laboratory on board the research vessel belonging to the Division of Sea Fisheries. Some response to this illumination seems to be reflected in the subsequent sections of their eyes (fig. 72 *A*) inasmuch as the greatest condensation of distal pigment occurs around the junction of the cones and the cone stalks, and the rhabdomes are at least partially screened by the proximal pigment. The extent of the tapetal pigment is less readily ascertained as it is somewhat obscured by the proximal pigment, but it appears to be distributed above and slightly below the basement membrane. In serial sections of the adult eye it is evident that the position of the distal pigment is similar to that of the puerulus stage and that the retinular cells are heavily charged with proximal pigment. Moreover, as there is little indication of proximal pigment below the basement membrane, it may be assumed that the eyes approximate the light-adapted condition. Contrasted with this is Waterman's illustration (fig. 2 *C*, 1961) of a section of the eye of a young *Panulirus argus* in which response to dark-adaptation is shown in the concentration of the proximal pigment on both sides of the basement membrane.

Another interesting phenomenon which has been observed by a number of investigators and particulars of which are given by Brown (1961) is that, in animals kept for relatively long periods under continuous illumination or darkness, a regular diurnal rhythm takes place in the activity of the retinal pigments. Apparently, however, the details differ according to the species but, despite somewhat inconsistent responses witnessed in both diurnal and nocturnal animals, the significant fact emerging from the observations is that this recurrent daily migration of one or more of the retinal pigments is quite independent of constant experimental conditions. It has been seen to coincide with natural daily changes in light intensities and possibly other environmental factors at sunrise and sunset, and the investigators have concluded that it is therefore caused by some internal agents.

The mechanisms controlling the migrations of the retinal pigments have not yet been fully elucidated, but it has been suggested by Welsh (1930) that the movements of the distal pigment may be effected by the contractility of three or four fibrils contained in the distal pigment cells, while cytoplasmic streaming may account for the mobility of the proximal and tapetal pigments. Furthermore, the results of interesting experiments detailed by Welsh (1939, 1941), Carlisle & Knowles (1959), Kleinholz (1961), and Kleinholz *et al* (1962) are regarded as proof that the movements of the distal pigment are regulated by a hormone which is released from the sinus gland when the eyes are illuminated. There is also some evidence that the tapetal pigment is likewise under endocrine control, but the source of the hormone is somewhat conjectural. There also appears to be no experimental proof that any hormone produced in the eyestalk is concerned with the movements of the proximal pigment, but Kleinholz (1961) has suggested two possibilities, either that an activating hormone is processed outside the eyestalk, or that the retinular cells are 'independent effectors'.

Some of the structural differences between the eyes of shallow-water and deep-sea Crustacea examined by Beddard (1890), Welsh & Chace (1937, 1938), and Ramadan (1952) may be interpreted as important modifications correlated with the adaptations of the eyes to the particular environment of the animals concerned. Considerable morphological variation is shown, however, in deep-sea forms, some having proportionally large eyes with presumably functional elements, while in others the eyes are degenerate or even absent. According to Welsh & Chace (1937, 1938), this apparent anomaly may be explained by the fact that luminescent organs and a thick layer of reflecting pigment are often associated with large eyes. In some instances the only obvious difference between the eyes of nocturnal deep-sea and shallow-water species is the reduction in the former of the amount of distal and proximal retinal pigment, while degenerate eyes, which are remarkable for the loss of screening pigments and also of rhabdomes, are furnished with a large quantity of reflecting pigment.

Ramadan's (1938, 1952) studies of the eyes of representative Penaeidae have revealed, not only that the eyestalk is less complex in deep-sea species, but also that in certain structural details the ommatidia differ markedly from those of related shallow-water species. While the nuclei of the crystalline cone cells of the latter are said to be angled and located in the corners of the cells and the rhabdomes conform to the typical decapod structure, in deep-water forms the nuclei of the crystalline cone cells are rounded and centrally placed and the rhabdomes are non-striated and peculiarly branched in transverse sections. Although the reason for these differences is obscure and Ramadan

(1952) has concluded that they cannot be accepted as indications of adaptive modifications, they are, nevertheless, of interest in a consideration of the eyes of *Jasus*.

Compared with the puerulus stage, the ommatidia of the adult eye have proportionally longer cone stalks, but this may be merely a normal incident in the transformation of the larva into the adult state, for Kampa, Abbott & Boden (1963) have observed that a similar elongation of the cone stalks takes place between the zoaea and the adult stages of *Homarus gammarus* (*vulgaris*). A more remarkable difference in *J. lalandii* is the apparent structural resemblance of the short rhabdomes of the adult eye to those of deep-sea Penaeidae examined by Ramadan (1952). While Parker (1891) was somewhat doubtful as to the presence of rhabdomes in *Palinurus* (probably *Panulirus*), Exner (1891) remarked that the eyes of *Palinurus* may be compared to those of *Palaemon* and *Sicyonia*, but that 'die Sehstäbe sind hier ziemlich klein' (p. 124). In sectioned material of the eye of *J. lalandii*, differentially stained with Heidenhain's iron haematoxylin and phloxine, the rhabdomes are visible as short, clear, cerise structures which are sharply contrasted with the surrounding, narrow, heavily-pigmented retinular cells. The latter are uniformly constructed throughout their length, and in distal transverse sections (fig. 73) they are disposed around the rhabdome, but this is quite unlike the striated, fusiform structure observed in the puerulus ommatidium. It is composed of seven branched rays which correspond with the seven main retinular cells, and in dissections of bleached preparations superficially resemble the curved staves of a minute barrel. Proximally the rhabdome appears to taper off, but the rosette formation of the retinular cells is maintained up to the basement membrane. A similar stellate configuration of the proximal ends of the retinular cells is also evident in the sectioned eye of young *Panulirus argus* (Waterman, 1961), in *Pleuroncodes planipes* (Kampa, 1963), and in *Homarus gammarus* (Kampa, Abbott & Boden, 1963), and probably represents the characteristic grouping of the axons of the seven normal retinular cells in most Decapoda.

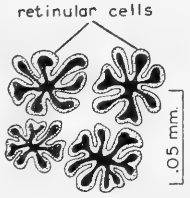


FIG. 73. Transverse section of rhabdomes of adult eye.

The marked difference between the rhabdomes of the puerulus stage and those of the adult suggests that the onset of adult life in *Jasus* evokes a transformation of the eyes from a condition typical of pelagic and shallow-water

Decapoda to one approximating that of benthic species. To some extent this seems to be supported by the presence in the puerulus stage of a fairly conspicuous *eye-papilla* (fig. 74) which Hanström (1939, 1947) has stated is well developed in pelagic and bathypelagic Macrura Natantia and may function as a tactile organ. It projects ventrally towards the antenna as an evagination of the frontal wall of the optic cup; in section it is more or less oval in outline and contains a number of distinct bipolar sensory neurones, the axons of which pass into the medulla terminalis and become associated with the larger elements of Hanström's X-organ, or the sensory papilla X-organ (SPX) as it is now designated by Carlisle & Knowles (1959) and Passano (1960). Although the sensory papilla is absent in the adult, its former position seems to be indicated by an obvious transparent area, which may be comparable with the so-called sensory pore of other Crustacea, but in sections of the eye there is no noticeable thinning of the cuticle over this region.

(c) *Vascular system*

In preference to including details of the optic blood vessels in the general account of the vascular system, it has been deemed expedient to deal with them briefly after considering some aspects of the structure of the eye. Information concerning these blood vessels in other Crustacea has been supplied mainly by Baumann (1921), Debaisieux (1944), Mayrat (1956), and Mauchline (1958), whose accounts clearly indicate that a fairly uniform plan underlies their distribution in different Crustacea.

It has already been intimated (p. 145) that the blood supply to the eye muscles is derived from a delicate *oculomotor artery*, while that to the optic ganglia stems from the *optic artery*, which itself is one of the terminal branches of the median ophthalmic artery. The course of the optic artery may be traced in dissections of injected adult specimens or, more precisely, in serial sections of the eye but, as most of the delicate endings of the arteries and veins form a complex network within the lobus opticus and merge so imperceptibly into one another, it is often difficult to ascertain where one system terminates and the other begins. By reconstructing serial sections of the smaller eyes of the puerulus stage and omitting the intricate ramifications and anastomoses within the lobus opticus, it is possible, however, to obtain a general impression of the main arterial and venous channels (fig. 74).

The *optic artery* is a wide vessel which runs through the eyestalk parallel to the optic nerve and, passing frontally, divides into four main branches which are substantially similar to those observed in *Astacus* by Baumann (1921). The *first branch* arises at the base of the lobus opticus, where it immediately enters the proximal part of the medulla terminalis, subsequently irrigating this region and giving off a few small vessels to the distal end of the optic nerve. Curving over the optic ganglia, the main stem of the optic artery courses distally, giving rise to the *second branch* which subdivides and transports a copious supply of blood to the distal part of the medulla terminalis and the medulla interna. The

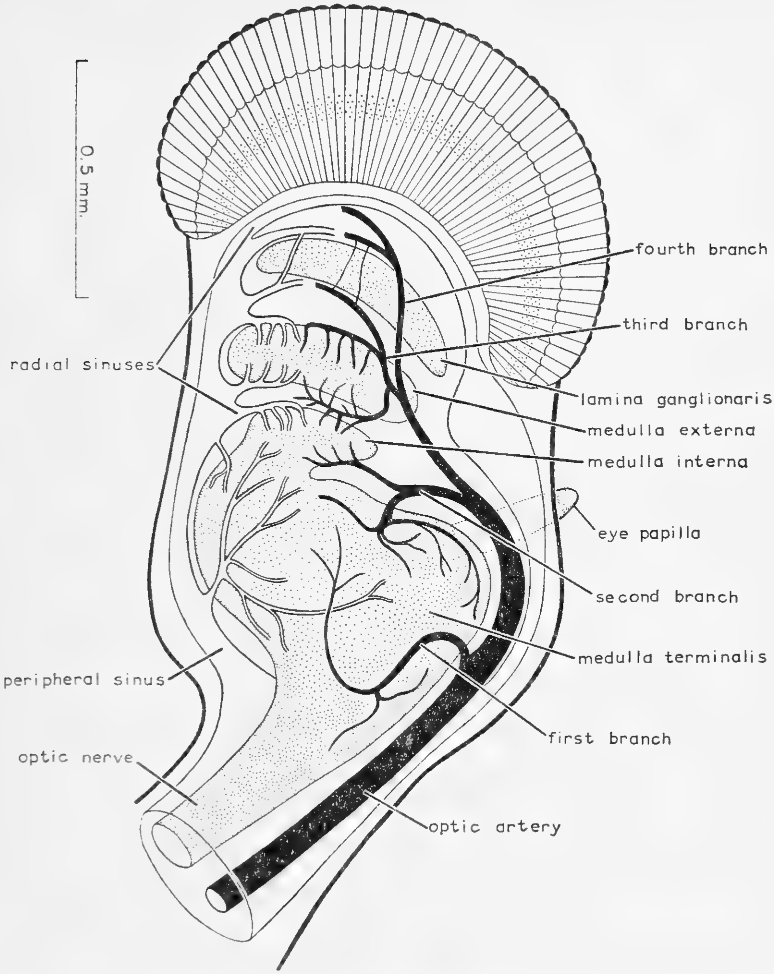


FIG. 74. Diagrammatic reconstruction of main blood vessels of left eye of puerulus stage.

medulla externa receives its main share of blood from the distal offshoot of the *third branch*, but this vessel also serves the two chiasmata and may send additional tributaries into the medulla interna and the medulla externa from its proximal subbranch. The terminal portion of the optic artery represents the *fourth branch* which bifurcates, one vessel passing along the distal margin of the lamina ganglionaris and the other dividing into a series of fine channels in the subretinal region in close proximity to the basement membrane of the eye. In partial agreement with the findings of Debaisieux (1944) and Mayrat (1956), there is no marked circulation to and from the lamina ganglionaris, but it is, however, traversed by occasional delicate anastomoses which connect the vessels on its proximal and distal margins. Contrasted with this, the lamina ganglionaris, as well as the three medullae of some crustacean eyes examined by Mauchline (1958), is provided with a rich supply of blood.

While it is generally accepted that the interommatidial spaces of the eye contain blood and most observers have reported the presence of a regular series of minute arteries on the proximal side of the basement membrane, the actual passage of blood into the eye has proved difficult to determine with accuracy. Close to the distal end of the optic artery in *Palaemon* (*Leander*) *squilla*, however, Mauchline (1958) has detected an opening in the basement membrane which would allow of the entrance of arterial blood into the interommatidial spaces. No such aperture was observed in *Jasus*, and the impression gained from an examination of serial sections of the eyes of the adult and the puerulus stage was that some of the fine terminal frontal arteries radiating between the primary optic fibres in the subretinal region might penetrate the basement membrane and so introduce blood into the eye.

Within the several parts of the lobus opticus, the various branches of the optic artery resolve into numerous delicate vessels from which the blood enters a system of ramifying venous passages. Along these the blood is directed out of the lobus opticus into *radial sinuses* which are associated with the three distal ganglia and empty into a large *peripheral sinus*. It is also evident that, communicating with the latter, there are one or more conspicuous venous channels from the medulla terminalis. Although the arterial supply to the visual part of the eye cannot be demonstrated satisfactorily, there are indications that, as in *Meganyctiphanes* (Mauchline, 1958), the deoxygenated blood leaves the interommatidial spaces and enters the peripheral sinus through a relatively wide ventro-lateral passage. The peripheral sinus lies in the space between the lobus opticus and the wall of the optic cup and envelops the eye muscles. After the confluence of the two eyestalks, the blood from both eyes flows into the anterior cephalothoracic sinus around the brain.

J. Endocrine Organs

A comprehensive discussion of crustacean endocrinology is beyond the scope of the present study, but the increasing interest shown in this discipline during the past thirty years warrants some mention, at least, of the presence and the arrangement of the main endocrine organs observed in *J. lalandii*. Instructive reviews of research on crustacean hormones by Hanström (1939), Kleinholz (1942), Brown (1944), Gabe (1954), Carlisle & Knowles (1959), and Welsh (1961) provide evidence of the progress made since Hanström's discovery of the sinus gland in Decapoda in 1933; and the gradual solution of cytological and physiological problems has resulted in the interpretation by Bliss (1951), Passano (1951), Bliss & Welsh (1952), and Bliss, Durand & Welsh (1954) of the sinus gland and the X-organ as functionally interrelated parts of an extensive neurosecretory system from which hormones, synthesized in its specialized neurones, are released into the blood stream.

Several types of neurosecretory cells have been described in various regions of the nervous system, particularly in the optic ganglia and brain by Enami (1951), Bliss & Welsh (1952), Carlisle & Passano (1953), Bliss, Durand & Welsh (1954), Durand (1956), and Carlisle (1959). Hormones have also been reported in the post-commissure organs and in fine fibres termed the pericardial organs by Alexandrowicz (1953), Alexandrowicz & Carlisle (1953), and Maynard & Welsh (1959).

There has been an almost unanimous acceptance of the conclusions of Bliss (1951), Passano (1951), Bliss & Welsh (1952), and Bliss, Durand & Welsh (1954) that the different hormones secreted in the central nervous system travel along axons which eventually terminate in the sinus gland located in each eyestalk. Accordingly, the earlier hypothesis that the sinus glands are endocrine organs is no longer considered to be valid, and most authorities now regard them as reservoirs from which neurosecretions are subsequently distributed to the body by the circulating blood. Gabe (1954), however, has questioned the value of some of the histological techniques used to determine the presence of neurosecretions and, while conceding that neurosecretions are conveyed to and stored in the sinus gland, he is convinced that the sinus gland itself is also the site of active secretion. In this connexion, Carlisle & Knowles (1959) have remarked that biochemical changes of the substances stored in the sinus gland are possible, but that secretion of material by the sinus gland has yet to be proved.

The number of hormones produced is not known, but information supplied by various investigators suggests that the pericardial organs influence the pulsation of the heart and that the blood-borne neurosecretions released from the sinus gland control manifold activities such as chromatophore responses, retinal pigment migration, growth, water balance, moulting, sexual differentiation, and the female reproductive cycle. According to Carlisle (1959) and Welsh (1961), five or six distinct types of neurosecretory cells have been detected in the X-organ which is located in the lobus opticus, while Carlisle (1959) has distinguished at least four constituents in the tissue of the sinus gland. From this it has been concluded that the X-organ alone probably produces several different kinds of neurosecretions, the best known of which is the moult-inhibiting hormone.

I. PERICARDIAL ORGANS

A detailed examination of the bilateral pericardial organ of *Jasus* was not undertaken, but part of it, the lateral pericardial plexus, has been described briefly (p. 167) and depicted diagrammatically (fig. 64). Since the discovery by Alexandrowicz (1953) of a system of delicate, ramifying nerve fibres in the pericardial cavity of a variety of crustaceans and their designation as pericardial organs, evidence has been provided by Alexandrowicz & Carlisle (1953) and Maynard & Welsh (1959) that they are the source of certain substances which stimulate the acceleration of the heart-beat. The fine plexuses making up the pericardial organs usually extend over the branchio-pericardial openings and surround the suspensory ligaments of the heart, and it has been concluded by the above investigators that they are neurosecretory in function and that active substances are released from their nerve endings into the blood before it enters the heart.

2. POST-COMMISSURE ORGANS

In addition to the X organ-sinus gland complex, Carlisle & Knowles (1959) have supplied details of other neurosecretory centres called the post-commissure organs. It is stated that they have not yet been found in Brachyura, but they have been described in *Penaeus braziliensis*, *Palaemon* (*Leander*) *serratus*, and *Squilla mantis* as a pair of small, thin lamellae arising from the post-oesophageal commissure. In these species a fine nerve passes from each lamella to a dorso-ventral muscle, and the lamella itself contains a number of delicate, branched nerve fibres, some of which are apparently neurosecretory and are connected with fibre tracts from the brain. From histological and experimental evidence, these investigators have suggested that chromactivating substances manufactured in the brain are passed to the post-commissure organs and released into a neighbouring haemal sinus.

Post-commissure organs superficially resembling those of *Palaemon serratus* are present in the puerulus stage and the adult of *Jasus* (fig. 61). They are continuous, however, with the anterior rather than with the posterior margin of the post-oesophageal commissure, and are not interconnected by a transverse lamella. Each is a minute triangular plate with its base attached to the post-oesophageal commissure, from which it receives several fibres; the latter ramify within the lamella and are dotted with elongate-oval nuclei. Projecting forward and upward towards the posterior wall of the oesophagus, the lamella tapers to a delicate nerve which curves round the ventral pyloric dilator muscle of the fore-gut and may give off a delicate branch to the oesophageal wall. In front of the ventral pyloric dilator muscle it turns outward and upward and becomes applied to the anterior dorso-ventral muscle, to which in some dissections it seemed to supply several fine fibres. Its termination was not determined, but the overall impression was that it was associated with a delicate plexus lying on the anterior dorso-ventral muscle, and anterior to this it appeared to extend to connective tissue strands in the vicinity of the mandibular minor abductor muscle or even to a nerve plexus on the bladder of the antennal gland.

The physiology of the post-commissure organs of *Jasus* is unknown, and any speculation as to their purpose can only be based on the conclusions of Carlisle & Knowles (1959) concerning their probable function in other species. Experiments performed by these authors and other investigators cited by them indicate that colour changes in a number of crustaceans are regulated by blood-borne hormones. Activating substances have been extracted from the sinus glands and the post-commissure organs and, apart from their effect on chromatophores, certain hormones are apparently implicated in the regulation of movements of the retinal pigments. Extracts of the sinus gland have been found by Kleinholz (1961) to influence the migration of the distal retinal pigment of *Palaemonetes*, but probably only evoke movements of the pigment from a dark-adapted to a light-adapted position. On the other hand, evidence that the post-commissure organs are a possible source of a dark-adapting hormone for the distal retinal pigment and also of one controlling movements of the reflecting or tapetal pigment of the eye has been discussed by Carlisle & Knowles (1959) and Kleinholz (1961). Assuming that similar principles broadly prevail in *Jasus*, it seems likely that some hormones destined to control movements of retinal pigments may be released from the post-commissure organs.

3. SINUS GLAND

In both the puerulus stage and the adult of *Jasus* the sinus gland is clearly defined as a flat object which is slightly thicker distally. In dissections of the adult eye it stands out against the other tissues as a snowy white, spongy disc, measuring roughly 800 to 900 μ in diameter and 90 μ thick in an eye with an optic cup 4 mm long and, excluding the eyestalk, a total length of 7·25 mm. Compared with the puerulus stage (fig. 71), the optic ganglia of the adult (figs 59, 61) occupy a smaller area of the optic cup, being proportionally narrower and rather more widely separated from one another; but, as in Pyle's (1943) observations of various developmental stages of *Homarus*, this structural change has no effect on the location of the sinus gland. Brown (1944) has indicated, however, that its position relative to the optic ganglia varies with the species, and from his remarks it would appear that the site of the sinus gland of *Jasus* corresponds more with the arrangement in certain Brachyura than with that of other Macrura. It is more prominent in the adult (figs 59, 61) than in the puerulus stage, but in both it is situated dorso-laterally on the inner wall of the peripheral haemal sinus near the proximal radial sinus and in line with the medulla interna and the distal part of the medulla terminalis.

Microscopic examination of thin serial sections of the adult sinus gland gives the impression of a histologically nondescript object enclosed in a flat connective tissue sheath. Its main components are variously sized, compactly arranged, homogeneous masses, which have staining properties somewhat similar to the neuropiles of the lobus opticus and are doubtless comparable to the swollen endings of the axons of the neurosecretory cells described in other decapods by Bliss & Welsh (1952), Bliss, Durand & Welsh (1954), Carlisle (1959), Passano (1960), and Welsh (1961). They seem to be partly interlaced by a delicate, loose connective tissue and interspersed by a number of nuclei which may be associated with the connective tissue. The presence of nuclei in the sinus gland has sometimes been disputed, but Gabe's (1954) recognition of their reality has been confirmed by Carlisle (1959) and Carlisle & Knowles (1959). In striking contrast to the bulk of the tissue are intensively stained, oval or rod-shaped aggregations of basophilic particles; these are rather irregularly distributed throughout the gland, but tend to accumulate towards its proximal end and, following the conclusions of the aforementioned authorities, may be considered as manifestations of the passage of neurosecretions into the gland.

The organ is slightly separated from the neurilemma of the lobus opticus but joined to it by connective tissue strands and, although it lacks the obvious radiating, digitiform processes of other Decapoda mentioned by Hanström (1939), Welsh (1941), and Pyle (1943), there is evidence of a few slender prolongations extending into the haemal sinus from its distal more swollen end. As in previously investigated forms, the proximal part of the sinus gland and the neurosecretory cells of the X-organ in the medulla terminalis are interconnected by a conspicuous tract of nerve fibres (figs 59, 71) which is well defined in proximity to the gland by the presence of basophilic granules and can be traced into the substance of the gland. Based on similar staining effects and their correlation with experimental evidence, Bliss & Welsh (1952) and Bliss, Durand & Welsh (1954) have confirmed the earlier suggestion made independently by Bliss (1951) and Passano (1951) that the sinus gland fibre tract conveys hormonal material from the X-organ to the sinus gland where it is stored and later circulated to parts of the body by the haemal system.

4. X-ORGAN

Clusters of neurosecretory cells, linked by fibre tracts with the sinus gland, occur in the lobus opticus, particularly in the medulla terminalis, and certain of these constitute the X-organ. From various publications, it is evident that the X-organ varies with the species and that it frequently consists of two portions. In an endeavour to resolve some of the confusion concerning the precise identification of the X-organ in different Crustacea, Carlisle & Passano (1953) proposed that the two parts be called the pars distalis X-organi and the pars ganglionaris X-organi, but it has been indicated by Carlisle & Knowles (1959) and Passano (1960) that these terms were later changed respectively to the sensory papilla X-organ or the sensory pore X-organ (SPX) and the medulla terminalis ganglionaris X-organ (MTGX). The former is homologous to the X-organ which Hanström (1939) found to be closely associated with the sensory papilla or sensory pore, and which he postulated was a modification of the sensory cells of the eye papilla. On the other hand, the MTGX, which is comparable to the X-organ described by Bliss & Welsh (1952) in *Gecarcinus lateralis*, is usually located ventro-proximally in the medulla terminalis and is typically connected with the sinus gland by the previously mentioned obvious fibre tract.

Cytological and functional differences are also attributed to the two portions of the X-organ. The SPX is said by Carlisle & Knowles (1959) and Passano (1960) to contain the sensory cells of the sensory papilla or pore, certain secretory cells and, more characteristically, the so-called 'onion bodies'. Although its precise function is problematic, these authors have indicated that in some species it may act as a storage and release centre for a moult-accelerating hormone which is produced in the MTGX and the central nervous system, but is only effective during the proecdysis stage of the moult cycle. The MTGX is distinguished from the SPX by its large neurosecretory cells, the chief derivative of which is apparently the moult-inhibiting hormone that prevents initiation of proecdysis.

Three types of neurosecretory cells, alpha, beta and gamma, have been described by Enami (1951) in the central nervous system and optic ganglia of the crab, *Sesarma haematocheir*, while Durand (1956) has detected four distinct kinds, Types 1 to 4, in the crayfish *Orconectes virilis*, and in *Pandalus borealis* Carlisle (1959) has differentiated five kinds, of which Type IV is characteristic of female and non-sexual specimens. Durand has shown that his cellular Types 1 and 2 occur respectively in the distal and proximal regions of the X-organ of *Orconectes*, and that the other two types are distributed elsewhere in the optic ganglia and the brain. As only giant beta neurosecretory cells were found by Enami in the X-organ of *Sesarma*, Durand has concluded that these are comparable to his Type 2 cells and that Types 3 and 4 are similar to the alpha and gamma neurosecretory cells described by Enami. Specific variation could account for cytological differences in the X-organ of these two decapods, or they could be explained by the observations of Carlisle & Passano (1953) and others that in Natantia and in Reptantia (except Brachyura) the SPX and MTGX are disconnected entities, whereas in Brachyura they are combined in a single mass. Although the two parts of the X-organ were not specified by Durand (1956), the regional localization of Types 1 and 2 neurosecretory cells might be interpreted as a possible differentiation of SPX and MTGX components of the X-organ in *Orconectes*. This conjecture seems to be invalidated, however, by Passano's (1960) illustration of two kinds of neurosecretory cells in the MTGX of *Sesarma reticulatum* and, as these have been likened provisionally to Durand's first two types of cells, it appears that there is little cytological difference between the X-organ of the species of Brachyura and Astacura so far investigated. To some extent this conclusion is compatible with Carlisle & Knowles' (1959) statement that in these two groups the SPX is either reduced or absent.

An investigation of the neurosecretory system of *Jasus* was not originally intended but, even with routine staining procedures, the large neurosecretory cells are easily distinguished from the smaller, normal ganglionic cells. They were observed in sections of the lobus opticus of the adult, and in the lobus opticus, the brain, and the ganglia of the ventral nerve cord of the puerulus stage (figs 58, 71), and may also occur in the peripheral zone of the superior ventricular ganglion and in the oesophageal ganglion of the stomatogastric nervous system of the puerulus. In the absence of critical differentiation of cytological details in the present preparations, illustrations of the cells have been omitted, but they are generally similar to those described in other decapods, and a brief survey of their association with the optic ganglia may not be inappropriate. It is immediately apparent that there are several clusters of neurosecretory cells, some of which are located dorsally and ventrally at different levels in the medulla terminalis, while others occur more distally around the medulla interna and the medulla externa. Although differing in detail, the scattered distribution of these groups of neurosecretory cells (fig. 59) is somewhat similar to that mapped out by Bliss & Welsh (1952) and Bliss, Durand & Welsh (1954) for *Gecarcinus lateralis* and *Orconectes* (*Cambarus*) *virilis* but, on the whole, the arrangement seems to be closer to that of the former than that of the latter species. Owing to the irregular occurrence of basophilic granules along the axonal tracts from the various cell groups, not all of them were determined even in sections counterstained with phloxine; but it is evident that most of the tracts lead by devious routes to the sinus gland and that the one connecting the neurosecretory cells of the MTGX with the sinus gland is the most conspicuous.

As the eye papilla is obvious in the puerulus stage, it is possible to differentiate between the distal SPX and the proximal MTGX portions of the X-organ in sections through the medulla terminalis. Numerous subepidermal sensory cells, with their axons passing inward towards the medulla terminalis, make up the core of the eye papilla, and nearer its base there is an outer, well-defined band of deeply stained nuclei which eventually becomes confluent with the neurilemma of the medulla terminalis. Anteriorly the eye papilla is provided with a medial, hyaline membrane, but in more posterior sections through the base of the papilla this seems to break down and continuity between the eye papilla and the distal region of the medulla terminalis is established. At this point, which is some distance from the proximal neurosecretory cells that presumably constitute the MTGX of the puerulus stage, further cellular elements become apparent at the distal edge of the medulla terminalis. These comprise a number of fairly large secretory cells and several conspicuous, rounded or oval bodies measuring approximately 33 to 35 μ or less across. Most of the latter contain concentric lamellae, and it is assumed that they are analogous to the so-called 'onion bodies' of the SPX of other decapods which, according to Carlisle & Knowles (1959) and Passano (1960), are regarded either as the coiled terminations of the axons of the MTGX and the brain neurosecretory cells or as accumulations of secretory products.

With the disappearance of the eye papilla, the SPX is more difficult to determine in the adult, but in a position comparable with that of the SPX of the puerulus stage certain cellular structures are differentiated at the frontal and distal part of the medulla terminalis. They occupy an area which is approximately 270 to 300 μ thick and has maximum length and breadth measurements of 330 μ and 290 μ and, as is diagrammatically indicated in figure 59, it is not connected with the outer surface of the optic cup. It is partly surrounded by a delicate membrane and contains a number of probable sensory cells, but is largely filled by conspicuous, oval or irregularly-shaped, contiguous elements, measuring from 46 to 60 μ long by 26 to 40 μ wide. In several of these the contents are slightly laminated, but the concentric layers of typical SPX 'onion bodies' are not discernible and the majority most closely resemble the epithelioid cells in the SPX of *Lysmata seticaudata* (Carlisle & Knowles, 1959). Some of them are markedly vacuolated and in others the cytoplasm contains basophilic granules which, by analogy with the staining reactions of the sinus gland, may demonstrate the presence of secretory material. As in other species described by Carlisle (1959) and Carlisle & Knowles (1959), an X-organ connective is probably present, but it seems to be obscured by blood vessels.

The neurosecretory cells in different parts of the adult lobus opticus (fig. 59) are impressive by their size, which ranges from 27 to 66 μ. Some are almost spherical in section but many which show the conspicuous axon are more or less pyriform in outline. Each is characterized by a large spherical nucleus which may or may not be concentric and varies in size with the cell body, being from 8 to 15 μ in diameter. The nuclear membrane is distinct and encloses a clear nucleoplasm which commonly contains a single deeply-staining body, probably a karyosome, and sometimes a number of chromatin granules. The cells forming a cluster proximo-ventrally in the medulla terminalis (fig. 59) and partly separated from the SPX by normal neurones are most obviously connected with the sinus gland and are considered to correspond to the MTGX cells of other decapods. The majority of the cells in this cluster are somewhat pyriform in shape and vary from 32 to about 40 μ in length; the nucleus is 11 to 15 μ in diameter and may contain chromatin granules as well as a large, slightly eccentric karyosome. The cytoplasm of these neurosecretory cells is decidedly flocculent in appearance and resembles the 'mulberry' formations described by Carlisle (1959) in the neurosecretory cells of *Pandalus borealis*. In the neurosecretory cells of other groups the cytoplasm is only slightly flaky and tends to be more homogeneous with a fine network of granular inclusions. The MTGX cells are by no means the largest of the neurosecretory cells, for a few rounded cells, 60 μ in diameter, and couple of 'giant' pyriform cells, 66 μ long, were observed among average-sized neurosecretory cells near the distal margin of the medulla terminalis in longitudinal sections passing approximately through the middle of the lobus opticus. In these cells the cytoplasm is not markedly flocculent; the nucleus measures about 13·3 to 15 μ in diameter, its sharply defined karyosome is eccentric, and there are no obvious chromatin granules in the nucleoplasm. The similarity between the neurosecretory cells observed in *Jasus* and those described by Enami (1951) and Durand (1956) is uncertain, but it is probable that the MTGX neurosecretory cells are comparable with the cells of Durand's Type 2, and those in other groups may conform to his Type 3. Although there are few, if any, corresponding to his Type 4 cells, a cluster of neurosecretory cells lying proximo-ventral to the sinus gland contains several small rounded cells, 15·5 to 22 μ in diameter, in some of which a deeply-stained basophilic mass almost fills the cell body, obscures the nucleus, and extends into the axon.

5. Y-ORGAN

This term was proposed by Gabe (1953, 1956) for a paired organ which he observed in fifty-eight species of Malacostraca and considered to be similar to the prothoracic or moulting gland of insects. He has shown that in Decapoda and other Malacostraca in which the adult excretory organs are antennal glands the Y-organ occurs in the second maxillary segment, but is found in the antennal segment in forms having maxillary excretory organs in the adult. Specific variations in its size, shape, and microscopic details have been reported, but it is generally located near the ventral body wall and has been interpreted by Gabe as a thickening of the hypodermis. Since Gabe's discovery, the Y-organ has been described in certain species by other investigators. According to Chaudonneret (1956), in *Orconectes limosus* (*Cambarus affinis*) it is an elongated mass situated between the mandible and the first maxilla and measures 1·6 mm long, 0·6 mm wide, and 0·7 mm high: Passano (1960) has mentioned that the Y-organ of *Carcinus maenas* is an ovoid structure which measures about 0·5 mm across and is located near the anterior end of the branchial chamber ventral to the mandibular posterior (external) adductor muscle.

In the adult *J. lalandii* the Y-organ is about 8 mm long by 4 mm high, but even in immature specimens with a cephalothoracic length of 33 mm it is larger than that of either *Orconectes* or *Carcinus* and measures approximately 2·5 mm long by 0·75 mm wide. In the puerulus stage it is proportionally smaller, being about 310 to 370 μ long and 90 μ wide in specimens having a cephalothoracic length of 9 mm. It seems to be less compact than that of *Carcinus maenas* (Passano, 1960), and in surface view (fig. 75) has the appearance of whitish, convoluted ridges arranged in a slight crescent towards the posterior end of the prebranchial chamber. It lies almost horizontally near the anterior limit of the epimeral attractor muscle and is also close to the maxillary epimera and the base of the second maxilla. Unlike that of *Carcinus maenas* (Passano, 1960), it is some distance from the mandibular posterior adductor muscle, but the posterior dorso-ventral muscle is inserted directly above it, and adjacent

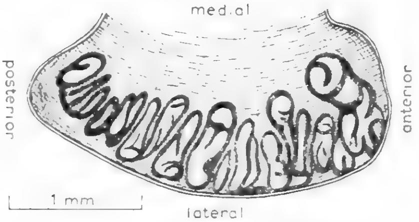


FIG. 75. Surface view of left Y-organ as seen on a portion of the body wall at the junction of the branchial and prebranchial chambers in a juvenile specimen with a cephalothoracic length of 33 mm.

to its inner margin (fig. 76) the lateral diverticulum of the dorsal lobe of the digestive gland bulges into the anterior part of the branchiostegite.

Gabe (1953) has stated that the Y-organ is innervated from the suboesophageal ganglion, while Chaudonneret's (1956) assertion that in *Orconectes* it is supplied by a branch of the first maxillary nerve would seem to imply that it is a derivative of the first and not of the second maxillary segment. Despite repeated search, no nerve supply to the Y-organ was detected in *J. lalandii*. The nearest nerve is the first dorsal, but this bends back to the epidermis and the epimeral attractor muscle at the posterior edge of the Y-organ without branching to it. Nevertheless, this observation is consistent with Passano's (1960) remarks that, although two nerves from the suboesophageal ganglion run close to the Y-organ of *Carcinus maenas*, there is no evidence that either of them innervates it.

Sections of the puerulus stage indicate that the Y-organ (fig. 76) is a folded, somewhat villiform invagination of the inner epidermis of the branchiostegite and that it apparently consists of elongate, compressed cells with small, rounded or oval, basal nuclei. Unlike Gabe's (1956) preparations, the cell membranes are indistinct, but they are probably delineated by numerous faint striations between the nuclear stratum and the cuticle.

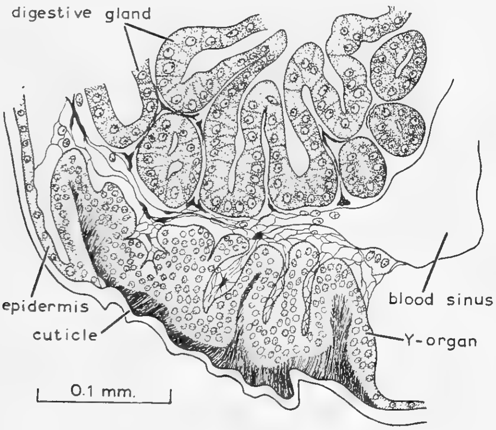


FIG. 76. Section of inner wall of branchiostegite of puerulus stage showing position of Y-organ.

Cytological changes in the Y-organ during the moult cycle were observed by Gabe (1953, 1956), and his surmise that the Y-organ plays an important role in regulating ecdysis has been confirmed experimentally in brachyurans by Echalier (1954, 1955), Carlisle (1957), and Carlisle & Knowles (1959). It has been shown by Carlisle (1957) that the spider crab, *Maja squinado*, habitually ceases to moult on attaining sexual maturity, and this is directly correlated with the atrophy of the Y-organ after the last moult. Contrasted with this, sexually mature *Carcinus maenas* undergo several additional ecdyses before they reach a stage in which moulting is permanently stopped, probably owing to the suppression of the activity of the Y-organ by the increased production of the moult-inhibiting hormone in the X organ-sinus gland complex. From these and other observations mentioned by Passano (1960), the various investigators have suggested that the crustacean Y-organ serves as a moulting gland which initiates certain histological and physiological changes during the proecdysial stage. Apparently, active secretion by the Y-organ is checked by the moult-inhibiting factor produced in the X organ-sinus gland complex, but it may be stimulated by the moult-accelerating hormone released from the SPX organ.

In addition to deliberations on its function as a moulting gland, there has been some speculation concerning the significance of the Y-organ during gametogenesis in Brachyura. Arvy, Echalier, & Gabe (1956) have demonstrated that, while ablation of the Y-organs in mature *Carcinus maenas* had no obvious effect on the gonad, removal of the Y-organs in juvenile crabs resulted in atrophy of the gonads and tardy gametogenesis in both sexes. There is some doubt, however, as to whether the gonadal changes in juvenile forms lacking Y-organs are caused by post-operational disturbance of the general metabolism, or whether they indicate that the Y-organ is the source of a gonadotropic hormone that is indispensible to gametogenesis but becomes ineffectual once the gonad is mature.

Differentiation of the sexes and the development of secondary sexual characters in Malacostraca have been proved by Charniaux-Cotton (1960) to be governed by other endocrine secretions. Male sexual features seem to be contingent on a substance produced by a paired androgenic gland which occurs on the distal part of the vas deferens. On the other hand, it has been concluded by Carlisle & Knowles (1959) and Charniaux-Cotton (1960) that the female reproductive cycle is regulated by the activities of the MTGX neurosecretory cells, while the development of the female secondary sexual characters is promoted by a hormone secreted by the ovary.

K. Reproductive System

Structural differences between the two sexes mentioned in connexion with various aspects of the external features may now be collated and summarized. The males are usually larger than the females, have a broader carapace and commonly stronger first pereiopods; the genital apertures are on the fifth pereiopods and the pleopods are uniramous. In the female the abdomen is broader than that of the male, the genital openings are on the third pereiopods, the fifth pereiopods are chelate, and the pleopods are biramous.

Accounts of the reproductive anatomy of *Jasus* have previously been presented by Von Bonde & Marchand (1935), Von Bonde (1936), Fielder (1964*b*), and Heydorn (1965), and the general configuration of the organs resembles that of other Palinuridae described by Matthews (1951) and Lindberg (1955).

The gonads of the two sexes are paired and broadly similar in position and form in juveniles, but differ considerably in size and structure in the mature state. Even though there are no external indications of sexual dimorphism in the puerulus stage, the developing gonads are faintly recognizable in serial sections (fig. 37), but they are so delicate and histologically indeterminable that the sex can only be ascertained by tracing the gonoducts towards their future external openings. In juvenile males and females with a cephalothoracic length of from 30 to 40 mm the gonads are better defined and similar in appearance, the ovaries, however, being more distinct than the testes. The paired immature gonads of either sex are whitish, elongate, narrow, straight tubes which are interconnected in the mid-line by a short transverse bridge behind the fore-gut and below the median ophthalmic and antennary arteries. Combined thus, they are roughly H-shaped in outline with relatively short anterior and much longer posterior horns. The former lie ventro-laterally in the cephalothorax, curving on either side between the mandibular posterior adductor muscle and the cardiac fore-gut, to the wall of which their anterior extremities are secured by delicate connective strands. As they converge towards the transverse bridge, the two gonads are located more dorsally above the anterior part of the hind-gut or intestine. Immediately behind the transverse bridge, the posterior horns invariably encircle the hepatic arteries and, travelling beneath the pericardial septum, they tend to diverge somewhat to the sides of the hind-gut. They continue towards the hinder end of the cephalothorax and their posterior extremities are usually attached by thin strands in the first abdominal segment. In the males of *Panulirus penicillatus* (Matthews, 1951) the testes are likewise anchored anteriorly and posteriorly by delicate mesenteries.

1. MALE

The mature *testes* (figs 10, 77) are long, white, highly-convoluted tubes which are also linked by a narrow transverse bridge and tend to be almost contiguous for some distance above the anterior region of the hind-gut. The *vas deferens* (fig. 77), which runs from each testis to the male aperture, is wider, more translucent, and less convoluted than the testis. It arises about half way along the posterior horn of the testis, approximately opposite the fourth pereiopod and commonly just anterior to the level of the sternal and the genital arteries. Its proximal portion is somewhat twisted, but gradually enlarges into a wider distal part that travels laterally over the first anterior oblique muscle and the outer slip of the first posterior oblique muscle. It then turns downward, passing in front of the posterior endosternite in the eighth thoracic segment, and proceeds between promotor *c* and levator *a* and over depressor *a* muscle of the fifth pereiopod. Its terminal portion is partly overlapped by the medial fibres of depressor *a* muscle that are attached to the proximal rim of the coxopodite. It opens ventrally on the coxopodite of the fifth pereiopod (fig. 2), and its aperture is guarded by a curved, backwardly-directed, slightly tumid flap.

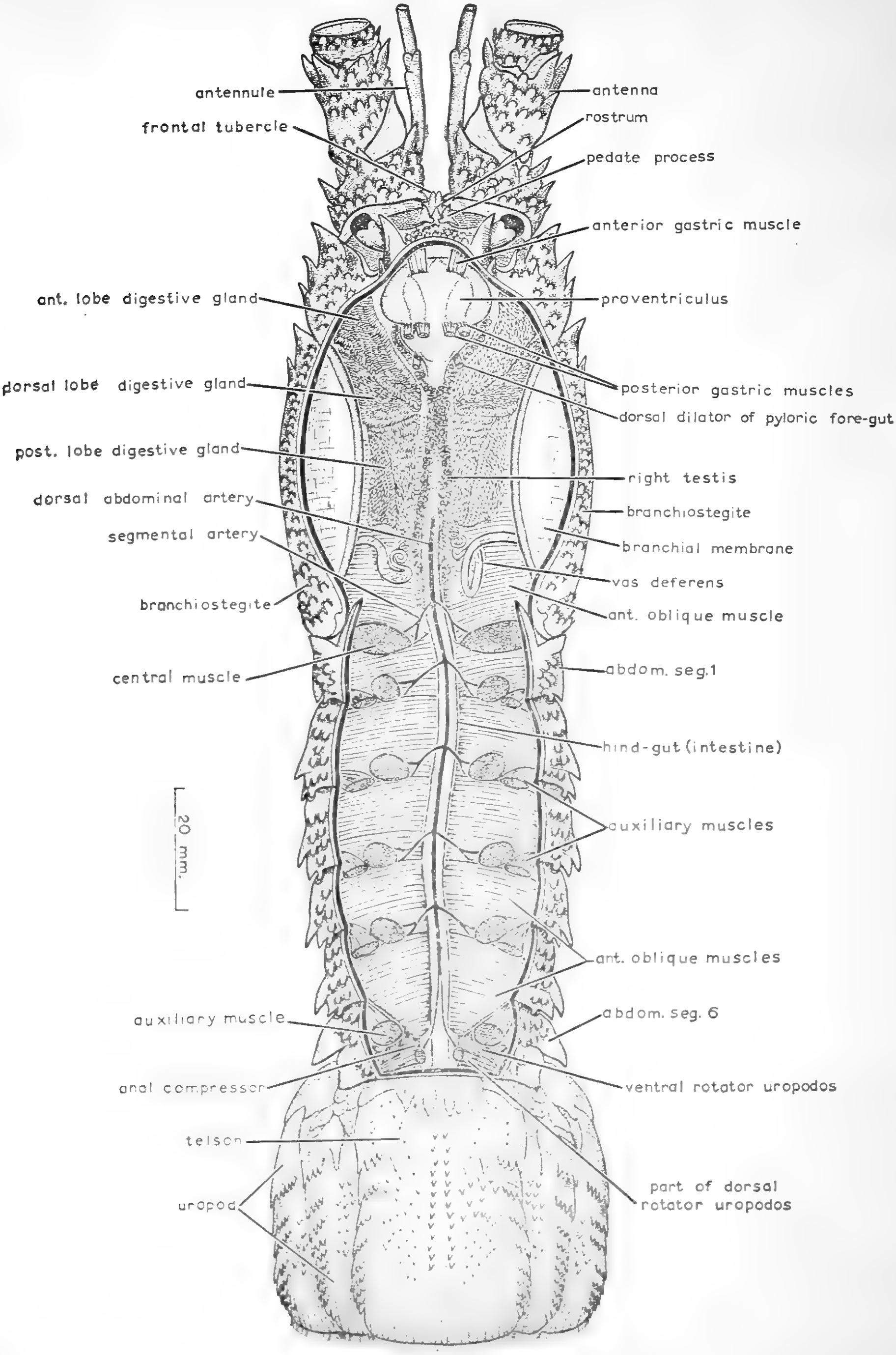


FIG. 77. Dorsal view of dissection of small male; the heart and the extensor and mandibular muscles have been removed.

2. FEMALE

The *ovaries* are always more conspicuous than the testes, but are also suspended anteriorly to the cardiac fore-gut and posteriorly in the abdomen and are similarly more or less H-shaped (fig. 79). In juvenile animals they are whitish, narrow, and practically straight tubes which terminate in the first abdominal segment. As the eggs ripen, the ovaries gradually change in colour and shape, and in mature specimens they are bright coral-red in colour and so greatly enlarged that their convolutions fill most of the cephalothoracic cavity and almost reach the bases of the antennae (figs 31, 78). The proportionally longer posterior horns are often apparently asymmetrical, that of the right side being continued into the second (fig. 78) or the third abdominal segment (fig. 31); but this asymmetry generally results from differences in the contortions of the right and left organs and their accommodation in the body

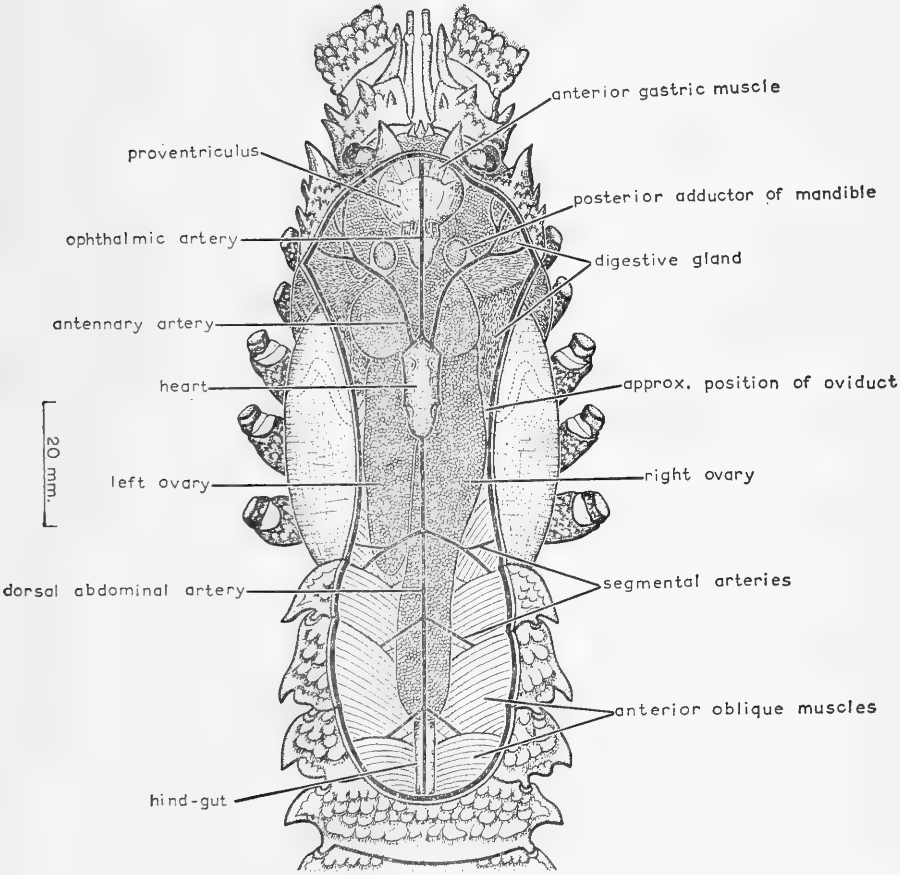


Fig. 78. Dorsal view of partly dissected female; the oviducts are represented diagrammatically.

cavity, for, when they are displaced and fully spread out, they are almost similar in length and width. After extrusion of the eggs, the spent ovaries (fig. 79) are considerably reduced in size, collapsed, and greyish-white in colour.

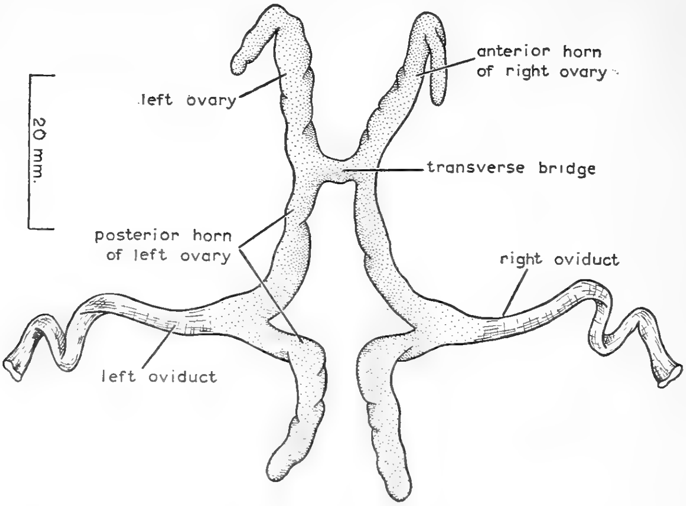


Fig. 79. Diagram of spent ovaries of ovigerous female, removed from body and with the oviducts somewhat laterally extended.

Each *oviduct* is a relatively short, broad, thin-walled, transparent tube which passes outward about midway along the posterior horn of the ovary opposite the third pereiopod. It runs horizontally across the posterior lobe of the digestive gland and curves downward over the lateral margin of the anterior thoracic muscle. In most specimens it enters the base of the third pereiopod anteriorly and describes a course comparable with that of the vas deferens in the fifth walking leg of the male. Travelling between the promotor and levator limb muscles, it opens on the ventral base of the coxopodite of the third pereiopod (fig. 80).

3. SPECULATIONS CONCERNING FERTILIZATION OF THE EGGS

From previous remarks on the external evidences of sexual dimorphism, it is obvious that the male has no intromittent organs. For this and other reasons the process of fertilization of the eggs is problematic. In most Macrura spermatophores of some sort or another are deposited on the ventral surface of the female usually in proximity to the genital apertures, and insemination is assumed to take place as the eggs pass over the spermatophores to their attachment on the setae of the pleopods. The spermatozoa apparently remain viable within the spermatophores for periods that vary according to the species. Lloyd & Yonge (1947) have reported that in *Crangon crangon* (*vulgaris*) the eggs are laid within two days of mating, while, according to Hughes & Matthiessen

(1962), the interval between the two processes in *Homarus americanus* may be as long as thirteen months.

The spermatophoric matter of *Astacus* was described by Huxley (1881) as whitish, vermiform filaments adherent to the posterior thoracic and the anterior abdominal sterna. Similar whitish, thread-like spermatophores were reported on the ventral surface of females of American fresh-water crayfishes by Andrews (1931), who suggested that some secretion released by the female during oviposition might act on the sperm capsule and so effect liberation of the spermatozoa. Elongate, complex spermatophoric masses are also known to occur in Natantia (Lloyd & Yonge, 1947) and in Anomura (Matthews, 1956), while even in Brachyura, in which internal fertilization is customary, spermatophores have been described by Spalding (1942) as minute, simple, oval structures that are introduced into the female vagina together with a sperm plug.

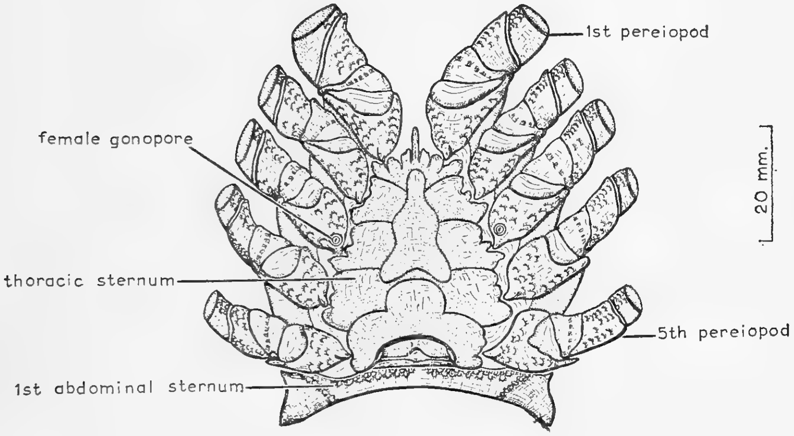


FIG. 80. Thoracic sternum of female, showing position of genital apertures on third pereiopods.

One of the first accounts of spermatophores in Palinura is to be found in Allen's (1916) article on the habits of *Panulirus interruptus* (Randall), in which the spermatozoa are embedded in twisted, tubular spaces in a putty-like mass which is plastered by the male on to the thoracic sternum between the last three pairs of pereiopods of the mature female. This seminal mass was stated to change rapidly in colour and consistency from a whitish, soft material to a black, hard substance, and an almost identical porous spermatophore has been described for *Panulirus argus* (Latreille) by Crawford & De Smidt (1922). In more recent studies, Matthews (1951, 1954*a*, 1954*b*, 1954*c*) has shown that mature females of *Panulirus penicillatus* (Olivier), three species of Scyllaridae, and *Enoplometopus occidentalis* (Randall) probably also carry sperm masses for some time before oviposition begins. From the pitted condition of one spermatophoric mass examined by him, Matthews considered it likely that the 'specialized claws' in the female were used to scrape the hard surface and so release the spermatozoa.

No such external spermatophores have been reported in *J. lalandii* and, as it is not known how fertilization is effected, the matter is still subject to speculation. Nevertheless, inspection of whole mounts of vasa deferentia, stained with acetic acid alum-carmine and cleared in oil of wintergreen, demonstrates that the enlarged distal portion of the duct is filled with an apparently double, intricately-folded, lacy ribbon; innumerable, minute, rounded cells, presumably mature spermatozoa, are arranged along the edge of the frill, and the whole presents some similarity to the spermatophore described by Matthews (1951) in the vas deferens of *Panulirus penicillatus.*

As in many other decapods, mating doubtless occurs in secluded places at night, but it seems to have been witnessed in captive animals by Gilchrist (1913*a*, 1918) and Von Bonde (1936). The latter investigator assumed that the seminal fluid was introduced into the female genital apertures, and his conclusion that fertilization takes place in the oviducts was based on the absence of external spermatophores and on an examination of recently laid eggs before cleavage had started. These eggs were enveloped by a thin inner chorion and a firmer, outer, 'chitinous' membrane; the latter was thought to have been secreted in the distal part of the oviduct, and Von Bonde therefore suggested that impregnation could only be effected higher up in the oviduct. According to Herrick (1911), however, the mature eggs of *Homarus* are provided with a single transparent membrane, the chorion, the properties of which were determined by Yonge (1937) to be those of the endocuticle ('chitin'). The outer coat, which is laid down after external fertilization, is epicuticular ('cuticular'), and is probably a derivative of the secretion from the tegumentary or cement glands on the pleopods. (It has been pointed out by Dennell (1960) that the terms 'cuticle' and 'chitin', used by Yonge and some other workers, refer more precisely to the epicuticle and the endocuticle respectively.) The above statements concerning the eggs of *J. lalandii* and *Homarus* are more or less in accordance with Burkenroad's (1947) conclusion that in all decapods fertilization precedes the formation of the egg membranes: but he established that, of four such membranes in *Palaemonetes*, the first is produced by the unfertilized eggs when they are extruded into the sea water, and the third is only developed in late stages of cleavage.

Although Von Bonde (1936) has mentioned an additional 'cuticle', the outer egg-capsule of *J. lalandii* is probably comparable to that of *Homarus* and other decapods, in which, as has been indicated above, it is considered to be formed externally by the tegumentary secretion which also serves to attach the eggs to the pleopods. Even if this suggestion is correct, it nowise minimizes the difficulty of attempting to formulate a plausible theory as to how and where impregnation of the eggs of *J. lalandii* takes place. So far as is known, there has been no direct observation of the process of fertilization in any marine macruran, but in those Palinura with visible spermatophoric masses and in such forms as the fresh-water crayfish, *Cambarus*, and the lobster, *Homarus*, in which the male has copulatory stylets and the female has an external sperm receptacle, it is fairly easy to imagine how external fertilization is accomplished. At the same time, Lloyd & Yonge (1947) have shown that in *Crangon crangon* spermatophoric masses are successfully deposited on the ventral surface of the female, even though the male has no copulatory organs.

In a recent article dealing with the problem of fertilization in *Jasus*, Fielder (1964*c*) has compared certain of its structural features with those of *Panulirus cygnus* George, and has concluded that internal impregnation in *Jasus* is feasible. However, unlike Brachyura in which internal fertilization is practised, no spermathecal enlargements were observed on the oviducts, nor were any spermatophores or spermatozoa detected in the oviducal lumina. While Fielder's deductions are well founded, possibly some of them require elaboration, and a consideration of the variations in the genital apparatus of other species of Palinura might be useful. He has suggested that the outer sclerotized rim of the male gonopore in *Jasus* is erectile and capable of being used as an intromittent organ. Nevertheless, the aperture is not located at the tip of this protuberance as would be expected if the structure served as a genital papilla. Moreover, the chance of its being inserted accurately into the female aperture seems remote in view of Von Bonde's (1936) statement that the brief mating period lasts only 30 to 60 seconds. In this connexion, it is of interest to note that Lloyd & Yonge (1947) have observed that an even shorter period of five seconds is all that is required in *Crangon crangon* for the application of the spermatophores, while the time given by Hughes & Matthiessen (1962) for the completion of mating in *Homarus americanus* is five minutes. The male genital apertures of *J. lalandii* and those of the Natal rock lobster, *Palinurus gilchristi* Stebb., are relatively small and markedly different from those of the east coast rock lobster, *Panulirus homarus* (L.), in which, as in *Panulirus cygnus* (Fielder, 1964*c*), the coxopodite of the fifth pereiopod of the male is modified ventrally behind the large transverse gonopore and has a broad oval pad with folded walls, antero-medial to which there is usually a forwardly-projecting brush of setae. Presumably this is an adaptation in *Panulirus* for the application of the spermatophoric matrix to the thoracic sternum of the female, but it does not seem to be a feature of all species that are known to deposit sperm packets. As previously mentioned, Matthews (1954*a*, 1954*c*) has reported hard spermatophoric masses in Scyllaridae, and an examination of available South African species belonging to this family indicates that the fifth pereiopods of the males are unmodified and resemble those of *Jasus*.

Another interesting feature discussed by Fielder is the difference between the surface of the thoracic sternum of *Jasus* and that of *Panulirus*, from which he inferred that the smooth sternum of the latter is more suitable for the reception of a spermatophoric mass than the setose sternum of *Jasus*. At the same time, the argument does not seem to be fully upheld by the structure of the thoracic sternum of *Projasus parkeri* (George & Grindley) which, apart from the characteristic median spines, is practically devoid of setae; admittedly this cannot be regarded as positive evidence, for the method of fertilization in this species is unknown, and it is only assumed to be similar to that of *Jasus*. In available literature there is also little precise information concerning the mating behaviour in the genus *Palinurus*, and again it is supposed that external spermatophores occur. When compared with *J. lalandii*, the thoracic sternum of *Palinurus gilchristi* Stebb. is seen to be more tuberculated and less setose, and the valve over the male genital aperture is somewhat larger, but these dissimilarities are not considered important enough for assuming that the two species have different methods of fertilization. Further elucidation of this point may be derived from an examination of some Scyllaridae in which the female thoracic sternum seems to be variable. Although it is fairly smooth in *Scyllarus martensii* Pfr., it is tuberculate in *Scyllarides elisabethae* (Ortm.) and setose in *Ibacus incisus* (Peron), and, following Matthews' (1954*a*, 1954*c*) observations of the habits of other Scyllaridae, any one of these types of surface is presumably capable of supporting a spermatophoric mass. It was also noticed in *S. elisabethae* that between the last two sternal plates there is a medial recess rather resembling a sperm receptacle, but this is common to both sexes and probably simply represents a depression caused by a sternal apodeme, such as occurs in *J. lalandii*.

Relative to Fielder's conclusion that the chelae of the fifth pereiopods of the females of *Jasus* are too weak to pinch the surface of a hard spermatophoric mass, the Scyllaridae may be of further significance. In describing the diagnostic features of South African Decapoda, Barnard (1950) has indicated that in female Scyllaridae, with the exception of *Thenus* Leach, there is a small chela on the fifth pereiopod, and Matthews (1954*a*) considered that it could be used in *Parribacus antarcticus* Lund to scarify the hard surface of the spermatophoric mass. The chelae of South African scyllarids do not appear to be appreciably stronger than those of *J. lalandii*, but, assuming as Fielder suggests, that the small chelae in *Jasus* are only used for grooming the ovigerous pleopods, it is nevertheless probable that in many Scyllaridea the pointed dactylopodites would also be able to puncture the spermatophoric mass and so disperse the spermatozoa.

These remarks contribute little towards the solution of the problem of the fertilization of the eggs in *Jasus*, but they demonstrate the variability of structural details in those Scyllaridea which are thought to produce spermatophoric masses and, if this is any guide, it would seem that the possibility of external fertilization occurring in *Jasus* cannot be excluded. The time lag between mating and oviposition in *J. lalandii* would perhaps provide a significant clue but, unfortunately, the only records available are conflicting. On the one hand, the statement by Von Bonde & Marchand (1935: 14) that 'the eggs appear beneath the female's tail immediately after fertilization', seems to suggest that mating and oviposition are practically synchronous. On the other hand, Gilchrist (1918) and Von Bonde (1936) have remarked that oviposition takes place two or three days after mating: to fulfil the implications of this observation, some form of storage and protection for the spermatozoa would be required for a period of up to three days. Despite persistent search in this and other countries, no spermatophores have yet been discovered, and lack of information on this particular biological detail is the main obstacle to the solution of the problem. In the absence of copulatory organs and internal spermathecae, it seems unlikely that *Jasus* has internal fertilization, but further investigations into the mating process, the nature of the spermatophores, and the structure of the spermatozoa are essential before the matter can be settled. A step in this direction has been taken by Heydorn (1965), who has described the spermatozoa observed in smears of the contents of the vasa deferentia, and has used comparative sperm counts to determine the stage of puberty and to estimate the reproductive potential of mature males. As has already been indicated, Fielder (1964*c*) has presented some interesting arguments in support of Von Bonde's (1936) assumption that fertilization in *Jasus* is internal. It considered, however, that studies of the external anatomy of available South African Scyllaridea suggest that fertilization in *J. lalandii* may be external, and that observations on the mating behaviour of the Natal rock lobster, *Palinurus gilchristi* Stebb., might provide decisive clues.

DEVELOPMENT

It is easy to confirm Von Bonde's (1936) observation that the fertilized eggs are provided with stalks which are twisted intricately around bundles of the long non-plumose setae on the endopodites of the female pleopods. From Herrick's (1911) remarks on *Homarus* and those of Lloyd & Yonge (1947) on *Crangon crangon*, it may be assumed that the stalks and the egg-capsules are secreted by tegumentary glands on the pleopods, but the eggs of *J. lalandii* remain discrete, whereas those of *Homarus* are agglutinated. While the eggs are thus anchored to and protected by the female's abdomen, embryonic development proceeds for several months until the first free-swimming larval stage escapes by rupturing the egg-capsule. It has been established by Von Bonde (1936) that the time between oviposition and hatching is about 95 days and that there is an interval of two and a half years in females and five years in males between hatching and the fully mature state. As yet, there is no published information concerning the time required for the completion of larval life in *J. lalandii*, but Lindberg (1955) has reported that the larvae of *Panulirus interruptus* remain planktonic for at least six to nine months, while Balss (1957) has adduced that the duration of larval development in *Palinurus elephas* is three months. The latter period seems to be too short to cover the successive larval phases of *J. lalandii*, and it is probable that the time required will be about the same as that observed by Lindberg (1955) in *Panulirus interruptus*.

A cursory examination of the early embryonic development was first made by Gilchrist (1918), who also gave illustrated particulars (1913*b*, 1916, 1920) of the sequence of steps in post-embryonic life. A fuller account of the embryology and a review of post-embryonic stages later appeared in Von Bonde's (1936) article and, as the ontogeny of a number of Scyllaridea is well known, only the salient features concerning *J. lalandii* need be related here.

It has been inferred by both Gilchrist (1913–20) and Von Bonde (1936) that the stage corresponding to the nauplius is passed in the egg and that the emergent larva represents a more advanced type in the developmental cycle. This was described by Gilchrist (1913*b*, 1916) as the *naupliosoma*, which superficially resembles a nauplius and uses its large, biramous antennae to swim strongly to the surface of the water during its brief period of existence of only four to six hours. Its body, which measures 1·7 mm long by 0·72 mm in maximum width (Von Bonde, 1936), differs from that of a nauplius in being demarcated into three tagmata and in having appendages on all but the last two thoracic segments and the abdominal region: a carapace and conspicuous, stalked, compound eyes are other distinctive features. An even younger free-swimming stage, introduced into the cycle and called the *prenaupliosoma* by Von Bonde (1936), was observed to last about eight hours before moulting into the naupliosoma. Reporting the recent discovery of planktonic prenaupliosoma larvae, probably referable to *Panulirus argus*, Sims (1965) has discussed the question of whether or not these early larvae are normal free-swimming stages. He has cited a number of instances of their having been observed in some Scyllaridae and Palinuridae, but has also indicated that there is no evidence that they are typical of the ontogeny of *Panulirus argus*. He has shown, however, that these stages will emerge from developing eggs if the egg-capsules are broken either accidentally or intentionally, or if the rupture is effected by unnatural osmotic pressure when the eggs are immersed in dilute sea water. His suggestion is that in some species they may represent advanced embryonic stages which are sometimes able to survive if, by chance, they are released prematurely.

The majority of Scyllaridea hatch in the characteristic *phyllosoma* or 'glass crab' stage, which is considered by Calman (1909) and other authorities to be a peculiar modification of the 'schizopod' or 'mysis' phase in the developmental pattern of other decapods. The phyllosoma larva is admirably adapted to planktonic life, the abdomen being rudimentary and its body consisting mainly of a dorso-ventrally flattened, highly transparent, somewhat bipartite cephalothorax with three pairs of long, slender, projecting, biramous pereiopods, in addition to more anterior appendages. The phyllosoma larvae examined by Gilchrist (1916) and Von Bonde (1936) had a size range of from 1·5 or 1·7 to 37 mm, but the time required for the development of the incipient larva seems to be variable. While Gilchrist (1913*b*, 1916) reported that some artificially-reared, free-swimming naupliosomas moulted at the surface into the first-stage phyllosoma within four to six hours, the smallest phyllosoma recorded by Von Bonde (1936) appeared about eight days after the emergence of the prenaupliosoma. Apart from the fact that the antennae are no longer locomotory, the phyllosoma of *Jasus* has all the essential features of Gilchrist's naupliosoma, and successive periods of ecdysis and growth are accompanied by improvements in the construction of the anterior appendages, the gradual growth of the fourth and fifth pairs of pereiopods, and, in later stages, the development of the abdomen. Gilchrist's (1916, 1918) conclusion that only the smallest phyllosomas are surface dwelling and that after a few days they migrate to the bottom for an unknown period is reflected in Von Bonde & Marchand's (1935) tabular

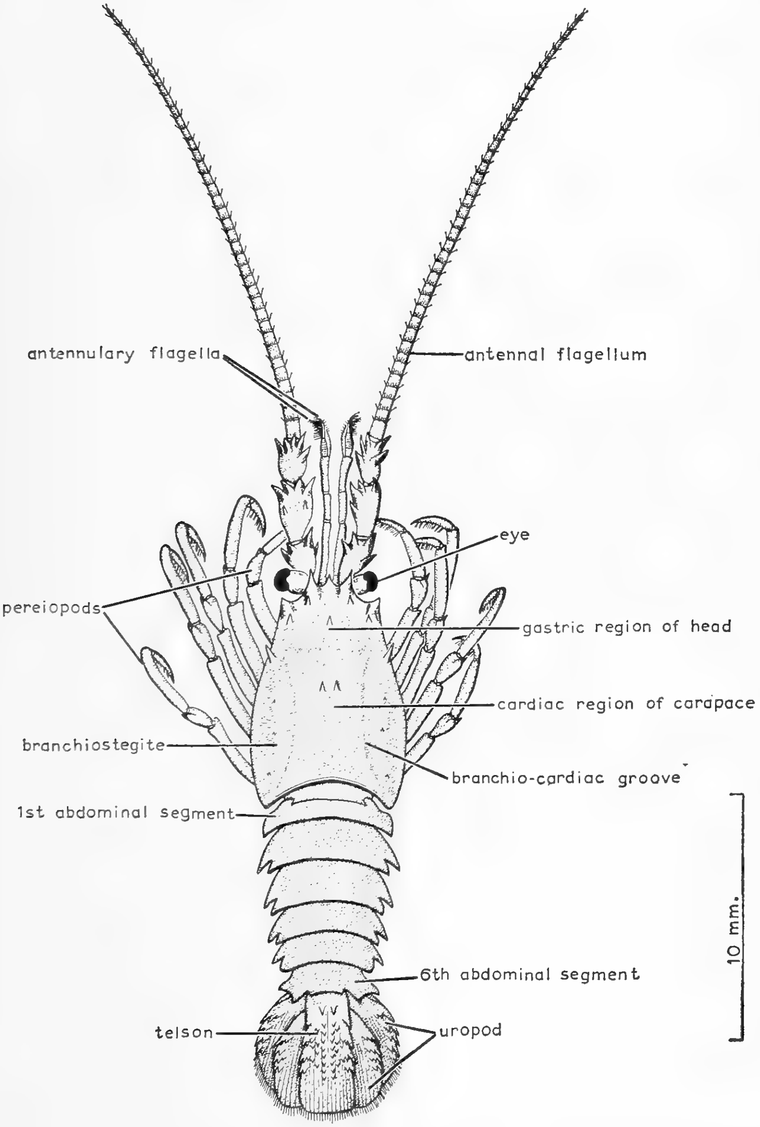


FIG. 81. Dorsal view of 22 mm long puerulus stage.

summary of events. Using the larval anatomy as a criterion, however, the accuracy of this deduction seems questionable, but Gilchrist's qualifying remarks are less cryptic and are perhaps a truer interpretation of the habits of the larvae. He observed that the smaller forms were plentiful in inshore waters during the summer months, while the larger, less abundant stages were collected only in deeper waters and probably submerged to greater depths at times coinciding with periodic moulting. It may be suggested that this seems fairly consistent with the structural characteristics of an organism that is obviously better equipped for flotation and drifting than for benthic life. Like many other planktonic forms, the phyllosoma larvae probably perform marked vertical movements and migrate towards the surface at night; diurnal fluctuations in depth are therefore to be expected, and records of vertical distribution will vary in accordance with the times of collection of the samples.

After an undetermined period, the largest phyllosomas undergo radical anatomical modifications and moult into the first post-larval phase, the *puerulus* (fig. 81). A total body length of from 22 to 26 mm for this stage has been recorded by Gilchrist (1916), who later (1918) mentioned that it frequents inshore waters. The puerulus differs markedly from the phyllosoma in having a more compact body which is demarcated into a cephalothorax and a well-developed abdomen. In all essentials it is a miniature of the adult, but the body is transparent and relatively smooth, and the carapace is rather flat dorsally and less rounded laterally than in the adult. It is also a natant, probably a nektonic form, with the pleopods (fig. 6) capable of being linked together in pairs by hooks on the appendices internae of the endopodites when they are thought to function as swimming organs. In a key to the puerulus stage of some palinurids, Gordon (1953) has indicated that one of the distinguishing features of the puerulus of *Jasus* is the absence of a flagellum on the short exopodite of the third maxilliped. Gilchrist (1916) also described and figured the exopodite of this appendage as a small unsegmented structure and, while close inspection of present material confirms its rudimentary condition, there is evidence of several, incipient, apical annulations which are somewhat similar to the divisions on the longer, more distinct flagella of the first and second maxillipeds.

In preparation for the assumption of adult life, the puerulus is succeeded by a stage differentiated by Gilchrist (1918, 1920) as the *post-puerulus*, the largest of which reared by Von Bonde (1936) measured 32 mm long. As the coupling hooks of the pleopods have now disappeared, the post-puerulus presents an even greater likeness to the adult than the puerulus but, as yet, the pleopods are not sexually dimorphic. Subsequently, calcification of the exoskeleton sets in and marks the end of larval life; it is assumed that the animal then gradually becomes adapted to sublittoral conditions and continues its activities as a young rock lobster.

SUMMARY

The various systems of organs of *Jasus lalandii* (H. Milne Edwards) have been studied, and most of the findings have been compared with published descriptions of the anatomy of other species of decapod Crustacea.

In discussing the external features, an attempt has been made to define some of the characteristic sclerites in the head region.

The functional significance of the appendages has been touched upon, and observations of living animals have given an impression of the use of some of the mouth-parts during feeding.

The parts of the endophragmal skeleton have been described, and an examination of the cast shells or exuviae, which were obtained after numbers of captive animals had moulted, shows that certain endoskeletal structures are resorbed in preparation for ecdysis.

There is a broad resemblance between the complex trunk and appendicular musculature and that of the few other species of Decapoda of which accounts are available. Several differences have been noted, and the functions of the muscles in the movements of the body and the appendages have been indicated.

No important differences were observed between the alimentary tract and that of related decapods.

Dissections and sections of the antennal glands demonstrate that the end sac is embedded in the labyrinth. As in other marine Decapoda, a nephridial canal is absent, and the antennal glands are probably not important in osmoregulation.

The gills belong to the trichobranchiate type and their serial arrangement is typical of the Palinuridae. The presence of nephrocytes along certain branchial channels suggests that the gills are partly excretory in function.

Specimens injected with black indian ink were used to study the main arteries and the venous sinuses, and from observations of serial sections of the gills it seems likely that the blood is oxygenated twice as it flows through the gill filaments. Pericardial pouches, which are important storage organs for water absorbed during moulting, are continuous with the posterior end of the pericardial cavity.

An account has been given of the ganglia and the peripheral nerves of the central nervous system, and the ramifications of the delicate stomatogastric nervous system have been traced.

Some of the details of the more obvious sense organs, such as the antennulary setae, the statocysts and the compound eyes, have been noted. As in some other species of Decapoda, a median eye persists in the adult.

In view of recent intensive research on crustacean neurosecretions, some preliminary observations of the endocrine organs have been included.

The male and female reproductive organs are essentially similar to those of other Palinuridae. No spermatophores have yet been detected in *J. lalandii*, and it is not known whether fertilization of the eggs takes place internally or externally.

Based mainly on information published by other workers and partly on direct observations of ecdysis in a number of experimental animals, some facts concerning the moulting cycle and its relation to the breeding season have been mentioned, and reference has also been made to early descriptions of the post-embryonic stages of *J. lalandii*.

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INDEX

Numbers in italics denote pages on which items are illustrated

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

MANUSCRIPT

To be typewritten, double spaced, with good margins, arranged in the following order: (1) Heading, consisting of informative but brief title, name(s) of author(s), address(es) of author(s), number of illustrations (plates, figures, enumerated maps and tables) in the article. (2) Contents. (3) The main text, divided into principal divisions with major headings; subheadings to be used sparingly and enumeration of headings to be avoided. (4) Summary. (5) Acknowledgements. (6) References, as below. (7) Key to lettering of figures. (8) Explanation to plates.

ILLUSTRATIONS

To be reducible to 4¾ in. × 7 in. (7½ in. including caption). A metric scale to appear with all photographs.

REFERENCES

Harvard system (name and year) to be used: author's name and year of publication given in text; full references at the end of the article, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year.

For books give title in italics, edition, volume number, place of publication, publisher.

For journal articles give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals.* 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination.

Examples (note capitalization and punctuation)

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ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs. 5 *a*, *b*; Liste: 11. Turton, 1932: 80