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CRUSTACEA

Volume X *No 3*

ANOMURA

BY

V. V. MAKAROV

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Anomura

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FOREWORD

This volume deals with one of the large taxonomic divisions of the Decapoda, viz., the Anomura, the hermit crabs. The following volume deals with the Brachyura, the true crabs. The volume treating of the more primitive groups of the Decapoda has been delayed, since the publication of some works is expected, in which many new species from the USSR are described; without them, the respective volume on the "Fauna of the USSR" would be incomplete. This is also the reason why some changes have been made in the systematic order of the publication of the volumes dealing with the Decapoda. The early publication of the volume devoted to the Anomura was also determined by the fact that this group includes a number of commercial items.

In the introduction, a short anatomomorphological outline and also very succinct data are given on the biology and zoogeography of the Anomura. Owing to its specific character, the data on the family Paguridae are preceded by a special introduction, in which its anatomy is examined in greater detail, while in the general introduction, the external morphology and some general problems (ecology, economic importance, phylogeny) of the group are especially stressed. In the zoogeographical outline of the Paguridae the localities of the fauna studied in this volume are listed; for some species, the types of which are preserved in the Zoological Institute of the Academy of Sciences of the USSR, the limit on the western shores of North America extends somewhat south of Kodiak Island, as far as Sitka.

The collections of the Academy of Sciences studied are chiefly those from the seas of the Soviet Far East; the most important are the collections of I.G. Voznesenskii (1840), Petelin (1852), A.A. Bunge (1897–1898); P.Yu. Shmidt (1900, 1901, 1929, 1933), V.K. Brazhnikov (1899, 1908–1910), N. Smirnov and A. Begak (1907–1910), F.A. Derbek (1908–1913), B.A. Geineman (1909–1910), V.K. Arsen'ev (1910–1911), L.M. Starokadomskii (1911–1913, 1934), E.E. Arnol'd (1911), F.P. Ryabushinskii (1911), E.K. Suvorov (1911), M.N. Pavlenko and V.K. Soldatov (1911–1915), Myaskovskii (1912), the collections of the Hydrographic Expedition of the Eastern Ocean (1914–1925) and that of Roshkovskii (1917). With regard to the Black Sea, there are the collections of K.P. Yagodovskii (1908) and S.A. Zernov (1908–1911).

The illustrations are by the artist N. Kondakov and the photographs by the author.

V. Makarov

SYSTEMATIC INDEX OF THE SPECIES

Superfamily **Thalassinidea**

1. Family **Axiidae**

2. Family **Callianassidae** Bate

Superfamily **Galatheidea**

3. Family **Galatheidae**

1

INTRODUCTION

The Decapoda studied in this volume can be divided into two groups according to their external appearance. The members of the first group have a shrimplike body (resembling the Macrura), while those of the second group are crablike*. This habitus is determined firstly by the form of the carapace and by the position of the abdomen. In members of the first group, the carapace is elongated and more or less laterally compressed; the abdomen is also elongated and not bent under the cephalothorax. In members of the second group, the carapace is broad and compressed in a dorsoventral plane, and the abdomen is shortened and bent under the cephalothorax. The superior surface of the carapace is smooth only in rare cases; it is usually covered with various ornamentations–transverse furrows or crests, blunt tubercles or pointed spines, squamate processes, or finally outgrowths and hollows of greatly varied forms. On the superior surface of the carapace, the following areas may be observed, especially in the crablike forms (Figure 1): along the median line are the unpaired areas, namely, frontal, gastric, cardiac and intestinal areas; the paired areas are the orbital, hepatic and branchial areas. The gastric area is, in turn, divided into unpaired mesogastric and urogastric subareas, and the paired epigastric, protogastric and metagastric subareas. Each branchial area is also divided into meso-, epi-, and metabranchial subareas. The sinuous cervical groove delimits the hepatic and branchial areas, as well as the gastric and cardiac areas. The paired branchiocardiac or branchial furrows separate the cardiac area from the branchial areas. The contour of the crablike carapace is formed by the anterofrontal edge, which usually bears a rostrum, by the anterolateral edges (which sometimes form an obvious angle with each other, and in other cases show a smooth transition), and finally, by the posterior edge. The lateral sides of the carapace are called thoracic pleurae, or branchiostegites. It is important to note that, in this case, the lateral edge of the carapace does not correspond to the boundary between the notum and the pleurae; this
2 boundary is found under the lateral edge and resembles a membranous line, called in the Anomura 'linea anomurica' or 'linea thalassinica'; this line starts from the anterior corner of the mouth and extends posteriorly a fairly large distance from the edge of the carapace, but gradually approaches it, until it finally reaches the posterior edge of the carapace, above the base of the fifth pair of pereiopods. Consequently, the superior half of the lateral side of the carapace, i.e., the one between the lateral edge of the carapace and the linea anomurica, marks the edge of the notum, bent ventrally, while

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* Since the peculiar family Paguridae is dealt with in the introduction to that family, we shall not discuss it here.

the pleurae are merely the lateral parts under the linea anomurica. The anterior part of the thoracic pleurae is called the pterygostomial area, and the posterior part is called the subhepatic area. The linea anomurica is very clearly marked in the genus Pachycheles (family Porcellanidae). The rostrum is not fused with the epistome, and has the most varied forms. Sometimes it is completely missing or rudimentary (Callianassinae); sometimes it has the form of an outgrowth at the end of the raised gastric area (Upogebiinae); sometimes it looks like a broad triangle (Hapalogastrinae, Pachycheles), or it may be divided into several lobes (Porcellana); sometimes it resembles a narrow triangle with denticulate edges (Galathea), or a long, smooth, pointed spine (Munida), or a spine bearing a variable number of accessory spinules (Lithodes, Paralithodes); in a few cases, it is semimembranous (Cryptolithodes), and, finally, in some genera of the Lithodinae it is an outgrowth varying greatly in form (Phyllolithodes, Lopholithodes, Rhinolithodes, Sculptolithodes). The frontal edge of the carapace does not form closed orbits, and therefore the eyes move freely. The sternal plates are narrow and fused, with the exception of the last thoracic segment, which has a free sternal plate.

In most cases the eyestalks are pedunculate, with a terminal cornea. The peduncle is usually made up of two joints, a short basal one and a longer terminal one. In rare cases, e. g., in Emerita (Hippidea), the basal joint is secondarily divided so that there are three joints in all. The peduncles of the genera Callianassa and Albunea undergo a specific modification. They are dorsoventrally flattened and have the form of triangular plates, the cornea being on the dorsal side in the center of the plate, or sometimes located slightly more forward or backward.

The antennules show no peculiarities; the stalk is composed of three joints, and the terminal joint bears two flagella. In the burrowing genus Albunea (Hippidea) the fused antennal flagella form a peculiar tube, serving for the respiratory water circulation.

4 The antenna is usually four-jointed, and in very few cases, five-jointed, the stylocerite being shorter than in the Natantia. In Emerita, the stylocerite is provided with long hairs and serves for the capture of the small planktonic algae and animals which comprise its food. In most of the Anomura, a scaphocerite is found on the second joint. Its shape varies greatly, from a small plate (Callianassidae) and a simple spine to ramified spines, curved denticulated plates (Cryptolithodes), or numerous, long, fir-needle-like spines (Lopholithodes). In general, the scaphocerite of the Anomura is considerably reduced compared with that of the Natantia, and loses its function as a static organ as a consequence of the predominantly reptant life of this group; in the shrimplike forms of the Anomura, as for instance the Galatheidae, the lack of scaphocerites is compensated for by the unusually long first pereiopods; during recoil movements—produced by strong flexing movements of the abdomen—these legs are held in a horizontal position and thereby serve a balancing function.

MOUTH PARTS. The masticatory section of the mandibles is composed of a cephalic end and an apophysis; the cephalic end of the anomuran mandible is not subdivided into a molar and an incisive part—the palp is usually two-jointed. The maxillules have two masticatory lobes and a palp, which usually has either one or two joints (Thalassinidea). The maxillae have a four-lobed masticatory part, a uniarticulate palp (endopodite) and

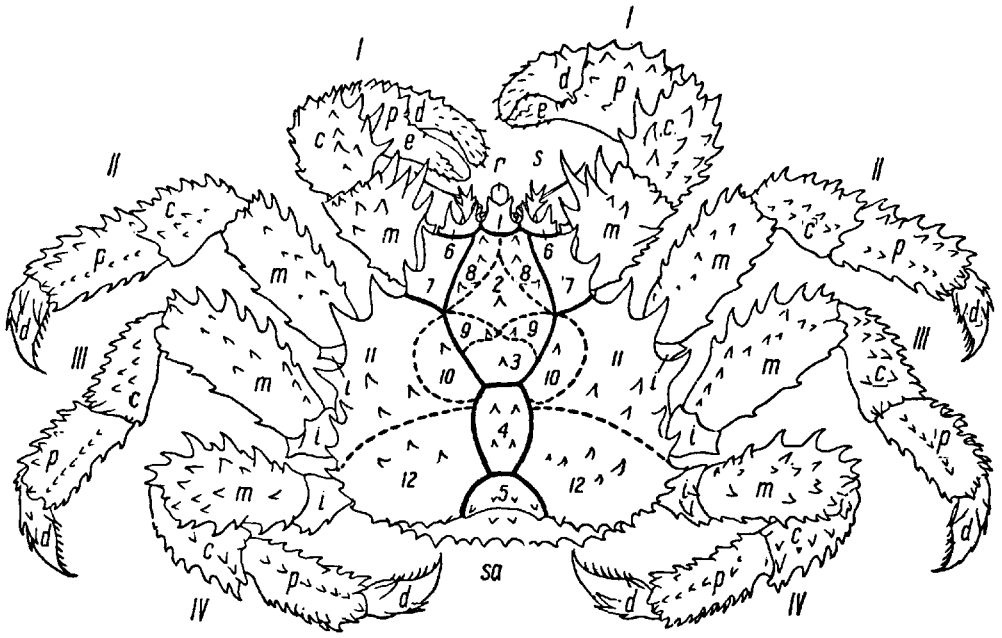

Figure 1. Diagrammatic presentation of the areas of the carapace

The areas are marked by continuous lines, the subareas by interrupted lines. The terminology of the pereiopodal joints: 1. frontal area; 2. mesogastric subarea; 3. urogastric subarea; 4. cardiac subarea; 5. intestinal area; 6. orbital areas; 7. hepatic areas; 8. protogastric subareas; 9. metagastric subareas; 2, 3, 8, 9 – gastric area; 10. epibranchial subareas; 11. mesobranchial subareas; 12. metabranchial subareas; 10, 11, 12 – branchial area; I. – chelipeds (first pereiopods); II. – first walking legs (second pereiopods); III. – second walking legs (third pereiopods); IV. – third walking legs (fourth pereiopods); r – rostrum; s – scaphocerite; sa – second abdominal segment; i – ischium; m – merus; c – carpus; p – propodus; d – dactylus (on the cheliped, the movable dactylus); e – immovable dactylus of the cheliped (pollex).

a membranous scaphognath (exopodite). The coxa [coxopodite] and the basis [basipodite] of the first maxillipeds each have a masticatory lobe (in Axius the coxal lobe is divided into two parts; the palp is made up of one joint (in Axius it is two-jointed); the exopodite has a broad base and a slender flagellum, which is sometimes many-jointed. The second maxilliped is made up of a two-jointed protopodite (not bearing any masticatory lobes), with a five-jointed endopodite (some of the joints are sometimes fused), and an exopodite bearing a flagellum. The third maxillipeds resemble the second in structure; the ischium [ischiopodite] sometimes bears a spiniform lobe which serves for crushing the food (Galatheidea); Zimmermann (1913) ascribes the following functions to the endopodites of the third maxillipeds in the Galatheidea: 1) the collecting of small food particles by means of retrieving movements; 2) the cleaning of the antennules and the antennae; 3) the protection of the afferent canal of the branchial cavity (in bent position). In the Galatheidea the cleaning of the antennules and the antennae is carried out as follows: the antennules and the antennae are bent markedly downward, the endopodites of the third maxillipeds are straightened, then the antennules and the antennae are pulled slowly upwards, and are in this way cleaned between the hairs of the three last joints of the endopodites, which have the form of paired saws or combs. The hairs which collect the food particles are long and slender and bear two rows of small branches. In the Porcellanidae, with their crablike habitus, and in which the antennae have in fact lost their tactile function, a reduction of the cleaning hairs may be observed, and correspondingly a broadening and flattening of the joints of the endopodite; consequently, their third maxillipeds approach the type found in the Brachyura (e. g., Cancer). In some primitive Paguridea, the third maxilliped ends in a small chela. The exopodite is sometimes lacking (Callianassa). The third maxillipeds may be either pediform or foliaceous (Figure 2). In the first case, the ischium and the merus [meropodite] are the same width as the subsequent joints, or slightly wider; in the second case, the ischium and the merus are widened, entirely covering the mouth, while the three subsequent joints (carpus [carpopodite], propodus [propodite], dactylus [dactylopodite]) are narrow and small, and form the so-called palp. The relation between the mouth parts 'in situ' is shown in Figure 3.

PEREIOPODS. Each pereiopod is made up of seven joints. In the Anomura however, the basis and the ischium are fused into a single joint, so that the appendage is six-jointed. The first pair of pereiopods are nearly always chelate; in the taxonomic diagnoses the legs of this pair are called chelipeds, while the other four pairs are called simply pereiopods, though some of them may be chelate. The first pair of pereiopods (or the chelipeds) are the same, or similar, in length and form (Galatheidea, Upogebiinae), or the right cheliped is stronger and longer than the left one (the majority of the Lithodidae); the difference in length and form between the first two pereiopods is particularly marked in the Callianassinae. According to their structure one may distinguish true from false chelae (subchelae). In the true chela, the immovable dactylus (pollex or index) is the same length as the movable dactylus, and when the chela is closed, the internal edge of the dactylus adheres to the external edge of the pollex, or, if the fingers are curved, only their tips touch. In the false chela, the immovable finger appears as a short spiniform outgrowth of the propodus, starting from the angle of its straight or somewhat oblique anterior edge; the movable

dactylus is articulated with the opposite corner; when closed, the internal edge of the movable dactylus is in contact with the anterior edge of the propodus, touching the immovable dactylus only with its tip, or crossing its base. Subchelate first pereiopods are found in the Albuneidae and Upogebiinae. In contrast, the Hippidea have simple, straight pereiopods, i. e., they end in a single dactylus; in the genus Mastigochirus this dactylus is elongated to form a flagellum, and is segmented. The first pereiopods serve for the capture of food and also as weapons of attack and defense. The function of the legs in Mastigochirus, with their peculiar structure, has not yet been elucidated. The second pereipods are simple (Hippidea, Galatheidea, Upogebiinae, Lithodidae) or chelate (Axiidae, Callianassidae). The third and fourth pairs of legs are simple. The fifth leg is simple (Hippidea, Axiidae–in the latter they are sometimes subchelate, as in the Upogebiinae), or chelate (Galatheidea, Callianassinae, Lithodidae). In the burrowing forms, the pereiopods are adapted for digging, either by the broadening of the propodi of the last three pairs of legs (Callianassidae) or by the broadening and flattening of the dactyli of three pereipods (Hippidea), as shown in Figure 41. The fifth pereiopods in the Hippidea, Galatheidea, and Lithodidae are reduced, and serve for cleaning the branchial cavity (Putzfüsse); in the species of the first two subfamilies they are usually only partly hidden in the branchial cavity, since the carpus and the merus, with a bent articulation between them, generally remain outside; in the Lithodidae, the fifth pereiopods are usually entirely hidden under the carapace, and cannot be seen from outside. In the forms living under rocks and stones, e. g., Hapalogaster, all the pereiopods, as well as the carapace, are considerably compressed. In Cryptolithodes, and more so in Lopholithodes, the flattened and complementary form of the lateral sides of the pereiopods is very pronounced; consequently, all the legs may be closely pressed to each other and to the carapace, thus forming an ideal protection for the ventral surface
7 of the body in Lopholithodes, or completely covering the inferior surface of the carapace in Cryptolithodes. A peculiar formation is found in the Californian Lopholithodes foraminatus (Stimpson). The external edge of the carpus of the chelipeds shows a deep semicircular hollow; the internal edge of the carpus of the second pereiopods shows a similar but smaller hollow; when all the legs are pressed together, the two hollows are in front of each other, thus forming a round, fairly broad orifice (see specific name), which allows a free circulation of the respiratory water.

BRANCHIAE. Three types of branchiae may be distinguished, according to their structure: dendrobranchiae (only in the Penaeidea), trichobranchiae, and phyllobranchiae. The trichobranchia (Figure 4b) is composed of a central stalk, which bears numerous slender filaments or tubes; the filaments become thinner toward the distal end of the stalk; each filament has a vascular canal, which communicates with the canal of the stalk. The phyllobranchia is composed of a central stalk bearing two rows of leaflets or plates, which are very close together, and which become smaller toward the distal end of the stalk; the leaflets are on the two opposite sides of the central stalk. Trichobranchiae are found in Thalassinidea, in the genus Aeglea (Galatheidea), and in Pylochelidae. Phyllobranchiae are found in the Hippidea, Galatheidea (with the exception of Aeglea), and Lithodidae.

According to their position (insertion), three types of branchiae may be distinguished: 1) podobranchiae-situated on the coxal joint of the maxilliped

and of the pereiopod; 2) arthrobranchiae–situated on the articular membrane, between the coxa and the body; 3) pleurobranchiae–on the lateral side of the body.

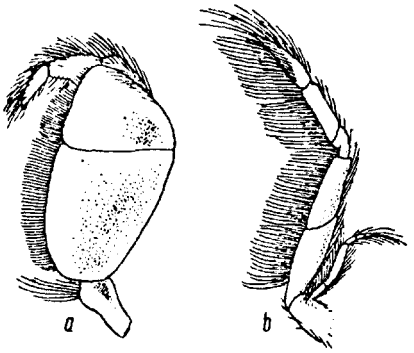

Figure 2. Two types of third maxillipeds:

a – foliaceous type (Callianassa harmandi); b – pediform type (Upogebia major).

In a complete branchial formula, every thoracic segment has one podobranchia, two arthrobranchiae (anterior and posterior) and one pleurobranchia. In almost all cases, however, the branchial set is incomplete, as one or another of the branchiae is usually missing. Mastigobranchiae may be found on the coxa of the appendages, from the first maxilliped to the fourth pereiopod inclusive.

In the genus Callianidea, apart from the normal branchiae, hidden under the carapace, numerous gill-like filaments similar to the trichobranchiae found on the edges and the external surfaces of the pleopods of the second to fifth abdominal segments; they differ from the trichobranchiae in that they are segmentary, either actually or apparently, and also by the fact that they are joined in pairs at their bases, in thick stalks.

The branchiostegite is not close to the coxal joints of the appendages, so that a free flow of water is furnished to the branchiae by the movements of the scaphognaths. In the Galatheidae and Lithodidae, because of the reduction of the fifth pereiopods, the posterior edge of the carapace may be raised, thus further facilitating the inflow of water. Apart from the fifth pereiopods mentioned above, a deviation of the respiratory flow, caused by the reverse movements of the scaphognath, is also used for the cleaning of the branchiae.

In his work, K. Zimmermann (1913) studied the adaptative modifications undergone by the Galatheidea in connection with the transition from the sublittoral habitat (Galathea squamifera) to the muddy facies of the tidal zone (Porcellana playtcheles). Thus, we note modifications for protecting the branchial cavity against obstruction with mud. In Galathea squamifera, which inhabits the clear water of the open sea, the branchiostegite alone forms a sufficient protection of the branchial cavity; the hairs bordering the afferent orifices of the branchial cavity (at the posterior end of the carapace) have a simple structure, like that of the hairs on the edges of the branchiostegite. The mastigobranchiae, which in G. squamifera are found on the third maxillipeds and on the first three pereiopods, serve for cleaning the branchiae, especially the arthrobranchiae. With a reduction of the scaphognath in Galathea strigosa, the necessary water circulation is maintained by the movements of the carapace itself. This leads to a reduction of the epipodites on

9 the pereiopods, because of the danger of tearing during these movements; the branchiae are protected against obstruction by mud by the more complicated structure of the hairs bordering the afferent orifices of the branchial cavity. Almost the same thing may also be observed in Galathea intermedia. In Porcellana, which inhabits the littoral zone, the mastigobranchiae on the third maxillipeds and on the pereiopods are missing; so, too, are the podobranchiae. The arthrobranchiae and the pleurobranchiae, however, are well developed. Zimmermann ascribes this to the habit of the genus to cling to various objects. When doing so, the legs are held wide apart. Because of such movements, the epipodites and the podobranchiae may be in danger of being damaged or torn, or at least would rub against one another or against the edges of the branchiostegite. To prevent this in Porcellana playtcheles, which lives in more muddy biotopes, the hairs on the edges of the branchiostegite and on the coxal joints of the pereiopods have a ramified or pinnate structure, thus enabling efficient filtration; in P. longicornis, which inhabits rocky shores, where there is no danger of obstruction by mud, the corresponding hairs have a simple structure, as in Galathea squamifera.

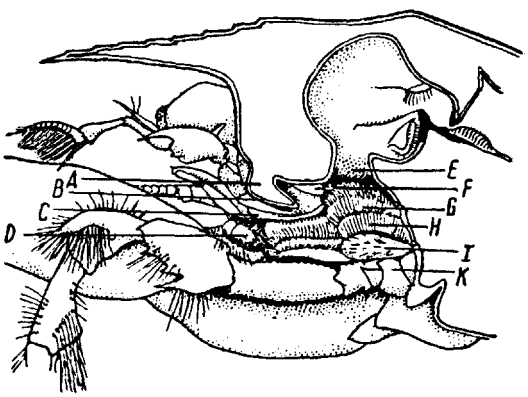

Figure 3. Sagittal section through anterior part of cephalothorax in Galathea dispersa showing the arrangement of the mouth parts

A – labrum (upper lip); B – mandibular palp; C – incisive process of the mandible; D – second maxilliped; E – esophagus; F – molar process of the mandible; G – maxillule; H – maxilla; I – first maxilliped; K – third maxilliped.

The hairs on the basal joints of the third maxillipeds, encountered in all the species mentioned above, protect the afferent orifice of the branchial cavity against incidental streams of water, which could stop or slow down the respiratory flow. In order to allow the respiratory flow to pass as close as possible to the branchiae, there is a crest on the internal surface of the branchiostegites in Galathea, Munida, and especially in Porcellana, resembling a similar crest described by Pearson in Cancer. Zimmermann detected a marked alternation of the respiratory function of the two sides

of the body in Porcellana; while resting, members of this genus always stretch one of the chelipeds more than the other; the afferent water flow is always observed only on the side of the body on which the cheliped is stretched. This becomes obvious by the movement of the flagellum of the second maxilliped, by the movement of the particles in suspension, and by the movement of the antennules which are turned in the direction of the respiratory flow. No respiratory flow is observed on the other side of the body. About half an hour later, the second side begins its respiratory activity, while that of the first side ceases. This alternation permits muscular relaxation of the scaphognath together with cleaning of the branchial cavity. This is carried out in forms such as Carcinus by a complete suspension of the respiratory activity of both sides for a certain time. These facts are also confirmed by the behavior of the animals when placed in a toxic solution, e. g., an extract of red algae. In this way, a more prolonged blocking of the respiratory flow is produced in Carcinus and related species, while in Porcellana, a more rapid and more irregular alternation of the respiratory activity of both sides is observed. In Galathea, in such conditions, a marked blocking of the respiratory activity was observed. The last joint of the fifth pereiopods, which serve for the cleaning of the branchiae and of the filtratory hairs, is covered with sickle-shaped hooks. On the internal side it bears pointed spinules, forming an excellent comb. In Porcellana, which lacks epipodites, this appendage also penetrates the branchial cavity; according to Zimmermann, this does not apply to Galathea. In that genus, as well as in Munida, the fifth pereiopods also serve for the cleaning of the superior surface of the carapace, which is covered with transverse furrows and crests.

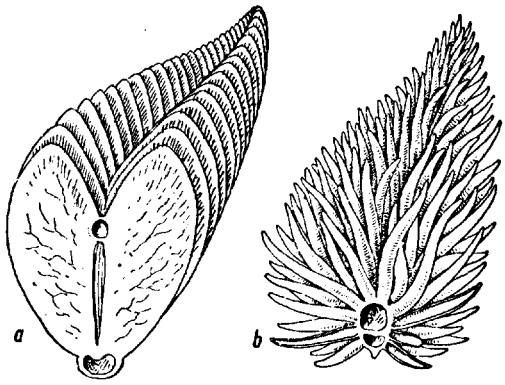

Figure 4. Two types of branchiae (schematic drawing)

a – phyllobranchia; b – trichobranchia

In amphibious and in almost terrestrial forms, there are – apart from branchiae – auxiliary formations which facilitate gas exchange. In Birgus latro (Linné), for instance, on the external wall of the branchial cavity are richly vascularized cuticular folds which carry venous blood toward the pericardium. Thus, one witnesses here a formation resembling a prototype

of pulmonary respiration, since gas exchange is carried out in an aerial medium. In the related Coenobita, the thin dorsal wall of the abdomen has a rich capillary network, which also undoubtedly effects gas exchange. It is, however, noteworthy that Birgus latro, for instance, has to reach water once a day in order to wet its branchiae. During the dry season Coenobita undergoes a kind of estivation, hiding under stones.

ABDOMEN. The form and position of the abdomen determine the above-mentioned division of the Anomura into two groups. Thus, the transition from the shrimplike habitus to the typical crab habitus can be followed. This gives the whole group its intermediate character. The abdomen is made up of seven segments, the telson also being considered as an independent segment. The abdomen of the Galatheidae most closely resembles the shrimp-like form: the epimera (pleurae) are still well developed, as are the uropods. The difference consists in the fact that the segments are dorsoventrally flattened and that the bend of the abdomen occurs at the fourth segment and not at the third, as in the Natantia. In Porcellanidae, which have entirely lost the natatory way of life, the abdomen is folded under the thorax, a typical crab habitus being thus obtained. However, the abdomen still has characters which are evidence of a relatively recent transition to the reptant life (Figure 5). On each segment epimera are still found, but they are relatively small and disposed horizontally, i. e., in the same plane as the tergal part of the segments; in addition, the sixth segment still bears uropods having the form of narrow, rather small plates, usually hidden under the telson. The telson in the Galatheidea has a peculiar form. It is flat, and made up of five triangular pieces, connected by means of a suture. Among the Thalassinidea, in species of the Axiidae, the abdominal epimera are still well developed, while in the Thalassinidae, their reduction becomes obvious. The abdomen is usually macruroid. In the Hippidea, as well as in the Porcellanidae, the abdomen is bent under the thorax; a peculiar variability is shown by the form of the abdomen in the superfamily of the Paguridea, as a result of the various ways of life of its members. The most primitive forms, e. g., the Pylochelidae, have shrimplike as well as hermit-crab-like features: the abdomen is elongated, straight and clearly segmented; the segments are relatively well calcified, but their epimera and uropods are reduced. The general habitus is similar to that of a hermit crab (see
11 Figure 42). The Pylochelidae may thus be considered as being hermit crabs "in statu nascendi". Their life is one of semiconcealment; the animal apparently often leaves its shelter and creeps freely on the bottom. The peculiar characters of the abdominal structure of the Paguridae are connected with their permanent life inside foreign, hollow bodies, and will be studied in the introduction dealing especially with this family; we shall, therefore, not deal here with this subject. If the Pylochelidae are hermit crabs "in statu nascendi", the Lithodidae are hermit crabs which have finally left their shelter but have not yet lost some of their specific features. The Hapalogastrinae (the more primitive Lithodidae) have a soft saclike but very shortened abdomen, slightly bent under the thorax; some Hapalogastrinae, e. g., Hapalogaster, have maintained the habit of semiconcealment, hiding under stones; consequently, the form of their body and appendages is flattened and the surface of the carapace is slightly calcified; the other genera of the Hapalogastrinae have a well-calcified carapace and appendages.

In the Lithodinae, various degrees of calcification of the abdomen are found, usually in the form of isolated plates. The first segment is small, narrow, and often hidden under the posterior edge of the carapace. For this reason the second segment is erroneously called the basal segment by some authors. The second segment is the largest; it is made up of an unpaired median plate and paired lateral and marginal plates; the plates may sometimes be fused, so that the whole segment appears as a unit. Beyond the second segment, the abdomen is strongly bent under the thorax and has a very flattened form. The three subsequent segments are composed of median plates, which are sometimes replaced by membranous areas covered with isolated calcified nodules; the first lateral plates are nearly always present; the marginal plates may be present or not, but if they occur in the female, they appear only on the right side. A peculiar modification of these three segments is found in Neolithodes: this whole part of the abdomen is membranous and covered with small, dense tuberculiform plates. The sixth segment is composed of a sole median plate. The telson is small and reduced. The form of the abdominal plates and the character of their arrangement are of taxonomic importance and are described as part of the generic diagnoses in the special section of this present work. Both the Hapalogastrinae and the Lithodinae have lost their uropods; the females still retain the asymmetry of the abdomen, while in the males the abdomen is absolutely symmetrical.

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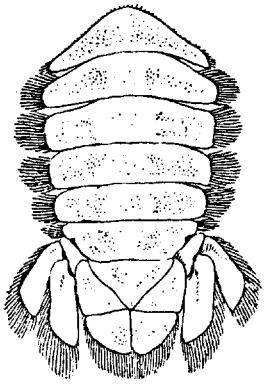

Figure 5. Abdomen of Pachycheles stevensii, male (extended)

ABDOMINAL APPENDAGES. Each pleopod is made up of two short basal joints (coxa and basis) and two branches (exopodite and endopodite) or a single branch (endopodite); the second type is found in the Galatheidea, Hippidea, and Lithodidae. The first or second pleopods are sometimes transformed into copulatory organs (Galatheidea, Pylochelidae). On the endopodite, an appendix interna — also called stylamblys — is found (Thalassinidea, Figure 6). In the table below, the disposal of the pleopods on the first five abdominal segments is shown; the left row in the column of each sex corresponds to the left side of the abdomen, the right row to the right side. The appendages of the sixth abdominal segment–the uropods–have been dealt with above.

FEEDING. The mouth parts have been described above. The stomach is composed of two parts: the cardia, whose function is to grind the food between the muscular walls of the stomach, and the pylorus, which has a filtering function; both parts are lined with the ectoderm. The median, endodermal part of the digestive tract is short; the canals of the hepatopancreas open on its ventral side, and the caeca open dorsally; in this part of the digestive tract food absorption is carried out. The ectodermal rectum is long, and opens at the anus on the ventral surface of the telson. In the following section, we shall deal especially with the character of the food and with the feeding mechanism itself.

A. Nicol's study (1932) deals with feeding in the Galatheidea. This author studied Galathea dispersa as a representative of the Galatheidea and

Porcellana longicornis as a typical representative of the Porcellanidae. The feeding of these two species differs somewhat owing to the structure of their mouth parts. The food of Galathea consists of two components: either large fragments of animal or vegetable origin, or organic remains and microorganisms from the bottom sediments. Detrital feeding is more frequent. In this type of feeding the principal part is played by the third maxillipeds, which are highly setaceous on their terminal joints and perform sweeping movements in the substrata. Both maxillipeds can act together as well as separately. The detritus accumulated between the hair tufts is cleaned away by the second maxillipeds, which always work alternately; the terminal hairs of the second maxillipeds transfer the food particles captured by the third maxillipeds to the internal mouth parts, which carry out selection of the food; the edible particles are directed toward the mouth, while the inedible particles are repelled and fall into the efferent respiratory water flow, which carries them away. When the food particles are big enough, they are captured first by the chelipeds, and then by the maxillipeds; if they are smaller, they
13 are captured directly by the maxillipeds. The hair tufts of the third maxillipeds catch the food particles, and the second maxillipeds turn and grind them. During this activity, the third maxillipeds press the food toward the mandibles, while the second maxillipeds thrust the food particle with their terminal hair tufts and are also able to remove it from the mandibles. The sufficiently ground particle is transferred by the third maxillipeds between the open mandibles. These, by closing, cut the food particle with their incisor processes, and the food then enters the esophagus and the stomach. In the stomach of Galathea, detritus, fine sand, small fragments of green and red algae, diatoms, fragments of small crustaceans, small gastropods and polychaetes, and sometimes also larger fragments of algae and muscles [sic] are found.

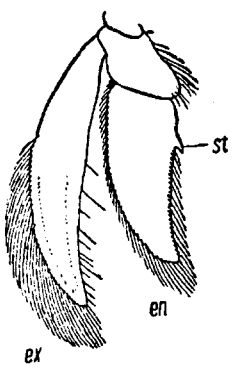

Figure 6. Second pair of pleopods of Callianassa californiensis bouvieri

ex – exopodite; en – endopodite; [st – stylamblys].

Porcellana feeds exclusively on detritus and microorganisms, and its method of capturing food differs considerably from that of Galathea. In fact, a filtration of the food particles is carried out through a catcher (formed by the thick, biseriated hairs of the third maxillipeds. The complex movements of the appendages around the body of the animal maintain the water flow which carries the suspended particles. The third maxilliped is extended, its hairs thus being straightened; in this way, a big spoon-shaped net is formed by these hairs and their lateral branches. Then the maxilliped bends, and in this way, the food particles are filtered from a considerable volume of water. As a rule, the third maxillipeds move alternately. The movement of the second maxillipeds is exactly synchronized with that of the third; at the moment the latter bend, the terminal hair tufts of the second maxillipeds penetrate between the bases of the hairs of the third maxillipeds; then the second maxillipeds begin to move toward the mouth, and the third maxillipeds stretch again. Thus, the combing of the third maxilliped is carried

out. This may occur several times in succession when the quantity of food is great. The second maxilliped then penetrates between the succeeding mouth parts, and it is pulled back when the turn of the maxilliped on the opposite side approaches. In this way, the second maxillipeds comb each other and are also cleaned by the succeeding mouth parts. The food particles thus
14 obtained penetrate farther into the mouth. Only once has an attempt at capturing a small mollusk been observed in Porcellana longicornis; this was, however, quickly rejected in the respiratory flow. The indications of Dalyell with regard to the feeding of Porcellana on lamellibranchiates, and those of Potts with regard to the occurrence of large algal fragments in its stomach are not confirmed by Nicol's observations.

Segments	I		II		III		IV		V	
Sex / Groups	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Thalassinidea . .	X	X	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Galatheidae . . .	+	+	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Porcellanidae . . .	—	—	—	—	+	+	—	—	—	—	+	+	—	-	+	+	—	—	+	+
Albuneidae	—	—	—	—	—	—	+	+	—	—	+	+	—	—	+	+	—	—	+	+
Pylochelidae . . .	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Lithodidae	—	—	+	+	—	—	+	—	—	—	+	—	—	—	+	—	—	—	+	—

The Callianassidae, which live in the holes they dig, are detritophagous animals; their feeding was described in the case of Upogebia pugettensis (Dana) by G. MacGinitie (1930). The animal creeps to the opening of the hole, and extends the first and second pereiopods, the hairs of which form a large filtration chamber (basket, according to this author); the energetic movements of the pleopods ensure an increased flow of water, which passes through the hairs of the pereiopods; these retain the suspended particles; the carapace is closely pressed to the superior wall of the hole so that the entire flow passes through the filtering mechanism. The spaces between the edges of the rostrum and between the carpi of the chelipeds are filled by the hairy ends of the third maxillipeds; this increases the retention of the food particles. At given intervals, the third maxillipeds sweep the collected food particles, which are subsequently carried by the second maxillipeds to the first maxillipeds and the maxillae, and the latter transfer them to the mouth. The large food particles (e. g., fragments of mollusks, in the experiments of MacGinitie) are retained for some time in the filtratory chamber, but afterward they are repelled by the flow regulated by the sudden movement of the uropods. B. A. Stevens (1928) found in the stomachs of Upogebia and Callianassa vegetal remains, a few diatoms and small grains of sand. According to Pesta, Upogebia feeds on small fragments of mollusks (Modiola, Venus), after opening their shells.

The Lithodidae studied most comprehensively with regard to feeding are the commercial stone crabs, especially Paralithodes camtschatica. In describing this species, Tilesius states that it feeds on cephalopods, other mollusks and starfish. According to Marukawa (1933), the food of P. camtschatica consists of Cynthia superba, Cucumaria japonica, mollusks, sea urchins, and dead fish; the author notes the predominance of Cucumaria japonica in the food. Navozov-Lavrov (1927) described the nutrition of the

Kamchatkan stone crab as being varied—in its stomach he found remains of algae, vertebrae and other small bones of fishes, and in most cases remains of starfish, sea urchins, and mollusks. According to this author, the calcareous parts of these animals are used by the crab for the forming of its carapace. As the principal food of this crab, J. Zachs [I. G. Zaks] (1936) lists small mollusks (Yoldia, Nucula, Venus), acorn barnacles, sea urchins, polychaetes, and Echiuroidea. The author also notes Fenyuk's findings that the food of the crab is extremely varied, not limited only to animals having calcareous formations, though when their stomach contents are analyzed, the remains of these animals are observed first, thus creating the erroneous impression that they comprise the predominant food. Analyses of the stomach contents of several hundred crabs carried out in the laboratories of the Pacific Institute of Fisheries and Oceanography do not confirm the conclusions of Marukawa with regard to the predominance of the sea cucumber in the food of the crab. It was found that young Paralithodes camtschatica feeds on polyps of Obelia longissima. In aquarium conditions, as observed by J. Zachs, A. Kazaev and D. Loginovich, the young fed on Lithorina, Acmea, eggs of sea urchins, Caprella, and larvae of mosquitoes which incidentally appeared in the aquarium. The Lithodidae are consequently omnivorous, though in comparison with the preceding groups, animal food definitely predominates.

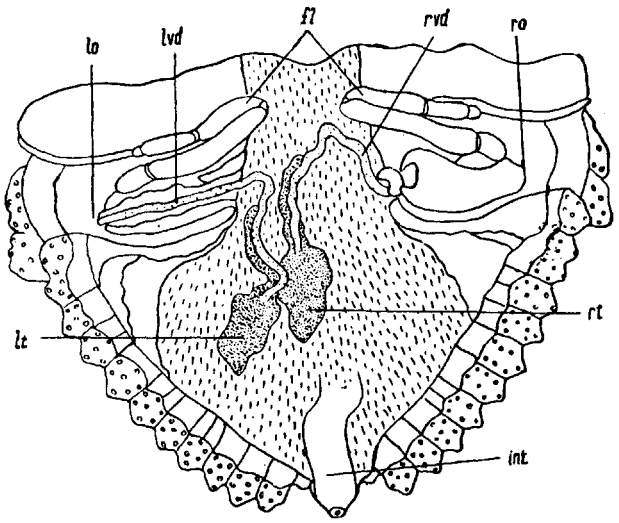

Figure 7. Lopholithodes mandtii, male, open, dorsal view

lo — external orifice of left vas deferens; lvd — left vas deferens; fl — fifth pair of legs; rvd — right vas deferens; ro — external orifice of right vas deferens; lt — left testis; rt — right testis; int — intestine (From Fasten, 1917).

REPRODUCTION. The testes are either in the cavity of the cephalothorax, partly extending into the abdominal cavity (in Upogebia, for instance, they reach as far as the telson), or they are found entirely in the abdominal cavity (Figure 7); they are tubular and are connected with one another by means of one or two transverse anastomoses. The vas deferens, commencing not far from the posterior end of the testes, appears either as a simple tube, or—as observed in Galatheidea and Paguridea—it forms a number of spirals
16 for a certain distance; the muscular terminal part of the vas deferens, the so-called ductus ejaculatorius opens on the coxal joints of the fifth pereiopods. The sperm have various forms and bear long protoplasmic flagella, as a rule three, which start from the neck of the sperm. The sperm are usually clustered in spermatophores of a great variety of forms.

The ovaries resemble simple tubes, and have a similar location to the testes; the two tubes are connected by means of anastomoses, with the exception of those in Thalassinidea. The oviducts, which commence at the sides of the ovaries, have the form of simple muscular tubes opening on the coxal joints of the third pereiopods; no receptaculum seminis is found.

The transformation of the pleopods of the male into copulatory appendages is observed only in the primitive Paguridea and in the Galatheidea. In the latter this modification usually affects the first two pairs of pleopods, which greatly resemble in structure those pleopods in the primitive Paguridea. Each appendage is made up of three joints (Figure 8): the first is, as a rule, rudimentary; the next corresponds to the basipodite, and the last to the endopodite; the last joint is foliaceous, with a spoon-shaped cavity, and is twisted in a more or less spiral form. On the second pair of pleopods, this joint bears a short outgrowth which corresponds to the exopodite of the pleopod. These two pairs of copulatory appendages are found in all males of the Galatheidae; the first pair of copulatory appendages is missing in most of the Porcellanidae.

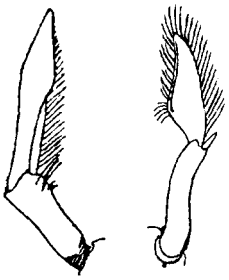

Figure 8. First and second pleopods of Munidopsis antoni male (From Milne-Edwards and Bouvier, 1894)

In all Decapoda the sexes are separate; hermaphroditism is found only in rare cases. In the genus Calocaris (Axiidae), for instance, a protandric hermaphroditism occurs. Testes develop in the second year of life; subsequently they degenerate and in the third to fourth year ovaries appear. The vasa deferentia, filled with spermatophores, are retained for a long time. These hermaphrodite forms, however, have normal gonochoristic behavior [i. e., forms with separate sexes], since owing to the protandrism, they have cross fertilization. In the vasa deferentia of Upogebia major, egg cells are sometimes found, which are subsequently obliterated.

In the reproductive process, the following four stages may be distinguished: 1) copula; 2) spawning, with simultaneous fertilization of the eggs; 3) the carrying of the egg cluster on the pleopods of the female during the embryonic stages of development, and 4) the hatching of the larvae and the further larval development.

Copula usually precedes the molt of the female. As already shown, the
17 Anomura, unlike the Brachyura, has no receptaculum seminis, and therefore the process of fertilization is carried out on the surface of the ventral side of the female. The process of copulation was observed in only a few species. In the Galatheidae (Brandes, 1897) the male, lying on its back and stretching its abdomen, holds the female over it, so that the abdominal surface of the female adjoins that of the male; with the spoon-shaped joints at the end of the pleopods, the male takes spermatophores out of its genital orifices; the spermatophores are subsequently transported by the fifth pereiopods toward the genital orifices and the pleopods of the female. The entire process lasts about one hour.

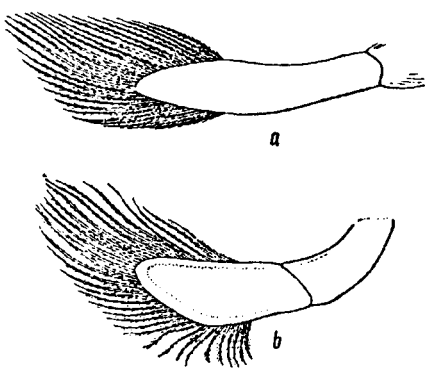

Figure 9. Pleopods of first abdominal segment of the female a – in Hapalogaster grebnitzkii; b – in Dermaturus mandtii

In the Lithodidae, copulation was observed by Marukawa, who describes it as follows (quoted from J. Zachs, 1936): "In the aquarium, the males, using their chelipeds, catch the females by the superior part of the meri of their chelipeds. During this 'handshake', the two sexes do not feed. The 'handshake' lasts from three to seven days. During this time the female molts, after which the male again catches the molted female. Consequently, the molt of the female coincides with copulation. The 'handshake', which coincides with molt, is, however, not a necessary condition for this, since females have also molted normally without the aid of the male. During spawning the female leans on the bottom with the posterior edge of the carapace. In this position, the eggs leave the ovaries through the genital orifices found on the ventral surface of the third coxopodites. Meanwhile, the male fertilizes the eggs, shedding the ribbon containing the spermatophores through the orifice found at the end of the basipodite. One male can fertilize several females at short intervals". According to the observations of J. Zachs and D. Loginovich, the 'handshake' may last even longer (up to two months in one of the cases observed in Paralithodes platypus), though, as a rule, the periods correspond to those indicated by Marukawa. According to the same authors, during the 'handshake', the male and the female lean on the dactyli of the periopods, the female does not 'sit', and the ribbon with the spermatophores is shed by the male from 1 to 4 days before the spawning. The male releases the female soon after the spawning, and the pair parts. Spawning sometimes continues after the parting. N. Navozov-Lavrov (1927) describes in a somewhat different manner the
18 copulation of Paralithodes camtschatica: "The male catches the female by both her chelipeds, and bends her under him, so that she is turned with her back downward, her sternum and abdomen adjoining those of the male. The male may move freely at this time, with the female clinging under him".

The number of eggs in the commercial Lithodidae reaches an average number of 200, 000. In the females with a carapace 10 to 12 cm wide (at this width both sexes reach sexual maturity), spawning occurs once a year. After fertilization, the eggs begin their embryonic development, which lasts for 10 to 11 months; subsequently, mass hatching occurs and the larvae continue their development in the water, up to the glaucothoë stage. The spawning dates and the duration of development depend upon temperature conditions. Thus, for instance, near Sakhalin, mass hatching of the larvae occurs in the first days of May, and not in April as happens farther south in the Sea of Japan. The farther north one goes, the later the dates of spawning. A similar phenomenon is also observed in the Mediterranean and North Sea species. In the first, for instance, all processes develop at an earlier date, while in the second, they are delayed. Spawning usually occurs in shallower waters, and a spawning migration toward the shores may therefore be observed. It is interesting to note that the terrestrial forms, e. g., the Coenobitidae, and even some dulcicole forms, such as Callianassa turnerana, of the fresh waters of the Cameroons, migrate during the spawning period to the sea.

In the development of the Decapoda, the following stages, briefly described below, may be distinguished (according to Balss, 1927). The development, however, never passes through all these stages; some of them are usually passed over.

1. NAUPLIUS. Body not segmented; no carapace; simple nauplial eye. Three pairs of appendages: uniramous antennules, biramous antennae, and biramous mandibles without masticatory processes; all appendages bear swimming hairs and serve for swimming only. At the level of the closed anus, a furcal seta is found on both sides.

2. METANAUPLIUS. Behind the nauplial appendages (the mandibles already have coxal teeth) appear the primordia of the succeeding three or four appendages (two pairs of maxillae and one or two pairs of maxillipeds). A number of segments may be distinguished on the body. The end of the body has furcal outgrowths.

3. PROTOZOËA. Body divided into cephalothorax (cephalon + first thoracic segment) and thorax+abdomen (second to fifth thoracic segments + abdomen). Compound eyes found under the carapace, which is just forming. Antennae still serve for swimming but mandibles are no longer biramous. Maxillae biramous; more or less pediform. Pereiopods still missing. Abdomen segmented, without pleopods; telson bifurcated.

19 4) ZOËA (typical in Brachyura). Primordia of pereiopods appear, subsequently developing from the rostral end toward the furcal end of the body. In Caridea, three maxillipeds are found, and generally two first pairs of pereiopods, which serve for swimming (Anomura and Brachyura). Thorax initially still unsegmented, eyes developing later than eyestalks. Abdomen segmented, but in first stages, sixth abdominal segment still fused with seventh.

5. MYSIS STAGE. Segmentation of abdomen completed. All pereiopods are present, most of them having exopodites and endopodites; together with the antennae, they now serve for swimming.

5a. METAZOËA. If-as happens in most Anomura and Brachyura (with the exception of Dromia)-the exopodites of the pereiopods do not appear, a metazoëa stage is distinguished.

6. DECAPODA STAGE. Larval appendages of cephalothorax and abdomen disappear, exopodites of the pereiopods disappear; pleopods are now used for swimming. In Paguridea, this stage is called glaucothoë, in Brachyura—megalopa.

We shall now deal along schematic lines with the development of various groups.

In the Hippidea, the larvae resemble those of the Galatheidea and Paguridea—the carapace has posterolateral marginal spines and the pereiopods have no exopodites; they have, as a specific character, a spatulate telson, with many spinules on its posterior margin.

In the various families of the Thalassinidea, the development is characterized as follows. In the Axiidae, exopodites appear on all pereiopods, but on the fifth pair they remain rudimentary. The rostrum is long and broad, with serrated edges. The pleopods are missing on the first segment. The dorsal surface of the abdominal segments has no carina. The telson bears many marginal hairs.

Callianassinae: rostrum as in Axiidae; last pereiopods usually have no exopodites. First pleopods, and usually second and fifth, are missing. Long spine on second abdominal segment; succeeding segments have a dorsal crest. Telson bears 17 spines (8+1+8).

Upogebiinae: small rostrum, not flattened in the horizontal plane. Exopodites only on the first three pereiopods. Abdominal segments without dorsal or lateral spines. Pleopods missing on first abdominal segment. Webb (1921) describes the differential traits of the four larval stages in Upogebia as follows: 1) caudal plate simple, with twelve spines; uropods missing; 2) caudal plate simple, with fifteen spines; uropods missing; 3) telson and outer uropods well developed and bear spines; inner uropods present, but small and without spines; 4) both pairs of uropods well developed, and bear spines.

20 The larvae of the Galatheidea and Paguridea are very similar; both have a very long pointed rostrum; in the Galatheidea the lateral edge of the carapace ends in a long spine on each side.

In the Galatheidea this spine bears a row of small spines on one or both of its edges. The four larval stages are normal: in the first stage, exopodites are present only on the first two maxillipeds; in the second stage, exopodites are present also on the third maxillipeds (unlike the Brachyura). Uropods appear only in the third stage. The pereiopods no longer have exopodites, and therefore there is a metazoëa stage instead of a mysis stage. The metazoëa has rudimentary pleopods on segments two to four or two to five. According to Webb, the differential characters of the four larval stages are the following: 1) caudal plate simple, with twelve spines; uropods missing; 2) caudal plate simple, with fourteen spines; uropods missing. The other two stages are as in Upogebiinae.

The Porcellanidae have a rostrum twice as long as the body, and the lateral edge of the carapace has a long terminal spine on each side; the spines on the posterior edge of the carapace, however, are missing. In the last larval stage as well as in the first, only two maxillipeds have exopodites; uropods are missing, but three or four pairs of pereiopods are already present.

In the Lithodidae, the larval development was studied in the commercial stone crabs; their development is the same type as in Paguridea. The larva

hatches when it reaches the protozoëa stage. The rostrum is bent ventrally; the telson and the antennae bear long pinnate hairs. The duration of this stage is very short, and it is followed by the zoëa stage. The zoëa has a wide cephalothorax, bearing an erect rostral spine; the posterolateral edges of the carapace end in long spines; the posterior edge of the carapace bears a small prominence; the surface of the carapace is covered with small spines; there are three pairs of maxillipeds; the abdomen is narrow and ends in a broad telson. The larva undergoes four molts during the zoëa stage; subsequently it becomes a glaucothoë larva. After the following molt, a young individual appears, already entirely resembling an adult animal.

THE PHYLOGENY OF THE ANOMURA. The group from which all Anomura originated was that of the Astacura, and the evolution of the Anomura took four directions (see scheme below). The Hippidea form a specific and individualized group, and most closely resemble the Galatheidea (epimera of abdominal segments still well developed; branchiae of the phyllobranchia type; pleopods of the female simple); the transition to the burrowing life (in sand) has left its mark on all the members of this group. Another evolutional trend is represented by the Galatheidea, which lead a free, vagile life; of them the closest to the Astacura are the Galatheidae (abdomen has well-developed epimera; carapace has well-developed rostrum). Passing to a reptant life,
21 the Galatheidae led finally to the Porcellanidae, which achieved a crablike habitus, but retained the "anomuroid" characters (carapace not yet fused with epistome; fifth pereiopods reduced; uropods still present). The third direction is that of the Thalassinidea, which retain more primitive characters than the preceding two groups (the branchiae are of the trichobranchiate type); the members of this group lead a burrowing existence and dig holes in mud and sand. The Paguridea originate from the same evolutional branch as the Thalassinidea, and passed, from the very beginning, to a life of semiconcealment; the family of the Pylochelidae still possesses a number of characters relating it to the Thalassinidea: the branchiae are trichobranchiate, and the abdomen is still segmented and has reduced pleurae; the uropods, however, are already adapted for the fixation of the body in heterogenous hollow bodies. The subsequent transition to a permanent life in such hollow bodies led to the typical Paguridae. These in turn, having finally left their shelters, again led a free life, thus bringing about the transition to the Lithodidae, which in their highest forms achieved a crablike habitus analogous to that of the Porcellanidae. We shall deal further with the phylogeny of the two families Paguridae and Lithodidae, which are the best represented in U. S. S. R. fauna.

H. Milne-Edwards (1832), A. Milne-Edwards and Lucas (1841), and Brandt (1849, 1850, 1851) have already shown the descent of Lithodes from Pagurus. In his studies, Boas (1880, 1880a) devotes special attention to this problem. Pointing out the error of de Haan, who relates Lithodes to the Galatheidea on the one hand and to Birgus on the other, he concludes–mainly on the basis of the study of the appendages and the abdomen–that the genus Lithodes* is closely related to Pagurus (or Eupagurus) or a form close to that genus. In both these genera, the right cheliped is larger than the left; the third maxillipeds have a similar structure, and above all they have on

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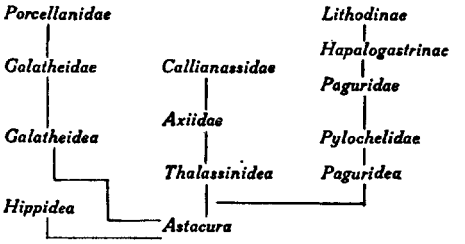
* Boas also included the genus Paralithodes in the genus Lithodes.



the ischium, under the denticulated crest, a spine which is absent in all the other Decapoda. The number of branchiae is the same in both. The females have an appendage on the left side of each of the second to fifth abdominal segments. The sternal part of the first abdominal segment is closely articulated with the last thoracic segment; the sternal parts of the subsequent segments are soft. The tergite of the first abdominal segment is
22 undivided, as in Pagurus; the tergite of the second segment is modified, as instead of the membranous space between the lateral plates, an odd plate is found; the tergites of the subsequent segments are separated in the middle by a membranous space, as in Pagurus, but unlike the tergites of Pagurus, calcareous nodules are found on these spaces. Apart from this, marginal plates are found, having no analogy in Pagurus. All the plates, which in Pagurus are hardly chitinized, are well calcified in Lithodes. The abdomen is asymmetrical, as in Pagurus, especially in the female, and the left side is always more developed. According to Boas, the genus Hapalogaster is intermediate between Pagurus and Lithodes; pleopods are missing in the male, as in Lithodes; the females have some appendages on the second to fifth abdominal segments, but not on the first one; therefore, the paired pleopods on the first abdominal segment in the female of Lithodes are considered by Boas as an atavistic phenomenon. We must note here Boas' error: the females of all studied species of Hapalogaster, as well as of Dermaturus and Oedignathus, have paired appendages on the first abdominal segment, even if very reduced (Figure 9, Russian page 17); consequently, the Hapalogastrinae form no exception in this connection and the presence of the paired pleopods in the Lithodidae should not be attributed to atavism. The tergites of the second to fifth abdominal segments in Hapalogaster are separated by membranous median spaces. The general conclusion of Boas is as follows: Lithodes is a Pagurus adapted to a free life, in the same way as Birgus is a modified Coenobita which lost its shell. Some characters of Lithodes, such as the direction of the articular axis of the last joints of the chelipeds and the presence of paired pleopods on the first abdominal segment, indicate that the ancestral form of Lithodes was possibly nearer to Paguristes than to Pagurus; by other characters, however, Paguristes is less closely related to Lithodes than is Pagurus.

According to Boas, Pagurus differs from the other hermit crabs by the following characters: 1) the sternal part of the first abdominal segment is nearly fused with the last thoracic segment, so that sometimes it seems that the last pereiopods start from the first abdominal segment; in all other hermit crabs an articular membrane is found between the last thoracic

segment and the first abdominal segment; 2) the tergal plates of the second to fifth abdominal segments are each divided into two plates; 3) on the ischium of the third maxilliped a spine is found under the denticulated crest. In all these characters, Lithodes resembles Pagurus. Boas (1924) indicates the forms having the three above-mentioned characters relating
23 them to Pagurus, as well as paired pleopods on the first abdominal segment: first and foremost is the genus Nematopagurus, which Boas compares in detail with Lithodes, as well as with the genus Pylopagurus. From these genera, or from related forms, Boas deduces the genus Lithodes. We cannot mention all the details of the comparison between Pagurus, Nematopagurus, and Lithodes, as Boas has done. His comparison deals with: the armature of the dactyli of the chelipeds; the relative length of the second and third pereiopods; the form of the subchela on the fifth pereiopods; the form of the mouth parts (with the striking gradual reduction of the appendix on the palp of the first maxillae, in the direction Pagurus–Nematopagurus–Lithodes), and the reduction of the hairs on the same palp in a contrary evolutional direction; we shall dwell only on the comparison of the abdomen; first, however, we wish to stress that Nematopagurus differs from Pagurus and Lithodes by the presence of paired tubular gonopods in the male, resembling the unusual gonopod of Spiropagurus, the left appendage being shorter than the right.

The abdomen of the typical hermit crab is characterized by the following features: the sternal plate of the first segment is compact and undivided; on the second to fifth segments the sternal plates are partly retained only marginally, being separated by means of membranous spaces; on the second segment these sternal plates are found on both sides, on the third to fifth segments—only on the left side; the pleopods are articulated with these rudiments of sternal plates; the sternal plates are connected with the tergal plates either directly or by a membranous space; at the boundary between the two plates, hairs may be found. The division into two parts is also characteristic of the tergal plates; only on the first and second segments do these two plates adhere closely. The following are common characters of the abdomen in Pagurus and Nematopagurus: the fusion of the ventral surface of the first abdominal with the last thoracic segment, the division of the tergal plates of the second to fifth segments into plates separated by membranous spaces (a fact observed by Boas also in a species of Paguristes). These, however, sometimes have narrow transverse connective strips (e. g., on the third segment of Pagurus bernhardus).

Figure 10 shows the straightened abdomens of females of Nematopagurus and Lithodes maja, dissected along the median line of the ventral surface; the membranous spaces are not illustrated. The first segment is identical in both genera. The second segment is very different: in Paralithodes the median plate corresponds to the membranous median part of the second segment of Pagurus (or Nematopagurus); the lateral plates correspond to the tergal plates of Pagurus; the marginal plates are neoformations, appearing at the level of the membranous spaces which in Pagurus separate the tergal plates from the sternal ones. In the case of Lithodes, all five plates are fused.
24 The three segments are similar in both genera; in Lithodes, however, the plates are thickened and nearer to each other, especially on the left side; the marginal plates and the nodules of the central parts are neoformations; the ventral parts are identical in both genera. The sixth and

seventh segments are also absolutely identical. The abdomen of Pylopagurus is almost identical with that of Nematopagurus; in Pylopagurus, however, the right halves of the tergal plates of the third to fifth segments are hardly visible.

In conclusion Boas states: "Lithodes has evolved from a hermit crab, which was probably very closely related to the contemporary genera Nematopagurus and Pylopagurus (possibly even belonging to one of these genera). Having left the shell, Lithodes retained very obvious traits of its descent. Though its abdomen is no longer protected by a shell, it does develop to a certain degree as if it were in a shell. The following traits are inherited from the hermit crab: the asymmetry of the abdominal segments and of the abdomen itself, the soft median spaces of the tergal plates of the third to fifth segments, and the softness of the whole ventral surface of the abdomen." The uropods (with their function of fixing the body in the shell) disappeared as useless, the fourth pereiopods again became long and ambulatory, while the fifth pereiopods became organs for cleaning the branchiae. The carapace became entirely hard.

E. L. Bouvier (1895, 1896), who has in general the same conception with regard to the phylogeny of the Lithodidae, differs in some details from Boas' point of view. On the basis of the example of Hapalogaster cavicauda, he shows the close relationship between the stone crabs and the hermit crabs: Hapalogaster has a small triangular rostrum with no subterminal prominence; the carapace is heart-shaped; the anterior part of the subbranchial areas is narrow; the cardiac area has a paguroid form; there are membranous lateral lines under the linea anomurica, the mouth parts are paguroid, and the scaphocerite is flat and smooth. As to the abdomen, Bouvier only partially agrees with Boas: the dorsal plate of the first abdominal segment is undivided in both genera; the fourth and fifth segments in both genera are composed of paired plates; the sixth and seventh segments are made up of unpaired plates; the rest of the dorsal surface is soft, with the exception of a small plate on the third segment of Hapalogaster cavicauda, corresponding to the left tergal plate of Pagurus. According to Bouvier, however, the structure of the second segment is different from that of Pagurus: each one of the tergal plates of Hapalogaster is made up of two plates, one lateral and one marginal, clearly delimited by a suture. On the membranous portion between them, calcified nodules are found; in Pagurus these plates are simple and are divided by a continuous membranous space. Bouvier considers that the tergal plates of Hapalogaster are formed by the fusion of the nodules, a fact which seems to be confirmed–in his opinion–by the presence of small tubercles on the margins of the plates. These tubercules seem to be nodules which are not
26 yet completely fused. Bouvier states: "Thus, we have no doubt with regard to the secondary origin of the tergal plates of the second segment; the principal feature of the abdomen of H. cavicauda may thus be described as follows: all the tergal plates of Pagurus reappeared in this species, with the exception of the plates of the third segment, which partly disappeared, and of the plates of the second segment, which disappeared completely; these last, however, are replaced by calcareous nodules, which gradually fuse to form two new tergal plates on each side." The justification of this conclusion is seen by Bouvier in the structure of the abdomen of Phyllolithodes papillosa, in which the fusion of the nodules started from the periphery, thus forming plates with central membranous spaces, covered with nodules not yet fused. The

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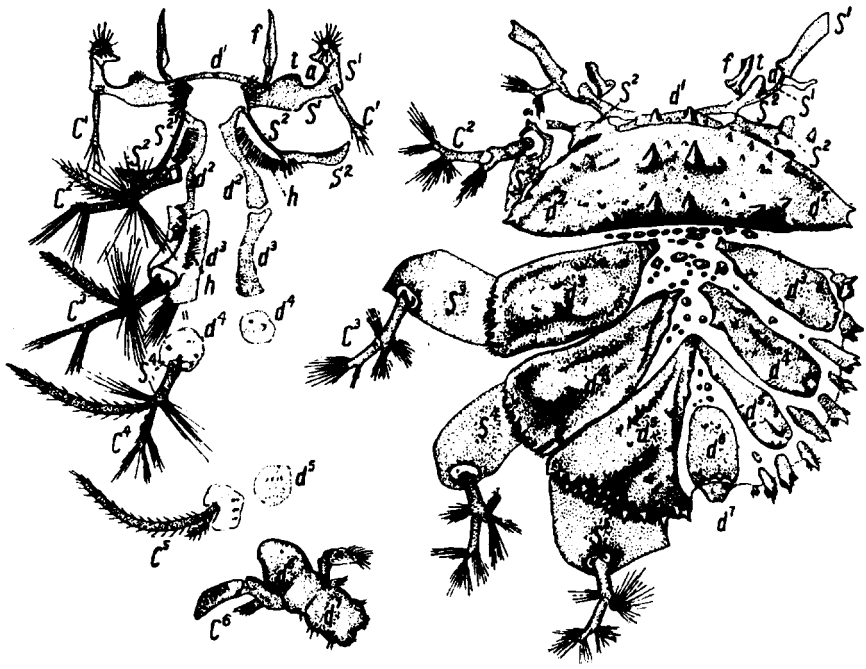

Figure 10. Abdomen of Nematopagurus, female (left), and Lithodes maja, female (right); the membranous parts are removed.

a – acetabulum of last thoracic leg; c^{1-6} – pleopods; d^{1-7} – tergal plates of the abdominal segments; f – outgrowth of first tergal plate; h – brush corresponding to the brush on the edges of the epimera in Reptantia; S^1, S^2, etc – sternal plates; S – edge of foremost sternal plate; S^2 – superior part of second sternal plate (From Boas, 1924).

fusion progresses intensely also in the central membranous spaces of the third to fifth segments, where the fused nodules form transverse plates. In Neolithodes, it is obvious that the tergal plates develop at the expense of the calcareous nodules. By their position these tergal plates resemble the corresponding plates of Hapalogaster and of the Paguridae; however, they are not at all homologous to these, but are—like the tergal plates of the second segment of the Hapalogastrinae and of Phyllolithodes papillosa—neoformations, characteristic of this lithodid. Bouvier considers that Neolithodes forms the link between the Hapalogastrinae and the Lithodinae, while Phyllolithodes forms an independent lateral branch in the phylogeny of the Lithodidae. In Paralithodes, the development of the secondary plates has progressed even more than in Neolithodes. Bouvier neglects to explain the presence of paired pleopods on the first abdominal segment of the Lithodinae females by atavism, tracing back the Lithodinae through Neolithodes to Oedignathus and Dermaturus; it is true that in the last genus he merely assumed the presence of paired appendages. As we see, Bouvier's hypothesis was confirmed, but we may relate Dermaturus–the most "lithodic"

[stone-crab-like] form of the Hapalogastrinae—to the hermit crabs, through the more primitive Hapalogaster, since all Hapalogastrinae have paired pleopods on the first abdominal segment in the female. In the genus Acantholithus the median nodules of segments three to five are fused to form plates, between which free nodules are still found. In Lopholithodes the fusion is even more marked, since the intermediate median nodules are fused. In addition, the fusion of the marginal plates of the third segment with the lateral ones may be observed not only on the left side but also on the right. In Paralomis the marginal plates of the third segment are fused with the lateral ones on both sides, and the marginal plates of the two subsequent segments are also often fused with each other. In Rhinolithodes all marginal plates are fused with the corresponding lateral plates; the same thing may be observed in Cryptolithodes. In these two last genera the abdomen of the female is but slightly asymmetrical, a fact which shows the trend of the abdomen of the Lithodinae to become secondarily symmetrical, though the pleopods of segments two to five in the female are found only on the left side, still making
27 obvious the "paguroid" character of the abdomen of the Lithodinae. Finally, Bouvier draws the conclusion that "although the abdominal plates of the second to fifth segments in the Lithodidae have a position analogous to that of the plates of the Paguridae, they are not in fact homologous to them. In order to become typical Lithodidae, the Paguridae at first had to lose all the abdominal plates of the second to fifth segments, then, on the large membranous surfaces of the abdomen, calcareous nodules had to appear; by fusing gradually, these formed tergal plates." Consequently we see that this conclusion is completely opposed to that of Boas. But the connection between the pleopod-bearing ventral plates with the corresponding dorsal plates confirms the homology in this respect between Paguridae and Lithodidae, and therefore Boas's conception should probably be considered more correct.

We could deal only briefly with Bouvier's conception of the evolution of the Lithodidae on the basis of the development of the abdomen, and we have also omitted to refer to the discussion by him of the same problem on the basis of the development of the rostrum and of the scaphocerites. We also recall the fact that, according to Bouvier, the ancestral form of the Lithodidae passed through the phases of Tomopagurus, Pylopagurus and Pagurus. Finally, we cite a quotation from Bouvier (1895:197), summing up his conception of the interrelation between the various lithodid genera: "Leaving their shells, the Paguridae, which were the ancestral forms of the Lithodidae, probably hid under stones, and to some degree achieved a likeness to the Porcellanidae*. In Hapalogaster this adaptation was retained, but it formed only a transition toward Dermaturus, which left the shelters and began to move freely as soon as its carapace was sufficiently calcified and developed enough spines. Here is the starting point for the whole great tribe of the Ostracogastrica (i. e., the subfamily of the Lithodinae, V. M.). Hapalogaster and Dermaturus, characterized by the lack of the secondary tergal plates on the third to fifth segments, formed the tribe Hapalogastrica (i. e., the subfamily Hapalogastrinae, V. M.). Phyllolithodes probably retained the way of life of Dermaturus. At any rate, it proceeds from this last genus and differs from all other Ostracogastrica by an incomplete and very peculiar fusion of the calcareous plates of the abdomen. Phyllolithodes forms a separate section

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* In his subsequent study (1896) Bouvier divides the Hapalogastrinae into porcellanidlike Hapalogastrica and crablike Hapalogastrica. The first still lead a life of semiconcealment (species of Hapalogaster), while the others move freely on the bottom (Dermaturus and Oedignathus).

within the tribe Ostracogastrica, having aberrant characters*. All the normal representatives of the Lithodinae originate from forms analogous to Dermaturus hispidus by a more intense calcification of the carapace and a more advanced fusion of the nodules and of the hard plates of the abdomen.
28 Neolithodes is the most closely related to Dermaturus hispidus, in which the fusion of the calcareous nodules begins, while Paralithodes in its turn is related to Neolithodes; through Paralithodes camtschatica this genus is the starting point for the Lithodes branch, while all the other genera descend from Paralithodes brevipes. Acantholithus descends from Paralithodes brevipes and still bears the numerous spines of Lithodes and Paralithodes; by the reduction of the spines and by the fusion of some marginal plates, this genus leads to Paralomis, which in turn, by a similar process, leads to Rhinolithodes. Other forms are related to Paralithodes brevipes; they are characterized by a progressive reduction of the carapace, by the fusion of the abdominal plates, and especially by a widening of the carapace, which protects the bases of the pereiopods. In Echidnocerus (i. e., Lopholithodes, V. M.) these adaptative modifications are still slightly marked but they are extremely well developed in Cryptolithodes, the legs being completely hidden under the carapace; this genus represents the end of the evolutional line of the Lithodidae."

ZOOGEOGRAPHICAL OUTLINE

The Anomuran fauna can be divided into two large groups according to their distribution: the fauna of the Boreal zone and the fauna of the Tropical zone. To the first group belong the Lithodidae (the geographical outline of the Paguridae is given separately), and to the second group belong all the remaining groups studied in this volume. Both groups have forms which penetrate the other zones; since the greater part of the seas of the Soviet Union belong to the Boreal zone, the Lithodidae form here an autochthonous fauna, while all the other Anomura represent immigrants from the tropical zone whose northern limit of distribution is in the neighboring Soviet waters. No species of either group is found in the Arctic zone.

In the Black Sea are encountered only two species of Callianassidae (Upogebia littoralis and Callianassa pontica) and two species of the Porcellanidae (Porcellana longicornis and P. longimana), which are identical to the Mediterranean forms of these species, and no doubt emigrated from the Mediterranean Sea.

The eastern limit of distribution of Munida bamffica, Galathea strigosa (rare), and Lithodes maja is in the Barents Sea, along the West Murman coast; Porcellana longicornis was found incidentally. The first two species are encountered quite rarely, penetrating into the Barents Sea with the warm outflows of the Gulf Stream. The scarcity of the lithodid fauna in the Barents Sea, which corresponds to the ecological requirements of this group, results from the great distance separating this sea from the distribution center of the Lithodidae, with which we shall deal briefly below.
29 Thus, in Soviet European waters only eleven species of Anomura are found (the four species of hermit crabs included), which represent about

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* Such an aberrant form within the Hapalogastrinae is the genus Placetron (Bouvier, 1896).

29 % of the total number of the species of this group in the Soviet seas; the remaining 71 % (i. e., 41 species) represent the fauna of the Far Eastern seas (hermit crabs included). About 42 % of the species (38 species) referred to in this volume belong to the fauna of the adjacent seas and especially to that of the northern shores of Japan and the western shores of North America. In the Table below are shown the quantitative ratios between the species of the families in Soviet European waters and Soviet Far Eastern waters.

European waters	
Thalassinidea	2 (18%)
Galatheidae	2 (18%)
Porcellanidae	2 (18%)
Paguridae	4 (37%)
Lithodidae	1 (9%)

Far Eastern waters	
Axiidae	1 (2%)
Thalassinidea	6 (15%)
Galatheidae	1 (2%)
Porcellanidae	1 (2%)
Albuneidae	1 (2%)
Paguridae	21 (52%)
Lithodidae	10 (25%)

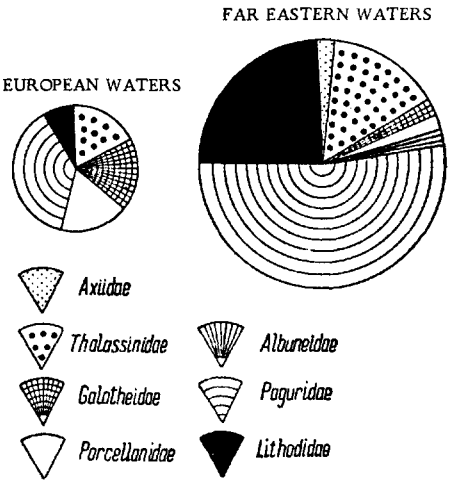

Figure 11. Quantitative ratio between number of species belonging to the various families in the European and Far Eastern waters

The same ratios are shown in Figure 11 in the form of diagrams, the surface of the circles being proportional to the number of species, and the sectors showing the ratio between the families. As seen in the diagrams and as stated above, the principal nucleus of the anomuran fauna of the Far Eastern seas—which is almost four times that of the fauna of the European Soviet waters—is comprised of Paguridea. Among these, the hermit crabs are twice as numerous as the stone crabs, while these are equal in number to all the species of the other families together. It is also obvious from the diagrams that the anomuran fauna of the European Soviet waters has no autochthonous nucleus but is comprised of an almost equal number of strange elements. The predominance of the Paguridae-this specifically tropical family-in the Far Eastern waters is due to the genus Pagurus, which has a predominantly boreal distribution. In the following discussion on the Anomura of the Far Eastern seas, we shall not take into account the Paguridae.

30 Among the Anomura of the Far Eastern seas, four groups may be distinguished:

1). Species found in all three Far Eastern Soviet seas: Hapalogaster grebnitzkii, Dermaturus mandtii, Paralithodes camtschatica, P. platypus and P. brevipes.

2). Species common to the Sea of Okhotsk and the Sea of Japan: only one species belongs here, i. e., Sculptolithodes derjugini.

3). Species common to the Sea of Okhotsk and the Bering Sea: Munidopsis beringana and Lithodes aequispina.

4). The group of identical or very closely related species, found on the two opposite shores of the Pacific and having a discontinuous range (amphipacific species, according to the name proposed by A. Andriyashev):

Asiatic shores	American shores
Callianassa californiensis bouvieri	Callianassa californiensis
Callianassa gigas eoa	Callianassa gigas
Oedignathus inermis	
Cryptolithodes expansus	Cryptolithodes typicus

Let us now proceed to an analysis of the fauna of each of the seas.

SEA OF JAPAN. The 25 species known from this sea may be divided into the following three groups:

1). Species common to the Soviet and Japanese coasts: Upogebia major, Callianassa harmandi, C. japonica, C. californiensis bouvieri, Pachycheles stevensi, Blepharipoda japonica, Hapalogaster dentata, Oedignathus inermis, Paralithodes camtschatica and P. brevipes.

2). Species found only on the Soviet shores of the Sea of Japan: Axiopsis princeps, Upogebia issaeffi, Callianassa gigas eoa, Hapalogaster grebnitzkii, Dermaturus mandtii, Paralithodes platypus, Sculptolithodes derjugini (the last species, however, is found on the shores of Rishiri Island, but is not found farther south on the Japanese coasts).

3). Species found only on the Japanese coasts: Upogebia yokoyai, Ctenocheles balassi, Galathea acanthomera, G. integra, G. pubescens, Munida japonica, Cervimunida princeps, Mixtopagurus jeffreysii, and Cryptolithodes expansus.

Species endemic to the Sea of Japan are: Axiopsis princeps, Upogebia issaeffi, Callianassa gigas eoa, and Ctenocheles balassi. Z. I. Kobyakova (Trudy Leningradskogo Obshchestva Estestvoznaniya [Proceedings of the Leningrad Society of Natural Sciences], LXV, 2, 1936) found a new subspecies Axiopsis spinulicauda amurensis in the Amur Bay, reported under the generic name Axius. As the description of this subspecies has not yet been published, it is not quoted in the systematic part of the present work. The species common on the Japanese shores, or located only on the Japanese shores, are fairly precisely located forms, which do not advance further south than
31 Honshu Island. Only Callianassa harmandi, C. japonica and C. californiensis bouvieri are found also in the Yellow Sea, while Galathea acanthomera extends to the Bonin Islands. The complete absence of species belonging to the Galatheidae on the Soviet shores of the Sea of Japan is striking.

SEA OF OKHOTSK. The anomuran fauna of the Sea of Okhotsk comprises the following nine species: Calastacus quinqueseriatus* Munidopsis beringana, Hapalogaster grebnitzkii, Dermaturus mandtii, Paralithodes camtschatica,

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* Reported by Z. Kobyakova (1936) for the Sea of Okhotsk, without precise indication of locality.

P. platypus, P. brevipes, Lithodes aequispina and Sculptolithodes derjugini. In this way, more than 50% of the Anomura of the Sea of Okhotsk is made up of species common to all three Far Eastern seas. Most of the species enter the Sea of Okhotsk from the Northern Pacific. Sculptolithodes derjugini is probably a local form (Shantar Sea) which reaches only the northernmost part of the Sea of Japan. None of the species common to the Sea of Japan, however, are found in the Sea of Okhotsk.

EASTERN SHORES OF KAMCHATKA. All species quoted for the Sea of Okhotsk, with the exception of Sculptolithodes derjugini, may be considered as belonging also to the fauna of the eastern shores of Kamchatka. It is true that Calastacus quinqueseriatus, Munidopsis beringana and Lithodes aequispina have not yet been reported from these shores, but considering the great depths near this coast, the presence of these species here is highly probable. We must also include here Paralomis multispina, a deep-sea form of the northern Pacific.

BERING SEA. The Anomura of the Bering Sea are represented by thirteen species, which may be divided into two groups:

1). Species found in the western as well as in the eastern part of this sea: Hapalogaster grebnitzkii, Dermaturus mandtii, Paralithodes camtschatica, P. platypus, and P. brevipes.

2). Species found only in the eastern part of the sea: Munidopsis beringana, Hapalogaster mertensii, Oedignathus inermis, Placetron wosnessenskii, Lithodes aequispina, L. couesi, Paralomis verrilli and Cryptolithodes typicus.

It is very possible that Munidopsis beringana and Lithodes aequispina will be included in the first group, when the depths of the Bering Sea are better explored. There is no species found only in the western part of the Bering Sea; it is true that Paralithodes platypus seems to belong to this group of species, since it is not reported in American works as being present in the eastern part of the Bering Sea. However, Richter's specimens from the Pribilof Islands belong to this species, which we consequently include in the first group.

32 If we turn our attention to the distribution of the species found in the Bering Sea in a latitudinal direction, it will appear obvious that most of them are located in the southern part of the sea, chiefly in the area of the Aleutian Islands, and that they rapidly disappear in a northerly direction. Thus, for instance, Hapalogaster mertensii, Oedignathus inermis, Placetron wosnessenskii, Paralithodes brevipes, Lithodes aequispina, L. couesi and Cryptolithodes typicus are found only in the area of the Aleutian Islands, i. e., about 54 % of the total number of species. In the area of Cape Olyutorsk on the Soviet coast, and of the Pribilof Islands on the American coast, the following species occur: Munidopsis beringana, Dermaturus mandtii, Paralithodes camtschatica (on the American coast, up to Norton Gulf), Lithodes aequispina and Paralomis verrilli. Only two species, namely, Hapalogaster grebnitzkii and Paralithodes platypus, reach the Bering Strait.

CHUCKCHEE SEA. With the exception of the Paguridae, no group of Anomura is found in this sea.

As already shown above, the principal nucleus of the anomuran fauna in the Far Eastern seas is made up of Paguridea. Since the Paguridae will

form the object of a separate geographical outline, we shall deal in a more detailed manner with the distribution of the Lithodidae, using for this purpose firstly Bouvier's outstanding essay (1896), and adding to it new data. Let us first of all deal with the quantitative importance of the Lithodidae in the different regions of the oceans. In doing so we shall not complicate our exposition with the enumeration of the species, but we shall confine ourselves to the more obvious percentage ratios; 82 % of all known species of Lithodidae are found in the Pacific, and only 18 % in the Atlantic. No genus is found in the Atlantic which is not represented in the Pacific also; 28 % of the genera found in the Pacific are found also in the Atlantic. As to the distribution of the Lithodidae in a latitudinal direction in both oceans, 87 % of the total number of species is found in the Northern Hemisphere, and only 11 % in the Southern Hemisphere; no genus is known here which is not represented also in the Northern Hemisphere. The percentage of genera found in the Southern Hemisphere of those found in the Northern Hemisphere is 21. From all these data it ensues that the great majority of the Lithodidae are found primarily in the Northern Hemisphere, and secondly in the Pacific.

Let us now deal separately with the distribution of the Lithodidae in the Pacific and in the Atlantic. Of the total number of species found in the Pacific, 89 % are found in the Northern and 11 % in the Southern Hemisphere. In the Atlantic, 80 % of the species are found in the Northern and 20 % in the Southern Hemisphere. Consequently, the ratio is almost equal in both oceans as well as equal to that found in all the oceans taken together. The
34 distribution in the western and eastern parts of both oceans is of particular interest. For the Pacific, this ratio is as follows:

Species of the western coasts.	20 %
" " " eastern "	62 %
Amphipacific species	18 %

For the Atlantic, the corresponding ratios will be: for the western coasts 50 %, for the eastern coasts 30 %, and amphiatlantic species 20 %.

A second conclusion is reached from the above data, namely, that most species are found in the northeastern part of the Pacific Ocean, while in the Atlantic, they predominate slightly in the northwestern part.

If we also take into account the fact that, besides the predominance of the Lithodidae in the northeastern part of the Pacific, the Hapalogastrinae – the most primitive group of the Lithodidae – are also located only here, it becomes evident that this part of the ocean might be the primary distribution center of the Lithodidae. It seems that in this part of the ocean the Lithodidae also underwent their entire evolution, since, apart from the Hapalogastrinae, almost all the genera of the family, including such specialized forms as Cryptolithodes, are encountered here. All Hapalogastrinae are littoral or sublittoral species. Advancing along the Aleutian Range, the eastern coast of Kamchatka, and the Kurile Islands, they reached the Sea of Japan, and, being cold-water forms, they made this the southern limit of their range (Hapalogaster dentata, in southern Japan, is the southernmost species of this subfamily, while Hapalogaster grebnitzkii, in Humboldt Bay, is the southernmost species on the western shores of North America). A number of lithodid species have remained littoral or sublittoral (Phyllolithodes, Cryptolithodes, and some species of Rhinolithodes and Lopholithodes). These species are

consequently located in the northeastern Pacific. Other species have populated the depths, and the distribution of the Lithodidae throughout the oceans has been possible owing to these species; for example, the abyssal genus Paralomis is the most widely distributed. In the temperate zone of the Southern Hemisphere a few species have become secondarily sublittoral, e. g., Paralomis verrucosa. Most species that have reached the Atlantic have however, remained abyssal (500-2, 300 m). In their southward advance in the Pacific, the Lithodidae used the western shores of America, where, as is known, the upwelling of cold abyssal water occurs. Therefore, most species found in the tropical zone of the Pacific are found exclusively on this coast, while on the Asiatic coast, not even the abyssal forms cross the equator. Bouvier (1896) explains the absence of Lithodidae at the southern latitudes of the Asiatic coasts of the Pacific by the former existence of a Sino-Australian continent, which was subsequently fragmented; in Bouvier's opinion this continent and the orogeny which occurred here limited the advance of the Lithodidae. We think, however, that the interpretation of the distribution of the Lithodidae along the western shore of America by thermal conditions is more acceptable, since these cold-water forms have found here more adequate conditions owing to upwelling. Reaching the Southern Hemisphere, some forms secondarily settled the sublittoral zone (Lithodes antarctica and Paralomis verrucosa in South America), while others, remaining abyssal, skirted South America and entered the South Atlantic (Paralomis formosa up to Rio de la Plata), and others reached the Indian Ocean (Lithodes murrayi and Paralomis aculeata). The Lithodidae of the North Atlantic reached this area by a different route. This is most obvious with Lithodes maja which, from the Bering Sea passed through Bering Strait northward, skirted North America, and settled throughout the North Atlantic. Its close relationship with Lithodes couesi of the Bering Sea, which is also probably its ancestral form, is evidence of this route of diffusion. As to the other species of the North Atlantic, which are deep-sea forms, either of two routes could have been taken. Bouvier presumed that they followed the route of Lithodes maja. We believe, however, that the way around South America, and the subsequent advance northward along the western shores of Africa — where upwelling also takes place — is more probable. It is quite possible that the common ancestor of the genus Lithodes populating the South American sublittoral zone — on the one hand — gave rise to L. antarctica, while on the other hand, remaining abyssal, and advancing along the above-mentioned route, it gave rise to L. ferox and L. tropicalis on the northern shore of Africa. This is also the most probable route for the species of the deep-sea genus Paralomis, namely P. bouvieri and P. spectabilis of the North Atlantic. It is rather more difficult to establish the route of penetration followed by Rhinolithodes biscayensis found in the Bay of Biscay, at 1, 400 meters. It is most probable that it also followed the southern route around South America; but at present, the range of this genus is discontinuous and Rhinolithodes is a typical amphiboreal genus. The most complex problem is that of the genus Neolithodes, represented in the North Atlantic by two species. This genus is the most primitive of the Lithodinae, according to the structure of its abdomen, and seems to form the link with the Hapalogastrinae. The [theory of a] process of a secondary involution of an Atlantic species of Lithodinae toward a more primitive form is hardly acceptable. Apart from this, in the other parts of the Atlantic, there are no species of

(33)

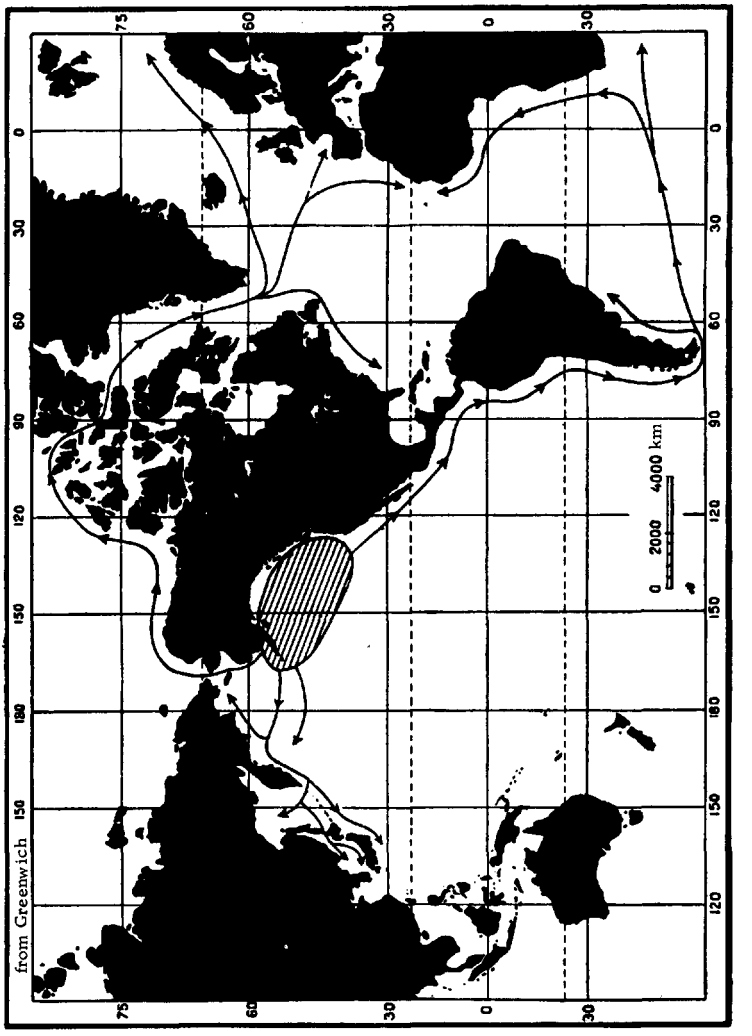

Figure 12. Primary center and subsequent distribution of the Lithodidae

Hapalogastrinae that could have given rise to Neolithodes, as has been shown above. On the other hand, this last genus is not encountered in the Pacific, a fact which complicates the problem even more. If Lithodes diomedae of the Chilean coasts (described by Benedict) proves to belong to
36 Neolithodes, as presumed by Bouvier, then here also the southern route is the most probable. The Hapalogastrinae of the North Pacific gave rise to Neolithodes in the Southern Hemisphere; this genus penetrated the North Atlantic, and at present has a discontinuous range. In Figure 12 the distribution routes followed by the Lithodidae are indicated; both alternatives are shown for the Atlantic although we believe that the southern route extending northward along the West African coast is more probable—with the exception of Lithodes maja. More accurate future deep-sea research in the tropical and temperate zones of the Pacific and the Atlantic will complete our knowledge with regard to the fauna of these regions and will elucidate the problems discussed here. Meanwhile, we must confine ourselves to the foregoing scheme, which is based on the rather fragmentary existing data.

Economic Importance

The commercial items of our decapodan fauna are the so-called commercial "crabs"* of the Far Eastern seas: Paralithodes camtschatica, P. platypus and P. brevipes. The first species has the greatest economic importance. The most intensive fishing is carried out along the western shores of Kamchatka, followed by the coasts of the Maritime Territory (Primor'e) and the east coast of Kamchatka. Fishing for P. platypus in the Bering Sea seems to be possible in the area of the Olyutorsk Gulf, and along the coast between Cape Olyutorsk and Cape Navarin. The pioneers of crab fishing were the Japanese. Fishing increased considerably from the time that crab canning was introduced in factories located on the shores, particularly from 1920, when factories on ships, the so-called "krabolovy", appeared for the first time. The Soviet crab fisheries began to develop only in 1923; in 1932 the first Soviet factory ships came into being. We have no statistical data at hand concerning the crab fisheries, and we therefore confine ourselves to some data taken from the scarce trade publications. Unfortunately, the material gathered by the crab team of the Pacific Institute of Fisheries and Oceanography, headed by J. Zachs, is still in manuscript.

Popov (1930) presents the following table with regard to crab catches on the western shore of Kamchatka (in numbers of specimens):

37

1923	1924	1925	1926	1927	1928	1929
696,630	964,430	2,963,100	4,454,090	5,121,110	6,759,050	7,845,360

We do not show in this table the catches in the areas rented by the Japanese, since by transforming the data into numbers of cans produced, a considerable difference appears compared with Japanese surveys.

* L.G. Vinogradov (1931) tried to introduce the term "craboid" in order to emphasize the taxonomic position of these commercial items; but this term was not accepted and the term "crab", which is, of course, incorrect from the taxonomic point of view, was retained.

The crab catches by Japanese fisherman on the western shores of Kamchatka are represented by the following numbers of specimens (according to Popov, 1930):

1923	1924	1925	1926	1927	1928	1929
2,391,230	282,070	7,353,853	15,360,822	2,254,279	20,562,568	24,033,503

In 1920 the Soviet crab fisheries obtained 4, 345, 925 crabs in the same area.

The output of the factories on the coast of the Maritime Territory is shown by the following values (cases containing 55 to 60 crabs each) (according to Zachs, 1936):

1928	1929	1930	1931	1932	1933
2,746	8,405	6,500	6,512	5,678	5,333

According to Marukawa, the total output of canned crab in Japan for 1930 was 58, 000 cases.

The fishing season of the crab is connected with its migration toward the shores. In the Maritime Territory, the spring spawning migration begins in March. The mature females arrive first, followed a little later by the males; in the month of June, after reproduction, the males return to the deep sea, where most of them molt. At the end of September they again enter the littoral zone. On the western shores of Kamchatka the spring migration occurs at the end of April. The return of the males to the deep sea is closely related to the thermal conditions of the littoral zone. The male leaves the littoral zone when the temperature exceeds 4° C; on the east coast of Kamchatka this occurs in June. The fall migration usually begins in September. Conflicting views are found in the scientific literature with regard to the behavior of the crab in winter. The Japanese are of the opinion that crabs hibernate in the mud — there are indications, however, that crabs occur in winter otter-trawl hauls. According to L. Vinogradov (1933), crabs congregate in winter at depths of 100 to 160 meters in Peter the Great Bay.

It is, therefore, quite possible to catch them in winter. They are known
38 to have a reduced mobility at that time and this facilitates fishing. In addition, the quality of crab is at its best in winter as the molting season is a long way off.

It has been observed that during their migrations, the crabs shelter in hollows and little depressions on the bottom. They travel at the rate of 1. 5 to 2. 0 km per day (according to Marukawa, 2 to 4 miles a day). Crab fishing is carried out by means of fixed nets. The setting of the nets must intercept their migration route; a study of the migration routes in every fishing sector is therefore one of the most important tasks. For the fishing of crabs two kinds of nets are used: the Korean type has a large mesh, 20 to 28 cm between the knots, and usually has a depth of $2\frac{1}{2}$ to $3\frac{1}{2}$ meshes; the Japanese type of net, having the same diameter of mesh, has a greater depth ($7\frac{1}{2}$ meshes). Sometimes an intermediate type is used: the meshes are slightly smaller than in the Korean type and the depth is $4\frac{1}{2}$ meshes. The net is tied to the headrope

at intervals of three meshes; the headrope is also floated and the footrope weighted; each net is from 38-47 meters long. The nets are set in strings (up to 100 nets per string), the two free ends are weighted with an anchor and buoyed. Figure 13 shows a diagram of a crab-fishing net. The nets are, as a rule, fixed at depths of from 50 to 120 meters and left for a period of 3 to 4 days (the Korean type) or 7 days (the Japanese type). At the end of this period the nets are hoisted up onto the fishing vessel (called "Kungas" or "Kavasak") either directly on board, or by means of special winches. If the vessels supply factories located on the shore, the unhooking of the crab from the nets is done immediately. On the vessels supplying factory vessels, nets are hauled on board and then delivered immediately to the factory vessel, where unhooking is carried out. Crabs are subsequently selected and canned.

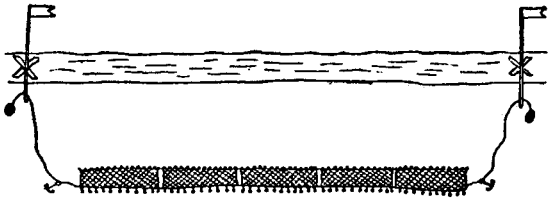

Figure 13. Diagram of a crab net (From Navozov-Lavrov, 1927)

39 Overfishing, chiefly in Japan, led to some exhaustion of the natural crab reserves. The following measures are proposed for the maintaining of the reserves: the prohibition of fishing of females and immature specimens; large-scale investigations in order to locate commercially worth-while concentrations of crabs and to determine the composition of such swarms; the prohibition of fishing with nets having meshes smaller than those decided upon; artifical rearing; the protection of natural spawning grounds, etc. The experiments to acclimatize the Kamchatkan stone crab in the Barents Sea do not seem to have succeeded so far.

DAMAGE. The burrowing forms, to which belong chiefly the Callianassidae, do considerable harm to ostreiculture. The holes dug by these animals sometimes cover the entire tidal zone; they reach a depth of up to one meter, and have a cylindrical form. B. A. Stevens (1928) and MacGinitie (1930) studied holes made by Callianassidae. The former used the following method: at low tide, he poured liquid gypsum into the holes; at the next low tide he undug the gypsum molds piece by piece; the pieces were then reconstituted, and in this way he obtained U-shaped molds (see Stevens, 1928, Figure 20), with one or more blind ramifications. MacGinitie describes a somewhat different form of hole: a principal canal, starting from the surface, proceeds at a certain depth in a horizontal direction, then reopens at the surface in a number of ramifications; at intervals there are widenings where the animal can turn. The process of digging was studied in detail by MacGinitie in special glass containers. Digging is carried out by means of the two first pereiopods,

the material excavated being deposited at the surface by the same legs. Progress within the burrow is made with the aid of the third and fifth pereiopods, while the fourth pereipods lean on the walls of the burrow for balance. The erect telson closes the entrance perfectly, thus serving as protection. If, however, the animal is frightened, it advances to the nearest widening of the hole, where it turns in order to direct its chela toward the danger. Aeration is effected by the movements of the pleopods. A burrow is usually inhabited by a single pair: one male and one female.

Figure 14. Names given by fishermen (in Russian) for joints of leg of commercial stone crab

1 – "rozochka" (little rose); 2 – "tolstaya nozkha" (thick leg); 3 – "kolentse" (knee); 4 – "tonkaya nozhka" (thin leg) (From Navozov-Lavrov, 1927)

The damage caused to the oyster bed is twofold. Firstly, the mud and sand dug out by the Callianassidae cover the eggs and the young of the oysters. Secondly, they undermine the various structures built for oyster cultivation. As oyster beds are often found at low tide, areas where the young are reared are surrounded by cement dams, which retain water at low tide; if Callianassidae are abundant there, their holes are so arranged that the inlets of the holes are within these areas, and the outlets at a lower level. At low tide, the water of the fenced areas flows out through these holes, and the oyster bed is exposed. Many oyster beds off the west coasts of North America were destroyed in this manner. Covering these areas with a layer of pebbles or shells does not prevent the damage done by the Callianassidae. Covering with cement or large stone blocks is too expensive. The best defense device used in America is laying a double layer of boards: in the fenced sector, a bottom layer is dug to a depth of 10-12 cm, then a layer of boards is set in, and on these a second layer is put at right angles to the first; the boards are then again covered with the bottom material. If no gaps are left, such a layer of boards is impenetrable for the Callianassidae.

40

ENEMIES. The principal enemies of the Anomura are fish. In the North Sea, rays, flatfish, sharks and sturgeons often dig out Thalassinidae from their holes. In the specimens of Hemilepidotus gilberti and Myoxocephalus stelleri from the southern end of Sakhalin, A. Andriyashev found their stomachs full of specimens of Dermaturus mandtii. Curstaceans are eaten by fish chiefly after molting. Octopuses also often attack the commercial stone crab. During its larval stage the commercial stone crab serves as food for the chum and pink salmon, and the anchovy. It is interesting to note that on many islands such semiterrestrial forms as Birgus latro have been exterminated by rats.

PARASITES. The nemertean Cephalothrix galatheae Dieck is a parasite living in the branchiae of Galatheidae. Of the parasitic Cirripedia, Rhizocephala are the most common; thus, species of Parthenopea Kossman live on Callianassidae, species of Lernaeodiscus Müller and Triangulus Smith are parasites of Galatheidea, species of Peltogaster Rathke live on Lithodidae. Of the parasitic Isopoda, genera of the family Bopyridae are chiefly found, e. g., Gyge on Upogebia and Galathea, Ione on Callianassa and Upogebia, Pleurocrypta on Galathea and Porcellana, and Pseudione on Callianassa, Galathea and Munida.

COMMENSALISM AND SYMBIOSIS. With the exception of the Paguridae, these phenomena are rather uncommon in the Anomura. According to Norman, the mollusk Lepton squamosum (Montagu) is always found in the holes of Upogebia stellata on the Devonshire coasts. The holes of Upogebia pugettensis on the western shores of North America are always inhabited
41 by the pinnotherid crab Scheroplax granulata Rathbun and a species of the polychaete Harmothoë; the same crab and another species of Harmothoë are found in the holes of Callianassa. As shown by MacGinitie, the small gobioide fish Clevelandia ios Jordan and Gilbert is sometimes found in the holes of Upogebia, hiding here from enemies or protecting itself at low tide. Itiro Miyazaki* recently described a commensal lamellibranchiate, which is fastened to the ventral surface of the cephalothorax of Upogebia major. The taxonomic position of this mollusk is not yet clear, and it is mentioned in his work under the provisional name Erycina sp. N. Navozov-Lavrov (1927) found a small symbiotic fish, Eumicrotremus pacificus, on the carapace of Paralithodes camtschatica, and stressed the outstanding resemblance between its external appearance and the surface of the carapace, which it uses as a shelter. Unfortunately the author does not show the frequency of this phenomenon, which therefore requires further study.

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SPECIAL SECTION

As a rule the carapace is not fused with the epistome. The last thoracic segment is free (the sternal plate of this segment is not fused with that of the preceding segment). The scaphocerite is usually present. The last maxillipeds are in most cases narrow and pediform. The third pair of pereiopods are never chelate. The fifth pair of pereiopods are always larger and situated differently from the third pair. The abdomen is shrimp-like, i.e., elongated, or compressed and bent under the carapace; sometimes it is saclike and membranous; the sixth segment usually has paired uropods (missing only in Lithodidae). The genital openings are on the coxal joints.

Key to the Superfamilies

1 (2). Dactylus of second to fourth pereiopods curved and compressed. First pair of pereiopods acicular or with subchelae. Telson and uropods not natatory. Abdomen curved under thorax. Third maxillipeds lack mastigobranchiae. . . . . III. Hippidea.

2 (1). Dactylus of second to fourth pereiopods neither curved nor compressed. First pair of pereiopods not acicular and only rarely with subchelae.

3 (6). Sixth abdominal pleopods natatory (except in the genus Thalassina, in which they are acicular). Abdomen symmetrical; abdominal pleurae usually well developed.

4 (5). Body dorsoventrally flattened. Pleurobranchiae on last pereiopods. Transverse suture often found on telson. Abdomen more or less bent. . . . . II. Galatheidea.

5 (4). Body laterally compressed. No pleurobranchiae on last pereiopods. No transverse suture on telson. Abdomen straight . . . . . I. Thalassinidea.

6 (3). Sixth abdominal pleopods–if present–have neither broad nor acicular branches, but are adapted for holding the animal in hollow bodies. Abdominal pleurae found only in rare cases. Abdomen almost always asymmetrical, either soft and spirally coiled, or bent under thorax . . . . . IV. Paguridea.

Superfamily THALASSINIDEA

The body is cylindrical in most cases, often shrimplike, with a long well-developed abdomen. The carapace is usually laterally compressed; the frontal part is not fused with the epistome. The fifth thoracic segment is free. The integument is often poorly calcified. The linea thalassinica is either present or missing. The last maxillipeds are narrow (pediform). The first pereiopods are chelate; the chelae sometimes have the structure of subchelae. The second pereiopods are also often chelate. The third pereiopods are always without chelae. The branchiae are of the trichobranchiate type, but are sometimes peculiarly widened; in most aberrant forms there is an incipient formation of phyllobranchiae; the number of branchiae is variable, but always less than 17. The pleurobranchiae are nearly always missing (always missing on the last pereiopods). The genital openings are found on the coxopodites of the third or the fifth pereiopods. The abdomen is long and symmetrical; the epimera of the segments are often reduced; the endopodites of the pleopods often have an appendix interna. The caudal fan is broad; the telson has no transverse suture.

According to Ortmann the Thalassinidea are in some respects similar to the Homaridea, and, according to Borradaile, they resemble the Paguridea. They are analogous to the first group in the shape of the caudal fan, the first pereiopods and often of the second ones. They differ from the Homaridea in the following features: the third pereiopods (which are never chelate), the frequently reduced number of branchiae, and the tendency of the abdomen to become soft and to lose its pleurae. They resemble the Paguridea by their spiniform scaphocerite (in those forms where it is well developed), in their free last thoracic segment and by the way in which the last pair of pereiopods are borne, i. e., quite far from the last thoracic segment, and above it. They differ from the hermit crabs by 1) their fifth pereiopods, which have the same form as the others, 2) their second pair of pereiopods, which are usually chelate, and 3) their symmetrical abdomen and their broad caudal fan.

These are mostly burrowing forms, in mud or in sand; sometimes they are commensal in sponges, etc. Of the four families which comprise the superfamily Thalassinidea, two families are represented in the Soviet fauna.

Key to the Families

1 (2). Linea thalassinica absent. Scaphocerites always present, though sometimes small. Epimera of abdominal segments large. Exopodites of uropods with or without diaeresis*. . . . . 1. Axiidae.

2 (1). Linea thalassinica present. Scaphocerite reduced to a small flattened appendage, or missing altogether. Epimera of abdominal segments small. Exopodites of uropods never diaeretic . . . . . 2. Callianassidae.

* [Diaeresis = division or separation of parts normally united].

1. Family **AXIIDAE**

Axiidae Bate, 1888: 36; Ortmann, 1891: 46; 1901: 141; Borradaile, 1903:536; Schmitt, 1921:110.

They resemble Macrura in the shape of the body, which is shrimplike. The rostrum is usually flat, triangular, and of normal dimensions. The carapace has no linea thalassinica.

The flagella of the antennules are of normal dimensions. The scaphocerite resembles a spiniform mobile appendage, between the second and third joints
47 of the antennal stalk*. In addition, on the second joint, outward from the scaphocerite, an immobile spine is found (antennal spine). The first pair of pereiopods are chelate, large, and unequal. The second pair of pereiopods have small equal chelae.

The subsequent pairs of pereiopods are simple; the fifth legs may be subchelate, but usually terminate in a small spiniform dactylus. There are no branchiae on the first maxillipeds. Mastigobranchiae are found on the first four pairs of pleopods, and podobranchiae on the first three (according to Bate - four) pereiopods. The branchiae are of the trichobranchiate type. The abdomen is long; the epimera are well or moderately developed. The exopodites and endopodites of the pleopods are usually narrow or fairly broad; the endopodites have a stylamblys (appendix interna). The caudal fan is well developed. The exopodite of the uropods (external plate) is with or without diaeresis.

In the Soviet fauna, this family is represented only by the genus Axiopsis Borradaile.

Genus AXIOPSIS Borr.

Axiopsis Borradaile, 1903: 538; Schmitt, 1921: 110.

Type species: Axiopsis affinis (de Man).

The carapace is laterally compressed in front of the cervical groove, forming a very distinct flat area, on the dorsal surface and ending in a rostrum. There is no median dorsal carina on the carapace behind the cervical groove. In rare cases a slightly marked carina is sometimes found in front of the posterior edge of the carapace. The eyes are well pigmented. The antennal spine on the second joint of the antennal stalk is either long or of medium length. The second pair of pereiopods are chelate. The exopodite of the uropods is diaeretic. Borradaile's indications (1903), according to which arthrobranchiae and podobranchiae are found on the second maxillipeds and the pleurobranchiae are missing, are true only
48 for A. affinis (de Man). Having at our disposal only a dry specimen of A. princeps (Boas) we could not ascertain to what extent these statements are true with regard to the species. Apart from the species described below, Z. I. Kobyakova quotes for the Soviet fauna a new subspecies of the American A. spinulicauda (Rathbun), namely, A. spinulicauda amurensis from Peter the Great Bay. At the time this work was written, the description of this subspecies was not yet published.

* [= antennal peduncle]

† 1. Axiopsis princeps (Boas) (Figure 15).

Axius princeps Boas 1880: 98, Pl. 2, Figure 52; Pl. 3, Figure 87; Pl. 4, Figures 137, 137a; Pl. 5, Figure 174; Pl. 7, Figures 214-217; Balss, 1914: 88.

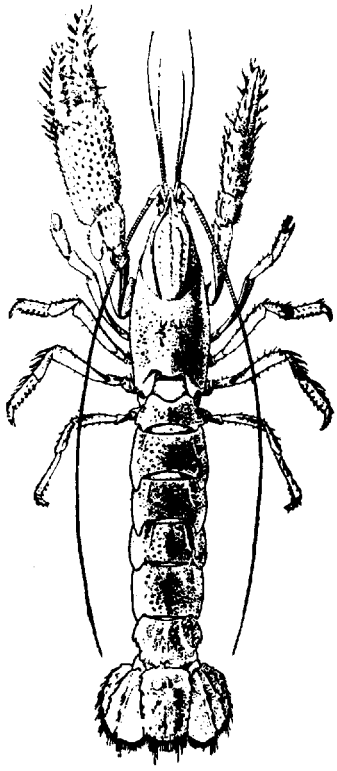

Figure 15. Axiopsis princeps (Boas)

The mandible bears a denticle on its incisor part. The first joint of the palp of the maxillule is long. The exognath of the second and third pair of maxillipeds has a short peduncle, while the exognath of the first pair has a large epignath. The carapace is long, very compressed laterally, and very high. The rostrum is triangular and extends beyond the eyes; its tip bears a blunt spine, while on both its sides, four similar spines are found. The anterior half of the carapace-in front of the cervical groove-bears on its slightly flat superior surface five longitudinal crests, which do not reach the cervical groove. The medium crest, which partly extends onto the rostrum, and the two intermediate crests bear coarse granules. Smooth lateral crests commence from the base of the basal lateral spinules of the rostrum. Tufts of short hairs are found between the crests and on the lateral surfaces of the carapace. The posterior half of the carapace is slightly wrinkled and is covered with short hairs. The antennae are long, the scaphocerites short and spiniform. The first pair of chelipeds are chelate, the left leg being much stronger than the right. The merus is long, triangular in section; the propodus, in contrast, is very short, markedly widening toward the edges. The left chela is very strong; the convex surfaces of the carpus have no edges and are covered with tufts of hairs; at the base of the movable dactylus, on both the external and
49 the internal sides, round coarse granules are found; the dactyli are strong, almost the same length as the propodus, slightly curved distally, and covered with long tufts of hairs; the prehensile edges bear large rounded tubercles, particularly in their proximal half. The smaller cheliped has almost the same form, but the propodus is more slender and narrow, and the dactyli are much longer than the propodus; they are straighter, without tubercles on the prehensile edges, and closed. The second pair of pereiopods are chelate. The three subsequent pairs of legs are simple; their propodi

† [This symbol shows that a particular genus or species has been found among the U.S.S.R. fauna. Those without the symbol are found in neighboring areas and possibly occur among the U.S.S.R. fauna, too.]

have on their inferoposterior surface five or six short transverse combs, made up of corneous spinules; the dactyli are short and curved, convex on the superior part and concave on the inferior part; the anterior edge of the inferior concave surface bears small spines, while the posterior edge bears larger ones. The abdomen is long and has relatively well-developed epimera. The third to fifth pleopods have an appendix interna, bearing hooked setae on its tip; the plates of the pleopods are narrow. The telson is fairly broad, almost rectangular, and spinulose; the internal plate (endopodite) of the uropods has a spinulose longitudinal median crest; the external plate (exopodite) of the uropods has a slightly marked spinulose longitudinal crest, which is, however, nearer to the spinulose outer edge; the distal part of the plate is divided by an evident diaeresis, and bears a row of sharp spines on its proximal side.

The dry specimen had a pale-olive coloration, and the hairs were a dirty reddish shade.

Dimensions

Length of carapace	29.0 mm
Width of carapace	13.0 mm
Height of carapace	16.0 mm
Length of carpus of large cheliped	9.0 mm
Length of propodus of large cheliped	19.0 mm
Width of propodus of large cheliped	14.0 mm
Thickness of propodus of large cheliped	10.0 mm
Length of movable dactylus large cheliped	18.0 mm
Length of propodus of small cheliped	11.0 mm
Width of propodus of small cheliped	7.0 mm
Thickness of propodus of small cheliped	4.6 mm
Length of movable dactylus of small cheliped	15.0 mm

Distribution: Vladivostok. It is probably a burrowing form.

2. Family **CALLIANASSIDAE**

Callianassidae, Bate, 1888: 27; Ortmann, 1891:48; 1901: 1142; Borradaile, 1903: 541; Schmitt, 1921: 114. – Thalassinidae, Heller 1863:200.

Rostrum large and flat, or small, almost lacking. Linea thalassinica present. Antennular flagella short, or moderately long. Scaphocerite small,
50 having the form of a flat scale. First pereiopods unequal or equal, chelate or subchelate (sometimes simple-genus Gebicula); second pereiopods simple or chelate; third and fourth pereiopods simple; fifth pereiopods simple, chelate or subchelate. No pleurobranchiae nor podobranchiae and usually no mastigobranchiae. Gills of the trichobranchiate type, or with filaments widening to varying degrees. Pleopods of third to fifth abdominal segments have broad branches; endopodites with or without appendix interna. Epimera of abdominal segments almost lacking. Exopodites of uropods not diaeretic. All members of the family have burrowing habits.

The family Callianassidae is divided into two subfamilies.

Key to the Subfamilies

1 (2). Rostrum large. First pereiopods equal. Propodus of third pereiopod of normal width. Endopodites of third to fifth pleopods without appendix interna . . . . 1. Upogebiinae Borr.

2 (1). Rostrum small, sometimes almost entirely missing. First pereiopods very wide, transversely oval. Endopodites of third to fifth pleopods with appendix interna . . . . . 2. Callianassinae Borr.

Subfamily **UPOGEBIINAE**

Upogebiinae Borradaile, 1903: 542.

Rostrum large. First pereiopods chelate, subchelate or simple, but equal; carpus and propodus not very wide. Second pereiopods equal and simple (with the exception of the genus Bigea). Propodus of pereiopods of usual width and not transversely oval. No mastigobranchiae (sometimes rudiments are found on the first two maxillipeds). Second pleopods have branches as wide as those of third to fifth pleopods; these last lack appendix interna on endopodites.

This subfamily is represented in the Soviet fauna only by Upogebia Leach.

1. Genus UPOGEBIA Leach

Upogebia Leach, 1814: 386, 400; Holmes, 1900: 157: Borradaile, 1903: 542. – Gebia Leach, 1815: 335, 342; Milne-Edwards, 1837: 312; Bell, 1853: 222; Heller, 1863: 204.

Type species: Upogebia stella (Montagu).

The anterior part of the carapace is very compressed laterally and ends in a large triangular rostrum, which almost completely covers the
51 eyes. The superior surface of the rostrum bears thick hairs. The rostrum bears lateral spines; from these up to the cervical groove extend crests, which divide the flat gastric area. The posterior part of the carapace is wide, with rounded posterolateral angles. The branchial areas are very large. The frontal edge of the carapace has a small spine above the base of the antennal stalk; this spine may be absent. The antennular stalks are short. The antennal stalks are five-jointed, with protuberant auditory tubercles on the ventral surface of the first joint. The scaphocerite is small and rudimentary, often resembling a short foliaceous appendage*. The eyestalks are cylindrical and somewhat broadened proximally; the corneas are terminal. The third maxillipeds are narrow and pediform. The first pereiopods are strong and equal, chelate or subchelate. The second to fourth

* In the generic diagnoses a number of authors (Bell, Heller, Milne-Edwards, Holmes) note the absence of scaphocerites.

pereiopods are simple. The propodus of the second pair is broad and flat. The fifth pereiopods are usually not chelate. The abdomen is long; the median segments are the broadest. The second pleopods are identical with the three subsequent pairs. The first pair of pleopods are lacking in the male; in the female, they are small, slender and filiform. The endopodites of the second to fifth pleopods have no appendix interna. The telson is broad, almost square; the uropods are wide and thick, not longer than the telson.

The genus Upogebia is divided into two subgenera: Upogebia Leach and Gebiopsis A. Milne-Edwards. The second subgenus differs from the first by the lack of spines on the frontal edge of the carapace above the base of the antennal stalks, and by the structure of the chela of the first pereiopods; in Gebiopsis the immovable dactylus–which in Upogebia resembles a spiniform appendage of the inferodistal end of the propodus–attains almost the length of the movable dactylus. This gives it the appearance of a true chela. In the Soviet fauna, only the subgenus Upogebia is represented.

Key to the Species

1 (2). First joint of antennular stalk with a spine at distal end of inferior edge. Triangular scaphocerite ending in pointed spine. Superior edge of propodus of first pereiopods with a strong spine near distal end. Superior surface of movable dactylus smooth and flat. . . . . †1. U. littoralis (Risso).

2 (1). First joint of antennular stalk smooth, with rounded anterior edge. Superior edge of propodus of first pereiopods without visible spine. Superior surface of movable dactylus with furrow or prominence.

3 (6). Immovable dactylus of first pereiopods without strong tooth in middle of prehensile edge.

52 4 (5). Immovable dactylus of first pereiopod with four or five spinules at base of external edge. Small spine at base of prehensile edge. Median crest of superior edge of propodus of first pereiopods without teeth at proximal and distal ends . . . . . †2. U. major (de Haan).

5 (4). Immovable dactylus of first pereiopods without spinules at base of external edge. Strong tooth at base of prehensile edge. Median crest of superior edge of propodus of first pereiopods with strong teeth at proximal and distal ends . . . .3. U. yokoyai nom. nov.

6 (3). Immovable dactylus of first pereiopods with strong tooth in middle of prehensile edge . . . . . †4. U. issaeffi (Balss).

†1. Upogebia (s. str.) littoralis (Risso)

Thalassina littoralis Risso, 1816:76, Pl. 3, Figure 2 – Gebios littoralis Risso, 1826:51. – Gebia littoralis H. Milne-Edwards 1837:313: Heller, 1863:205, Pl. 6, Figures 12-15; Czerniavsky, 1884:85. – Upogebia littoralis de Man, 1927:29, Pl. 3, Figures 11-11b.

The rostrum reaches the middle of the penultimate joint of the antennular stalk or slightly beyond. The tip of the rostrum is rounded, the lateral edge bearing four to six spinules. The upper surface has a smooth longitudinal furrow, extending also onto the gastric area, and visibly widening toward its base, so that in the posterior part of the gastric area, a distinct smooth triangular space is formed, divided posteriorly by the marked cervical groove. The lateral surfaces of the gastric area and of the rostrum are covered with small prominences bearing hair tufts. The laterofrontal spines are very short, the lateral gastric crests bearing 13 or 14 spinules. The spine on the frontal edge above the base of the antennal stalk is fairly long and pointed. The granules on the posterior edge of the cervical groove are very slightly marked at the level of the linea thalassinica as well as below it. The eyestalks extend a little farther than the middle of the rostrum. The first joint of the antennular stalk has a spine at the distal end of the inferior edge, and its third joint bears a triangular membranous scaphocerite ending in an acute spine. The last maxillipeds are narrow, pediform and hairy. The first pereiopods are equal and moderately long; the inferior edge of the ischium bears from three to five spines; the merus is long and flat, with a spine on the internal part of the triangular superior surface on the distal end; the inferior edge is spinulose and hairy. The carpus bears a spine at the distal end of the superior edge, which is hidden by a tuft of long hairs; beyond this spine, the anterior edge bears two barely visible small spines; there is another spine on the inner distal angle of the inferior surface.
The rounded superior edge of the propodus bears a longitudinal, hairy,
53 granulated crest on its internal side, and parallel to it, a smooth crest with isolated tufts of hairs, directed outward, and finally a small furrow with very sparse tufts of hairs; between the granulated crest and the smooth one, the superior edge of the propodus bears a fairly strong spine, directed outward, which is situated near the distal end. The external surface of the propodus is protuberant and smooth; the proximal half of the inferior edge is formed by a flat, triangular sector, with small spines and long setulae on its lateral sides; the immovable dactylus is pointed, with a perfectly smooth external edge; on the proximal two thirds of the prehensile edge is a slight denticulation and sometimes four fairly visible spinules; the anterior edge of the propodus bears a small spine on its anterolateral corner, at the base of the movable dactylus. The movable dactylus is slightly curved; its superior surface is smooth and flat; small smooth lateral crests may be observed only in its proximal third. The external and internal surfaces are covered with thick hairs; the inferoexternal edge (the prehensile one) bears a very small denticle near its base, and behind it three round granules are found. The inferior surface of the propodus is smooth, with the exception of a smooth longitudinal crest near the internal edge. Thus, between the crest and the internal edge a hairy furrow is formed. The row of hairs also extends along the external side of the inferior surface. The movable dactylus is identical in both sexes. The merus of the second pereiopods has a spine near the distal end of the superior edge; the inferior edge has one or two spines near the proximal end; the carpus bears one spine near the distal end of both the superior and inferior edges. The merus of the third pereiopods bears three spines on its inferior edge: one near the proximal end, the second in the middle, and the third—extremely small— at the distal end; the superior edge is smooth; the carpus has a small spine at the inferodistal end, and a tuft of hairs on its superior edge. The telson is almost square;

its lateral edges diverge in their proximal third, subsequently converging; the posterior edge is straight, with no incision; the median furrow of the upper surface is distinct.

Coloration: Pale whitish or greenish, abdomen often transparent (Pesta); greenish-gray (Heller, Webb). Czerniavsky stresses the animal's faculty for changing its color rapidly. Risso describes a dirty greenish color and a reddish carapace; in addition, he reports a carmine-red heterochromatic variety, which has a pearly-white abdomen and is found on the shore after heavy storms. This last fact may be explained by the animal's faculty for changing color, but could also be a posthumous change of color (Risso does not mention the condition in which these animals were found).

Dimensions	
Total length	34.0 mm
Length of merus of first pereiopod	6.0 mm
Length of carpus of first pereiopod	3.0 mm
Length of propodus of first pereiopod	5.5 mm
54 Length of movable dactylus	4.5 mm
Length of telson	3.5 mm
Width of telson	4.5 mm

Distribution: Black Sea, Adriatic and Mediterranean seas; coast of Portugal and southwest coast of France. The stage of development described by G. O. Sars from Norway, and which he ascribed to U. littoralis, no doubt belongs to another species (U. stellata?), since U. littoralis is not found north of the English Channel.

The species inhabits the Black Sea, at depths to 3 meters, buried in mud or sand some twenty centimeters deep, or more at night; the animals leave their holes and swim at a depth of 1 to 3 meters, sometimes reaching the surface. Their appearance at the surface en masse after storms is explained by the mechanical concentration of the animals which had been swimming freely on the bottom, or by their being washed out of their holes by the waves; the animals thus caught unawares are quite helplessly tossed by the waves; this also explains the occurrence of Callianassa at the surface during stormy weather, as observed by V. Czerniavsky (see below).

†2. Upogebia (s. str.) major (de Haan) (Figures 16 and 17)

Gebia major de Haan, 1850: 165, Pl. 35, Figure 7; Miers, 1879:52; Ortmann, 1891:54, Pl. 1, Figure 7; Balss, 1916:90; Yokoya, 1930:543, Figure 4. - Upogebia major de Man, 1927: 47, Pl. 6, Figure 18.

The rostrum is triangular with a rather blunt rounded end. The lateral edge bears four small spines. The lateral edges of the base of the rostrum bear five spinules, partly extending onto the gastric area; the upper surface of the rostrum is thickly covered with hairs, with the exception of the

median furrow; the anterior two fifths of the flat gastric area are also hairy; the posterior fifth and the narrow longitudinal median part are smooth. The laterofrontal spines are short and form a transition toward the lateral gastric combs, which are separated from the surface of the base of the rostrum and from the gastric area by deep, smooth furrows, and are made up of 12 to 14 small spines, hidden by hairs. The posterior edge of the cervical groove has three granules above the linea thalassinica and three below it; these are followed by a row of small granules. The lateral parts of the gastric area are also covered with small granules. The spine on the frontal edge above the antennal stalk is marked. The eyestalks reach almost the middle of the rostrum. The first joint of the antennular stalk is smooth; the third joint is more than four times as long as the second. The antennal stalk has a small foliaceous, transversely oval scaphocerite on its second joint. The maxillipeds are narrow and pediform, with thick hair on the inferior edges of their joints. The first pereiopods are equal and fairly strong. The inferior
55 edge of the ischium bears an acute spine near its distal end. The merus is flat, and somewhat widened distally; the superior edge is transformed– in front of the distal end– into an inclined, flat triangular area; the interior part of this area bears a spine near the distal end; the lateral surfaces of the merus are smooth; the inferior edge widens slightly distally, and bears six pointed denticles, which also extend onto the internal edge of the widening, while the external edge bears a row of small round granules; the internal edge bears a row of long, soft hairs; above these, on the internal surface of the merus, another row of hairs is found. The carpus is short; the superointernal edge bears six or seven small spines; the distal superointernal angle bears a strong spine; the superoanterior edge bears four to six denticles, which become smaller in an outward direction; on the internal surface of the anterior edge a strong spine is found, similar to that on the anterointernal angle; the superoexternal surface is smooth, and covered with distally diverging furrows; the superior furrow is covered with thick hairs. The inferior triangular surface is smooth, the external edge bearing 13 to 15 spiniform granules, which decrease proximally. The internal distal angle bears a strong spine, with a smaller spine beneath it. The propodus is elongated and oval, with slightly convex lateral sides; the superior and the inferior edges are broadly rounded. The superior edge bears a longitudinal row of spiniform granules and a denticulated crest, which commences on the internal part. In addition, both edges bear long hairs, the intervals between them being smooth. Parallel to the denticulated crest and somewhat behind it, a smooth crest is found on the external surface. Nearer to the
56 inferior edge of the propodus is a longitudinal furrow covered with hairs; the inferior edge of the propodus has a diagonal row of spines, the largest being the proximal ones; the distal two thirds bear small granules, and on these, tufts of long soft hair are found. The dentiform outgrowth of the inferointernal angle (the immovable dactylus) has four or five blunt spines behind its base, situated on a kind of crest, which is an extension of the smooth external edge of the dactylus; the smooth, concave prehensile edge bears a small spine near the base; the anteroexternal edge of the propodus bears a small spine, located nearer to the base of the movable dactylus. The armature is different in the two sexes. In the male, the superior surface bears nine or ten flat, oblique nail-like prominences; the internal edge has the form of a small denticulated crest; between this crest and the

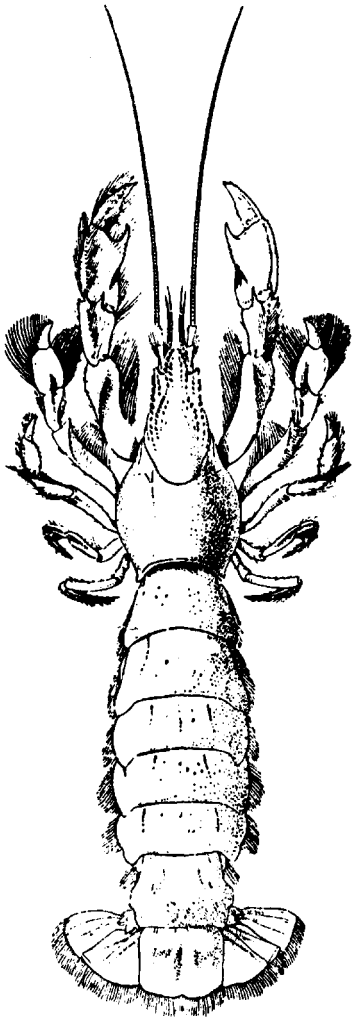

Figure 16. Upogebia major (de Haan)

row of flat prominences described above, another longitudinal row of very small granules is found, the proximal ones being larger than the others. These granules are covered with long hairs, which cover the distance between the above-mentioned crest and the row of granules; the superoexternal edge has a smooth crest, bearing hairs on its inferior part, and having only at its proximal end three or four granules; the inferoexternal edge is smooth, and in the middle is a small round tubercle; a row of hairs is found on the external surface above this edge. The inferior flat surface of the dactylus bears five oblique crests, the median one being the longest, and the two distal ones often appearing merely as granules (chiefly in small specimens). There are two rows of hairs on both sides. In the female, the superior surface of the movable dactylus has a deep smooth longitudinal furrow with a minute granulation on its raised borders. In young females this furrow is missing. The lateral sides are highly pubsecent; the inferoexternal edge is more raised for approximately one third of its proximal end than in the rest; the inferior surface bears a longitudinal median row of short obliquely transverse crests; at the base of the dactylus, this row deviates toward the internal angle. The superior edge of the merus is smooth, with one spine near the distal edge; the inferior edge is pubescent, with a strong spine at its proximal end and two smaller spines in front of it. The carpus has one spine at the distal end of the superior edge, and a matching one at the inferior edge. The propodus has a broad oval form, and is highly pubescent; the dactylus is particularly pubescent on its superior edge. The merus of the third pereiopods has a smooth superior edge and a spinulose inferior one. The fifth pereiopods are subchelate, the inferior and the distal parts of the propodus being very pubescent. The exopodites of the second to fifth pleopods are pointed, broad, and longer than the rounded endopodites. The

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lateral edges of the sixth abdominal segment have a flat, truncate lobe. The posterolateral corners of the telson are rounded; the crests on the telson are slightly prominent and hardly visible; the posterior edges of the uropods bear small spinules on the superior side.

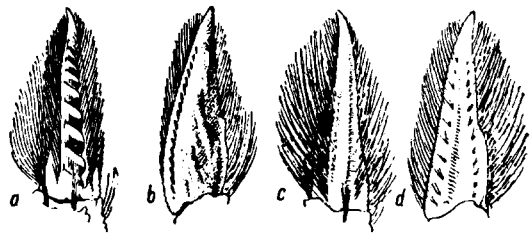

Figure 17. Movable dactylus of the chela in Upogebia major (de Haan)

a – dorsal view ♂; b – ventral view ♂; c – dorsal view ♀; d – ventral view ♀.

Dimensions

Total length	90 mm
Length of merus of first pereiopod	13.0 mm
Length of carpus of first pereiopod	8.0 mm
Length of propodus of first pereiopod	13.0 mm
Length of movable dactylus of first pereiopod	10.0 mm
Length of telson	10.0 mm
Width of telson	13.5 mm

Distribution. Southern Japan. In the Soviet seas it is encountered in the Vladivostok region (Golden Horn Harbor and Patrocles Bay) and in Olga Bay.

3. Upogebia (s. str.) yokoyai nom. nov. (Figure 18)

Gebia affinis Yokoya, 1930:544, Figure 5 (nom. praeoccup.) *

[Original description of Yokoya, 1930]

"Of the specimens from Asadokoro, one is 42.8 mm and another 33.5 mm long from the tip of the rostrum to the end of the telson. I was able to examine one female specimen of this species, which is 45.8 mm long, collected by Mr. Hiroaki Aikawa from the coast of Haneda near Tokyo.

"The species very closely resembles G. issaeffi Balss from Vladivostok and Gebia major de Haan, but it is distinctly different from these.

"The frontal margin of the carapace is similar to that of G. major, consisting of three anteriorly directed processes, the medial one being larger and longer than that on each side. In the present species, not only is the medial process somewhat narrower and more acutely pointed, but the lateral processes are more apart from the medial in the dorsal aspect than those of G. major. Viewing it from the lateral side, the medial process

* Gebia affinis Say, Journ. Nat. Acad. Scien. Philad. I, 1818:241.

58 shows in profile a line continuous with the upper margin of the carapace, and the lower margin obliquely ascends to acuminate to the tip, while in G. major the line of the upper margin is continuous with that of the carapace at first, but descends abruptly downwards at the tip and the lower margin shows a nearly horizontal line in the smaller specimens. In the full-grown specimens, the lower margin is slightly ascended to the extremity, where, however, it is not so acutely pointed as that of the present species.

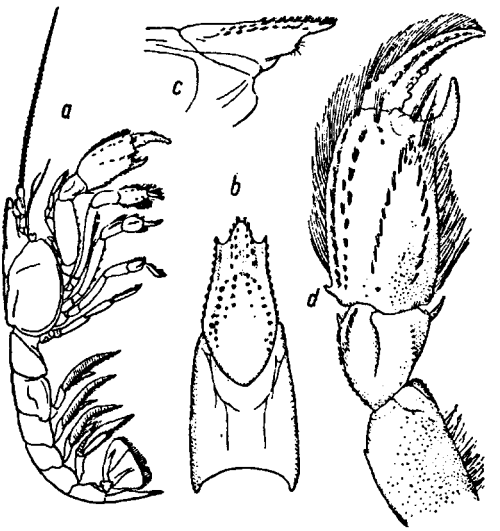

Figure 18. Upogebia yokoyai nom. nov.

a – general view of the animal from the right side; b – carapace, dorsal view; c – anterior half of carapace, lateral view; d – terminal half of first pereiopod, outer view (From Yokoya, 1930).

"The pereiopod is alike in both sexes and similar in shape to that of G. issaeffi. The meros [merus] is stouter than that of G. major in the specimens of similar size, about two and a third times as wide as long, * and its outer surface is smooth and devoid of hairs, while the teeth on the lower margin are sharply pointed. The carpos [carpus] is armed with a series of small acutely pointed teeth near the upper margin; this series of teeth is more prominent than that found in G. issaeffi and the terminal tooth is much stronger than any of the rest. The carpos is armed with two strong teeth on the distal margin, one on the lower margin and stronger than the other which is on the upper margin. The palm of the chela is about twice as wide as long and its surface is nearly smooth and superiorly provided with three obtuse longitudinal carinae which are fringed with series of long hairs. In these carinae the medial one is the most prominent and is guarded with a strong tooth on each of the proximal and the distal ends of the carina. Between this and the outer carina, it is longitudinally furrowed. The palma is also provided with two rows of hair bundles on the outer surface; and these two rows meet behind the hinge of the finger, where hairs are scattered in numerous bundles. The lower margin is slightly carinated and furnished with long hairs. The anterior prolongation of the propodus or the pollex is armed with a strong triangular tooth at the base of the inner margin. The dactylos [dactylus], or the movable finger, is provided with three rows of tubercles, one on each of the upper and lower margins, and another on the outer surface. In the latter the tubercles are prominent, while in the

* An evident lapse of the author: the length ought to exceed the width. V. M.

former, except the proximal one or two, they are mostly much less prominent. Beside these, on the upper margin and on each side of the lower margin, hairs are studded in a series, and another series of hairs is just below the said tubercular series on the outer surface. The hairs on the upper margin are prominent and are longest at the base, diminishing terminally in length. In other respects the species coincides with G. major" (Yokoya).

Distribution. Japan: 6 July 1926, Asadokoro, 2♂; 15 August 1926, Nonai 1♀ juv.

†4. Upogebia (s.str.) issaeffi (Balss) (Figures 19, 20).

Gebia (Upogebia) issaeffi Balss, 1913: 239; 1914: 18, Figures 89, 49; Upogebia issaeffi de Man, 1927: 27.

Figure 19. Upogebia issaeffi (Balss). Chela of left first pereiopod, inner view

This species resembles U. major, but differs from it by obvious characters, chiefly concerning the first pereiopods; therefore, in the following we shall deal only with the description of these legs. The first pereiopods are relatively shorter than those of U. major. In the male, the propodus bears a principal, hairy crest, which has —only at its distal end— a row of seven spines, gradually increasing in length; on the internal surface is a parallel row of very small pointed granules, which are also covered with hairs. The second crest, which is barely outlined on the external surface, is smooth, with sparse hairs. A hairy furrow is found on the external surface, near the inferior edge; at the base of the inferior edge of the propodus are three spines; from here extends, in an anterior direction, a row of thick hair which diverges outward before reaching the immovable dactylus, and then merges with the hairy furrow described above; at the point of the divergence, the hairs hide a group of short spines; the anteroexternal edge has a spine between the base of the movable dactylus and that of the immovable one. The immovable dactylus has a strong denticle in the middle of the prehensile edge, while the base of the external edge is quite smooth. In the female, the superior edge of the propodus bears a denticulated hairy crest, not a smooth one; in other respects the propodus is absolutely identical with that of the male. The movable dactylus has a structure differing in the two sexes (Balss and de Man studied only the males of this species, and therefore did not observe these differences). In the male, the superior surface of the movable dactylus

bears a smooth longitudinal furrow with raised borders; the external border of this furrow bears small granules; a very large round granule is found at the proximal end; the internal border of this furrow bears a row of small transverse protuberances (about 100, according to de Man); the inferointernal edge bears fairly large round granules; between this edge and the row of transverse protuberances, the surface bears a smooth crest densely covered with hairs, and one or two granules at the proximal end; the inferoexternal edge bears two blunt denticles, or more often one low, broad, truncate denticle, with swollen, rounded lateral corners. The outer inferior surface bears a row of large round granules, reaching neither the proximal nor the distal end of the dactylus, and bearing a row of hairs on both sides; the superior row extends to both ends of the dactylus, while the inferior one is the same length as the row of granules.

The inferior surface of the dactylus bears from nine to thirteen oblique transverse crests, closer to the internal edge; on the external and the internal edges of the surface, straight rows of hairs are found. When the dactylus is bent, the middle of the broad truncate denticle on the inferointernal edge is located in front of the denticle on the prehensile edge of the immovable dactylus. The superior surface of the movable dactylus in the female resembles that of U. major—there is a smooth longitudinal furrow, its raised borders covered with large granules; in other respects, the dactylus resembles that of the male, except that the transverse crests on the inferior surface are shorter, thick and swollen, and therefore look rather like large, round granules. The subsequent pairs of pereiopods and the abdomen are as in U. major.

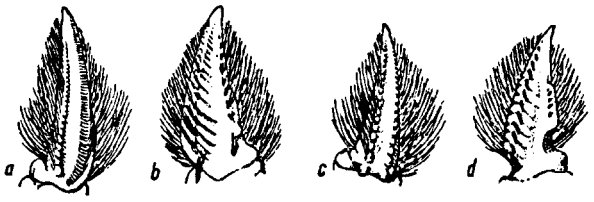

Figure 20. Movable dactylus of chela of Upogebia issaeffi (Balss)

a — dorsal view, ♂; b — ventral view, ♂; c — dorsal view, ♀; d — ventral view, ♀.

Dimensions

Total length	62.0 mm
Length of merus of first pereiopod	10.0 mm
Length of carpus of first pereiopod	5.5 mm
Length of propodus of first pereiopod	11.0 mm
Length of movable dactylus of first pereiopod	8.5 mm
Length of telson	7.0 mm
Width of telson	9.0 mm

61 Distribution. This species seems to have a limited range, since all known specimens were collected in the Vladivostok region.

Subfamily **CALLIANASSINAE**

Callianassinae Borradaile, 1903: 544.

The rostrum is short, sometimes almost entirely missing. The first pereiopods are chelate and unequal; the carpus and the propodus of the stronger leg are usually fairly broad. The second pereiopods are equal and chelate. The propodus of the third pair of pereiopds is broad. Mastigobranchiae are present or missing on the last pereiopods, but are always present on the first maxillipeds. The second pair of pleopods are either similar or dissimilar to the third to fifth pleopods, the endopodites of which bear an appendix interna.

Key to the Genera

1 (2). Second pleopods unlike subsequent three pairs . . . . . 2. Callianassa Leach.

2 (1). Second pleopods similar to subsequent three pairs . . . . . 3. Ctenocheles Kishinouye.

2. Genus CALLIANASSA Leach

Callianassa Leach, 1814: 386; Milne-Edwards, 1837: 307; Bell, 1853: 217; Heller, 1863: 201; Bate, 1888: 28; Holmes, 1900: 159; Borradaile, 1903: 544; Balss, 1914: 91; Schmitt, 1921: 116.

Type species: Callianassa subterranea (Montagu).

The carapace is short compared to the general length of the body. The whole integument is more or less soft, except for that of the first pereiopods, which is very hard. The rostrum is short, triangular and rudimentary, or absent altogether. The eyestalks are flat and triangular; the corneas are situated on the dorsal surface; they are small and sometimes absent; in a few cases, the eyestalks are rounded and the corneas are terminal (subgenus Scalassis Bate). The third maxillipeds are narrow and pediform, or broad and squamiform; there is no exognath. The first pereiopods are chelate and unequal; the larger cheliped, which may be either the right or the left one, is much stronger than the other. The carpus and the propodus are broad in comparison with the other joints; the merus has a dentiform lobe at the proximal end of the external edge; the carpus is articulated with the merus by means of a narrow suture. The second pereiopods are chelate and equal; the chela is flat, triangular or heart-shaped. The third and fourth pairs of pereiopods are simple; the propodus of the third pair is broad and transversely oval, its posterior edge either exceeding the posterior

62 edge of the carpus (lobate propodus) or level with it. The fifth pereiopods are subchelate. The branchiae are intermediate between phyllobranchiae and trichobranchiae—they are composed of two rows of long, thin filaments, which closely adjoin one another so that they seem to form a leaflet. As to their position, they are arthrobranchiae. There are two arthrobranchiae on each side of the third maxillipeds and of the first four pairs of pereiopods. There is a large mastigobranchia on the first maxillipeds, while on the second maxillipeds a small bulblike one is found. The abdomen is long; the first two pairs of pleopods differ in structure from the other pairs; the first pleopods of the male are small; the exopodite and the endopodite of the second pleopods are narrow and filamentous, in the male as well as in the female; the branches of the third to fifth pleopods are foliaceous in both sexes and have no gill-like filaments; their endopodites bear an appendix interna. The uropods are as long as the telson, or longer.

Owing to the great durability of the first pereiopods, a fairly large number of fossil forms are known in the Jurassic and pre-Triassic sediments; thus, for instance, Call. maxima A. Milne-Edwards was found in alluvial sediments during the digging of a canal in Siam, Call. crassa A. Milne Edwards was found in the Miocenic sands of St. Paul near Dax, and finally a number of species were encountered in the Parmes limestones in the vicinity of Gisors, in the sands of Blanchamps, and in the Cretaceous sediments of Bohemia and many other places.

The genus Callianassa is divided into five subgenera of which three are represented in the Soviet fauna, while the subgenera Calliactites Borradaile and Scalassis Bate are missing. The following are considered as criteria for division into subgenera: the characters of the third maxillipeds, and the form of the propodus of the third pereiopods, of the caudal fan and of the eyestalks. The subgenera represented in the Soviet fauna are recognizable by the form of the third maxillipeds and the caudal fan.

Key to the Subgenera

1 (4). Telson same length as uropods.
2 (3). Third maxillipeds narrow and pediform . . . 1. Cheramus Bate.
3 (2). Third maxillipeds broad and foliaceous. . . . 2. Trypaea Dana.
4 (1). Telson shorter than uropods . . . . . 3. Callichirus Stimpson.

Key to the Species*

1 (10). Telson same length as uropods.
2 (3). Third maxillipeds narrow and pediform.. C. subterranea (Montagu).
3 (2). Third maxillipeds broad and foliaceous.

* Subgenera are not indicated in the key.

63 4 (5). Frontal edge of carapace without rostrum; prehensile edge of movable dactylus of stronger cheliped with broad, truncate denticle at base, and another fairly strong denticle near tip. Posterior edge of telson with pair of spinules near both lateral angles. . . . . †2. C. harmandi Bouvier.

5 (4). Rostrum present, though sometimes very small. Posterior edge of telson without spinules near lateral angles.

6 (7). Carpus of larger cheliped 1.5 times as long as broad, and longer than the merus. Prehensile edge of movable dactylus of larger cheliped bears denticles similar to those of C. harmandi . . . . . †3. C. gigas eoa nom. nov.

7 (6). Carpus of larger cheliped slightly longer than broad, and as long as merus. Prehensile edge of movable dactylus of larger cheliped without protruding denticles.

8 (9). Proximal lobe on external edge of merus of larger cheliped narrow, with pointed end. Length of internal edge of carpus equal to width of carpus or slightly more. Carpus not longer than propodus; dactyli of chela almost meet when closed; movable dactylus shorter than internal edge of propodus. . . . . †4. C. japonica (Ortmann).

9 (8). Proximal lobe on external edge of merus of larger cheliped with a rounded end. Internal edge of carpus shorter than width of carpus. Carpus longer than propodus; gap between dactyli of chela when closed; movable dactylus longer than internal edge of propodus. . . . . 5. C. californiensis Bouvieri, nom nov.

10 (1). Telson shorter than uropods. . . . . †6. C. pontica (Czerniavsky).

1. Subgenus CHERAMUS Bate

Cheramus Bate, 1888: 30; Borradaile, 1903: 545.

The third maxillipeds are narrow and pediform. The propodus of the third pereiopods bears a lobe on its posterior edge. The internal plates of the uropods (the endopodites) are moderately broad, or broad; the telson is long.

1. Callianassa (Cheramus) subterranea (Montagu) (Figure 21)

Cancer (Astacus) subterraneus Montagu, 1808: 89, Pl. 3, Figures 1, 2; – Callianassa subterranea Leach, 1815, Pl. 32; Bell, 1853: 217; de Man, 1928: 6, Pl. 1, Figures 1-1h (literature).

Until fairly recently it was thought that in the European seas – the Mediterranean Sea and the Black Sea included – only one species of Callianassa exists, namely, C. subterranea (Montagu). Callianassa laticauda and C. stebbingi were considered identical with this species. At that time,

V. Czerniavsky (1884) distinguished three forms and two variations of C. subterranea, viz., forma typica (Mediterranean Sea and Black Sea, northern European seas) with the variety laticauda (Mediterranean), forma intermedia
64 (Mediterranean), the variety major (Callianassa major Say, eastern American shores) and forma pontica (Black Sea). The diagnosis formulated by Czerniavsky for this last form—the one of interest to us—is incomplete. In his monograph, de Man (1928) made a revision of the material on the basis of Mediterranean and N. European forms, and reached the conclusion that 2 species of Callianassa inhabit the Mediterranean: C. laticauda Otto (C. stebbingi Borradaile) and C. pestae de Man; Callianassa subterranea is specific to the northern European seas (French and English littoral), but Colosi's specimen, collected in the Mediterranean, on the North African coast, is considered by de Man as being C. subterranea, so that the problem of the distribution of this species in the Mediterranean is not yet fully elucidated. As to the Black Sea, on the basis of the study of the existing material, it is found that all the specimens belong to de Man's species Callianassa pestae. De Man himself considered possible the synonymy of forma pontica Czerniavsky with his species C. pestae. The identity of the two forms appears certain, and therefore, according to the rules of priority, this species ought to be called Callianassa pontica (Czerniavsky). Thus, C. subterranea does not inhabit the Black Sea (it is difficult to confuse it with C. pontica, as the two species belong to different subgenera). However, we consider it worth while to present an abridged description of this species, after de Man.

The rostrum is short and pointed, with a broad triangular form; the lateral outgrowths of the frons, situated between the eyestalk and the antennal stalk, are blunt. The cervical groove is deep, the linea thalassinica distinct. The internal edges of the eyestalks are straight, gradually diverging distally and almost touching; the external edges are arcuated; the corneas are found on the internal half of the dorsal surface of the stalk in the female (somewhat more proximally than in the male). The third maxillipeds are almost pediform. The ischium of the larger cheliped in the male has a small pointed spine at the proximal end of its concave internal edge*; in its proximal half the external edge has a row of five small even denticles. The merus is somewhat longer than the ischium; the internal edge is slightly curved, with a small moderately pointed denticle at its proximal end, followed by a larger prominence, with two tips, and, after a short space, by three moderately pointed even denticles as small as the first denticle. The
65 proximal quarter of the external edge extends in a large, flat lobe, bent upward distally, and having a very sharp distal edge; the external edge of the merus bears 12 denticles in front of the lobe, with hairs between them. The carpus is somewhat shorter than the merus, its width is equal to its length, and its edge is slightly hairy or spinulose. The propodus tapers slightly distally, and has a curved end. The movable dactylus is somewhat longer than the immovable one; its end is strongly bent, and its prehensile

* Here, as well as in the further descriptions of species of Callianassa, we use an orientation of the appendages rather different from that used by de Man; it is true that in this manner, the appendages appear somewhat dislocated, since in a normal position their broad surfaces face one another, so that what is called by us the superior surface is the exterior one; the internal edge in our descriptions corresponds to the superior edge in the descriptions of de Man, while the external edge corresponds to the inferior one; since, while observing (under a magnifying glass or spectroscopic microscope) a flat appendage, it is always set with its broad surface in a horizontal position, the terminology used by us is more convenient. We considered it necessary to make these remarks in order to avoid confusion.

edge is denticulated. The ischium of the smaller cheliped of the female is slender, broadening slightly distally. The merus is somewhat shorter than the ischium; it is oval; both its ends are truncate, and there is a small spine on the posterior third of its external edge. The carpus is slender, $1\frac{2}{3}$ times as long as the merus, and becoming broader distally. The length of the chela is two thirds that of the carpus. The edges of the joints of this leg are hairy, particularly the external edge of the carpus and of the chela, which bear long hairs, and the dactyli, which also bear many tufts of hairs. The length of the telson is the same as its width and it is trapezoid. The posterior edge has a small median cavity, in which a denticle of microscopic size is found; some distance from this denticle, at the transition toward the lateral sides of the telson, two equal microscopic spinules are found on each side, together with a denticle almost as small as the median one. The inner uropod is directed posteriorly and extends just beyond the telson; the outer uropod is very slightly longer; the basal joint of the uropods is smooth; the outer uropod, with two almost adjacent crests, is almost round; an additional row of short hairs almost reaches the middle of the posterior edge, whence it deviates inward; the length of the inner uropod is equal to its width; this uropod has a rounded posterior edge and a single distinct crest. In the female, the uropods are slightly longer than the telson.

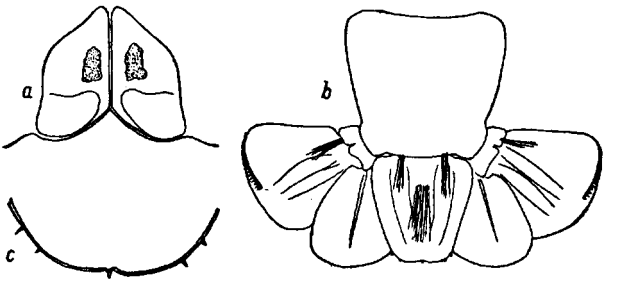

Figure 21. Callianassa subterranea (Montagu).

a – frontal edge of carapace and eyestalks; b – sixth abdominal segment and caudal fan; c – posterior edge of telson (From de Man, 1928).

Distribution. Shores of England, Ireland and France; Mediterranean Sea, on the shores of North Africa near Bengasi.

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2. Subgenus TRYPAEA Dana

Trypaea Dana, 1852: 513; Borradaile, 1903: 546.

The third maxillipeds are broad and foliaceous. The propodus of the third pereiopods has a lobate posterior edge. The endopodites of the uropods are broad, with rectangular posterolateral angles. The length of the telson is equal to or greater than the width; its length is equal to that of the uropods.

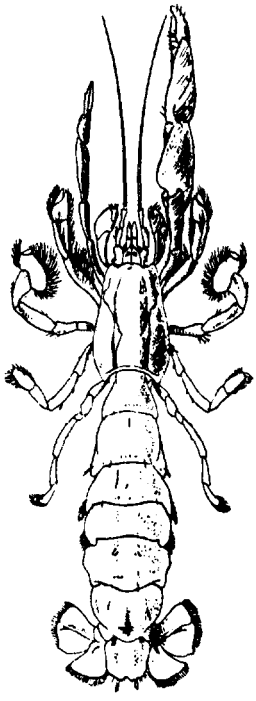

Figure 22. Callianassa harmandi Bouvier

†2. Callianassa (Trypaea) harmandi Bouvier (Figures 22-23).

Callianassa harmandi Bouvier, 1901: 332, de Man, 1928: 13, Pl. 3, Figures 6-6j; Yü, 1931: 92, Figure 3.

The frontal edge of the carapace has no rostrum, but small triangular prominences (lateral processes) are found at the level of the external edge of the eyestalks; in place of the rostrum, on each side of the median line, is a rounded prominence, very small and barely visible, and there is a small cavity between the two prominences. The length of the eyestalks is $1\frac{1}{2}$ times their width, the internal edges are straight, and adjoin almost up to their rounded tips, and the external edges are slightly concave in their anterior third. The corneas, which are found in the center of the stalks, project markedly; the internal edges of the distal parts of the stalks are distinctly raised. The first segment of the antennular stalk barely exceeds the eyestalks; the second segment is somewhat shorter than the first; the third segment is twice as long as the second and bears two flagella, which are shorter than the stalk; the stalk and the more slender flagellum bear long hairs. The antennal stalk is somewhat shorter than the antennular one and bears a small oval scaphocerite; the flagellum is almost half the length of the body. The third maxillipeds are as in C. japonica. The ischium of the large cheliped becomes distinctly broader distally; it has denticles on its external edge and a small denticle at the proximal internal end. The merus and the ischium are the same length; the slightly protuberant internal edge bears a row of small blunt denticles, and the superior surface bears a visible crest; the proximal lobe of the external edge resembles that of C. japonica, its posterior and anterior edges being denticulated. In front of this lobe, the external edge of the merus bears slender denticles; beneath this edge is a row of granules. The internal edge of the carpus bears small denticles and is slightly bent downward; the same is true also for the external edge; the length of the internal edge of the carpus is less than the width of the carpus. When the leg is bent, the rounded inferoexternal edge of the carpus almost completely covers the proximal lobe of the external edge of the merus. The chela is $1\frac{1}{2}$ times as long as the carpus; the length of the propodus somewhat exceeds its width; the edges of the propodus are finely denticulated and are hairy. The lobe of the anterior edge of the propodus, at the base of the movable dactylus, is wide with a smooth edge, and bears a small spiniform

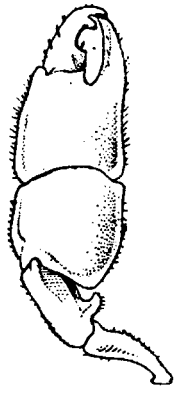

Figure 23. Callianassa harmandi Bouvier, large cheliped

outgrowth on its superoexternal angle; the curved immovable dactylus is smooth, with a smooth prehensile edge, only the inferointernal edge having a minute granulation. Highly specific for this species is the form of the movable dactylus, and, in particular, the armature of its prehensile edge. The whole dactylus is somewhat longer than the immovable dactylus, and has a strongly curved tip; beneath the very tip, the prehensile edge bears a strong denticle, which reproduces exactly the form of the tip of the dactylus. This is followed by an abrupt gap separating it from a broad proximal denticle, which does not reach the proximal end of the dactylus and has an almost rectangular shape, resembling the truncate base of a broad, triangular denticle. The free edge of this denticle is itself finely denticulated. When the chela is closed, the tip of the movable dactylus extends beyond the tip of the immovable one so that the superior edge of the second denticle of the prehensile edge rests against the prehensile edge of the immovable dactylus. Thus, a space of a very peculiar form remains open. The ischium of the smaller chelipeds is slender, with one or two small denticles on the external edge. The merus has a spine on its external edge. The carpus tapers markedly in a proximal direction. The chela is somewhat shorter than the carpus; the dactyli are the same length as the propodus; the prehensile edge of the immovable dactylus has a minute median denticulation. The prehensile edge of the movable dactylus is smooth. In general, this leg greatly resembles that of C. japonica, except that the chela is somewhat shorter than the carpus. The subsequent pereiopods, as well as the abdomen bearing the pleopods, are as in C. japonica. The posterior edge of the telson has a median spine and a pair of spinules near each of the lateral angles.

Dimensions

Length of ischium of large cheliped	9.0 mm
Length of merus of large cheliped	9.0 mm
Length of carpus of large cheliped	11.0 mm
Width of carpus of large cheliped	10.5 mm
68 Length of chela of large cheliped	16.0 mm
Width of propodus of large cheliped	10.0 mm
Length of movable dactylus	7.5 mm

Distribution. Japan: Province of Bingo; Nemuro. China: Shantung Peninsula, Kiaochow Bay. In Soviet waters: in Patrocles Bay and in Peter the Great Bay.

†3. Callianassa (Trypaea) gigas var. eoa nom. nov. (Figure 24)

C. gigas var. japonica Makarov, 1935:323, Figure 4 (nom. praeoccup.).

The rostrum is blunter than in the typical form. The tip of the eyestalks is also shorter than in the typical C. gigas; the pigmented corneas are situated in the middle of the stalks or somewhat more distally. The chelipeds are very unequal, the larger one being much longer than the small one. The surface of the ischium of the large cheliped is smooth and shiny; the

external edge is denticulated in its proximal two thirds; the internal edge is denticulated approximately along its first proximal third; in C. gigas the external edge is denticulated along almost its entire length, while the internal edge is smooth. The internal edge of the merus is almost smooth, and only at its proximal end a group of small granules is found; in C. gigas, the edge is clearly denticulated. The proximal lobe on the external edge of the merus is more pointed and not as prominent as in C. gigas; when the leg is bent, this lobe is half covered by the rounded posterior edge of the carpus, while in C. gigas in a similar position, the lobe remains entirely uncovered. The carpus is longer than the merus, and has sparse hairs; the edge is slightly sharpened; in C. gigas, the edges are extremely sharp and denticulated. The chela is approximately the same width as the carpus and is $1\frac{1}{2}$ times as long; the external edge of the propodus is slightly sharpened and denticulated, and the internal edge is smooth; the lobe at the base of the movable dactylus is broadly rounded, with a smooth edge, and with a barely visible outgrowth in its external corner; in C. gigas, the external corner of the lobe has a visible prominence, bearing spiniform granules. The dactyli are covered with tufts of long soft hairs; the prehensile edge of the immovable dactylus is slightly swollen in the middle, and has a slightly curved tip; the highly characteristic armature of the prehensile edge of the movable dactylus partly resembles that of C. harmandi: some distance from the base there is a long, low truncate denticle, its free edge slightly denticulated; this is followed by a short denticle, and finally by the strongly curved tip; when the chela is closed, the tip of the movable dactylus extends beyond the tip of the immovable one. The convex part of the prehensile edge of the immovable dactylus corresponds to the cavity between the truncate denticle and the subapical one on the prehensile edge of the movable dactylus. Thus, a narrow triangular gap remains open, and reaches only half the length of the dactyli; its form in no way resembles the gap in C. harmandi. The dactyli are perfectly smooth, their surfaces as well as their edges. In C. gigas, the prehensile edge of the immovable dactylus bears two low denticles on its proximal half. The prehensile edge of the movable dactylus has only a slight convexity at its base, while in the remaining part it has no teeth, but only a small denticulation. When the chela is closed, the tips of the dactyli cross, and the edges are pressed close together, leaving no open gap; the external edge of the movable dactylus, as well as its inferior surface, bears rows of coarse granules. The smaller cheliped does not differ from that of C. gigas in any respect. The external edge of the propodus of the second pereiopods does not protrude at all and is almost straight; both dactyli are the same width at the base; in C. gigas, the inferior edge protrudes markedly, and the immovable dactylus is much broader at the base than the movable one. The other pereiopods are like those in C. gigas. In one variety, the telson

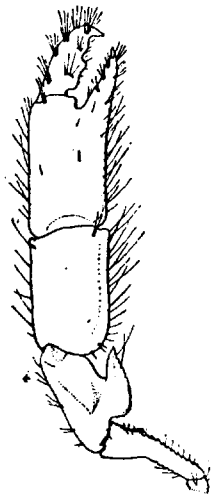

Figure 24. Callianassa gigas eoa, nom. nov., large cheliped

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is somewhat shorter, if compared with the uropods, than in the typical species. All the differences described above were entirely confirmed when the variety was compared with a specimen of the typical species, obtained from the Washington Museum.

Dimensions

Total length	46.0 mm
Length of large cheliped	44.0 mm
Length of ischium of large cheliped	9.0 mm
Length of merus of large cheliped	19.0 mm
Length of carpus of large cheliped	11.0 mm
Width of carpus of large cheliped	7.5 mm
Length of chela of large cheliped	15.0 mm
Width of chela of large cheliped	7.0 mm
Length of small cheliped	25.0 mm

Compared to the large male which served for the description, the four smaller males show some differences with regard to the armature of the prehensile edge of the dactyli of the large cheliped, viz., both edges have only a fine denticulation, they approximate closely when closed, and their tips cross. As to the other features, they resemble the specimens described above. This further illustrates the considerable changes in form undergone with age by the first pereiopods of Callianassa, a fact which in turn also indirectly confirms the dubious status of C. californiensis bouvieri, considered as an independent species (see below).

Distribution. Patrocles Bay, Peter the Great Bay.

70 †4. Callianassa (Trypaea) japonica (Ortmann) (Figure 25).

Callianassa subterranea (Montagu) var. japonica Ortmann, 1891: 56, Pl. 1, Figure 10a; Balss, 1914: 91; Yokoya, 1930: 543, 1933: 52. – Callianassa japonica Balss, 1924: 52; de Man, 1928: 19, Pl. 5. Figures 10-10c.; Yü, 1931:95, Figure 5.

The rostrum is short, having a broadly triangular form, and at its tip bears a small spiniform prominence. Between the external edge of the eyestalk and the antennal stalk the anterior edge of the carapace bears a triangular outgrowth reaching almost half the length of the rostrum. The eyestalk almost reaches the distal end of the basal joint of the antennular stalk; the width of the eyestalks somewhat exceeds half their length; their internal edges are obliquely rounded and very slightly concave near the tips. The corneas are somewhat oval and pigmented, with a marked reticular structure; they are situated in the middle of the superior surface of the stalks, or somewhat more distally. The second joint of the antennular stalk is almost the same length as the first; the third joint is slender, and twice as long as the second; the flagella are fairly long, of almost equal length; the stalk and the more slender flagellum bear long hairs on their inferior side, the hairs of the stalk being pinnate. The antennal stalk is somewhat shorter than the antennular one; the scaphocerite is small and oval, and overlaps the dorsal surface of the subsequent joint. The fourth and fifth joints

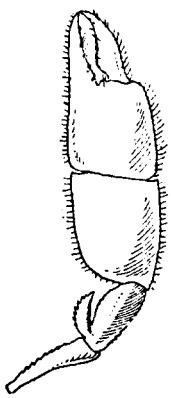

Figure 25. Callianassa japonica (Ortmann), large cheliped

are almost equal in length; the length of the flagellum is approximately half that of the body. The third maxillipeds are broad and foliaceous. The ischium is triangular, markedly tapering posteriorly; the anterior edge, which articulates with the merus, is obliquely truncate; the internal edge of the rounded merus is longer than the external one; the propodus is not broadened. The ischium of the large cheliped bears from five to seven denticles on its external edge. The internal edge of the merus bears a minute denticulation on its proximal half, made up of approximately 12 denticles, which decrease distally and finally disappear; the external edge bears a pointed lobe or denticle on its proximal half; this denticle itself bears seven or eight pointed denticles on its curved inferior edge; the superointernal edge bears two or three barely visible denticles. The external edge of the merus has a minute denticulation in front of the lobe; the swollen superior surface bears a distinct crest. The length of the carpus somewhat exceeds its width; the carpus has a smooth swollen superior surface, and a flat inferior one; the edges of the carpus are sharp, and bear a minute ciliation; the internal edge has a minute denticulation; the length of the internal edge of the
71 carpus is equal to, or slightly more than, its width. The chela is longer than the carpus, and the same width as the latter at its base; the distal part of the chela tapers; the external edge of the propodus, which has an indistinct denticulation and a ciliation, is almost straight, and extends onto the straight external edge of the immovable dactylus, which has a slightly curved tip. The superior surface of the propodus is convex, the inferior one flat. The movable dactylus is somewhat longer than the immovable one, and is visibly curved distally; the prehensile edges of both dactyli are evenly denticulated, the denticles on the movable dactylus being larger than those on the immovable one. When the chela is closed, the tips of the dactyli cross, only a small triangular gap remaining open at the base. The rounded outgrowth of the anterior edge of the propodus, at the level of the gap between the dactyli, has a denticulated edge (in the female, this edge is almost smooth). The ischium of the small cheliped is long, narrow and slender, with an almost smooth external edge. The merus is shorter than the ischium, and is oval; the external edge bears a small median spine. The length of the carpus is more than $2\frac{1}{2}$ times the width, and is markedly longer than the merus. The chelae are a little shorter than the carpus, and are pubescent. The prehensile edge of the movable dactylus is smooth, while the prehensile edge of the immovable dactylus has a minute denticulation, chiefly in its proximal two thirds. The chela of the second pereiopod is flat and truly conical. The propodus of the third pereiopod resembles a transversely oval plate, the rounded superior edge of which bears a short dactylus; the inferior edge of the propodus has a lobe, and therefore exceeds the inferior edge of the carpus.

The telson is almost square, with rounded posterior angles; the posterior edge is slightly concave, and bears a small median spine. The pleopods of the third to fifth segments are foliaceous.

Dimensions

Length of ischium of large cheliped	5.0 mm
Length of merus of large cheliped	5.0 mm
Length of carpus of large cheliped	5.0 mm
Width of carpus of large cheliped	4.5 mm
Length of chela of large cheliped	8.0 mm
Width of propodus of large cheliped	5.0 mm
Length of movable dactylus	4.0 mm

The habitus of C. japonica is similar to that of the European species C. subterranea. This induced Ortmann to consider C. japonica as a variety of the European species. Borradaile (1903), and subsequently also Balss (1924) noted that it is more correct to consider this Japanese form as an independent species and not as a variety, since it belongs to a different subgenus from the European species. Balss (1914, 1924) considers that Callianassa petalura Stimpson and C. californiensis japonica Bouvier are synonymous with this species.

Distribution. Japan: Hakodate, Tokyo Bay; Shimoda; Bingo; near the mouth of River Tanabe; Mioura; Kagoshima; Akita; China: Chefoo, Chinwangtao, Hainan. In Soviet waters this species is reported from Patrocles Bay, in Peter the Great Bay. It is found at depths of 9 to 192 m.

72 †5. Callianassa (Trypaea) californiensis Dana var. bouvieri nom. nov. (Figure 26).

Callianassa californiensis var. japonica Bouvier, 1901:332 (nom. praeoccup.); de Man, 1928:18, Pl. 4, Figure 9-9c; Yü, 1931:94, Figure 4.

This variety closely resembles C. japonica, differing from it only by its pereiopods. The ischium of the large cheliped becomes markedly broader distally; its internal edge is concave, and there is a fine denticulation at its proximal end. The upper surface bears at its base two granules disposed longitudinally; the external edge bears denticles in the proximal two thirds of its length. The merus is somewhat longer than the ischium and has an almost straight, denticulated inferior edge. The crest on the upper surface is very marked, and is separated by a hollow from another transverse crest, which extends onto the proximal lobe of the external edge. This lobe is broader than in C. japonica; it is distinctly rounded on its posterior edge, and is not as pointed as in this species. Both its edges, as well as the external edge of the merus, have a minute denticulation. The ratio between the width and the length of the carpus is greater than in C. japonica, and its postero-external edge projects backward to a much greater extent, extending beyond the level of the articulation of the merus, while in C. japonica, the rounded

edge of the carpus is found at the level of this articulation. The chela has a quite different form. The movable dactylus is slightly longer than the internal edge of the propodus (in C. japonica it is shorter), the pointed tip being strongly curved. The incision on the distal edge of the propodus, at the base of the immovable dactylus, is very deep, the lobe with the denticulated edge being large; the immovable dactylus is relatively more slender than that of C. japonica, and more curved as a whole, chiefly at its tip. Owing to this fact, a very wide gap remains open when the chela is closed, and therefore the dactyli touch only at the level of their crossed tips. The armature of the prehensile edges is as in C. japonica. The small cheliped differs from that of C. japonica by its chela, which is somewhat longer compared with the carpus, and by its dactyli, which are slightly longer in comparison with the propodus.

Dimensions

Length of ischium of large cheliped	8.0 mm
Length of merus of large cheliped	9.0 mm
Length of carpus of large cheliped	11.0 mm
Width of carpus of large cheliped	9.5 mm
Length of chela of large cheliped	14.0 mm
Length of propodus of large cheliped	8.0 mm
Width of propodus of large cheliped	9.5 mm
Length of movable dactylus of cheliped	8.5 mm

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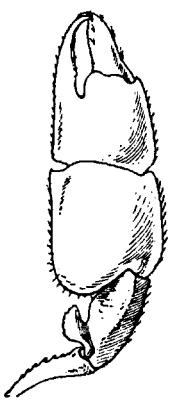

Figure 26. Callianassa californiensis bouvieri nom. nov., large cheliped

It is doubtful whether this form may be considered as an independent species. As shown above, H. Balss considers that it is identical with C. japonica. The resemblance is, no doubt, great and as correctly stated by de Man (1928)– the sole difference is that between the first pereiopods. It is very likely that this is merely a specimen of C. bouvieri showing age and sex differences, as only large males of C. californiensis bouvier have been known to date (unfortunately Yü, 1931, does not mention the sex of his specimens). If also in the future only males of this species are captured, it will be obvious that they belong to C. japonica, but at present, a lack of material prevents us from reaching such a conclusion.

Distribution. Japan: environs of Tokyo; China: Peitaiho. In Soviet waters, one male was captured in Patrocles Bay, in Peter the Great Bay.

3. Subgenus CALLICHIRUS Stimpson

Callichirus Stimspon 1866: 47; Borradaile, 1903:546.

The third maxillipeds are narrower than those of the subgenus Trypaea. The propodus of the third pereiopods has a lobe on its posterior edge. The endopodites of the uropods are narrow and pointed, or rounded at their posterior end. The width of the telson is the same as its length or more, and is distinctly shorter than the endopodites of the uropods.

†6. Callianassa (Callichirus) pontica (Czerniavsky) (Figures 27, 28)

Callianassa subterranea (Montagu) forma pontica Czerniavsky, 1884: 81 – Callianassa subterranea Heller, 1863:202, Pl. 6, Figures 9-11. Callianassa pestae de Man, 1928:34, Pl. 9, Figures 16– 16e (literature).

The rostrum is broadly triangular in form, and is pointed. The lateral denticles are blunt. The internal edges of the eyestalks either touch each other along almost their entire length, diverging only at the blunt tips of the stalks, or they diverge from the very middle, resembling in this respect C. laticauda. The corneas are small and convex, and are situated in the anterior half of the stalks, near the lateral edge. The eyestalks are the same length as the basal joints of the antennular stalk, or slightly longer. The antennular stalk is the same length as the antennal stalk; the third joint is much longer than the second. The third maxillipeds have a fairly broad (foliaceous) ischium and merus. The ischium of the large cheliped widens considerably in its distal third; the external edge, which is usually indistinctly serrated and almost smooth, bears a visible spinule at the beginning of the widened part. The proximal lobe on the external edge of the merus is pointed; its external edge bears from three to five denticles; the internal edge is smooth. The external edge of the merus is denticulated in its distal half, in front of the lobe; when the cheliped is bent, only the base of the lobe of the merus remains uncovered by the rounded postero-
74 external edge of the carpus. The carpus is shorter than the propodus (in a female from Venice the carpus is–according to de Man–somewhat longer than the propodus); both its edges are smooth. The propodus is the same width as the carpus (only in the specimen from Venice was the propodus narrower than the carpus); the edges are smooth. The lobe on the anterior edge of the propodus is wide and low, with a small prominence at the base of the internal edge of the immovable dactylus; the dactyli are shorter than the propodus; the movable dactylus is only a fraction longer than the immovable one; the external edges of the dactyli are smooth; the end of the movable dactylus is curved, and when closed it extends beyond the less curved end of the immovable dactylus. The armature of the prehensile edges of the dactyli is of two kinds (Figure 28): on the immovable dactylus a slight outgrowth is found, situated either in the middle or near the end; between it and the tip a distinct cavity is thus formed. In the first case, the dactylus is almost straight, while in the second it is slightly curved. In both cases,

a row of small denticles is found at the base. The prehensile edge of the movable dactylus either bears a minute denticulation along its entire length and has an incipient broad denticle at its base, the free margin of which bears an even smaller denticulation, or it bears at its base a broad truncate denticle, followed by a semicircular incision, then by a minute denticulation almost up to the tip. The two types of armature of the prehensile edges of the dactyli of the large cheliped do not depend on the sex of the animal. We found four males and four females among the specimens of the first type, and one male of the second type. It is possible that the type may depend on age, since this last male was the largest of all the specimens studied. The carpus of the small cheliped is long and narrow, narrower than the merus; its width is just one third of the length of its internal edge, or less. The width of the propodus is equal to that of the carpus. The propodus of the third pereiopods is oval. The telson is short and broad, almost semicircular, the breadth exceeding the length by one third; the posterior edge is pubescent, but bears no spines at all. The posterior edge of the outer uropod is broadly rounded; the raised part of its superior surface (which has the appearance of a transverse crest on its external half and is covered with hair) is some distance from the posterior edge; at the proximal end, a small denticle is found near the basal joint.

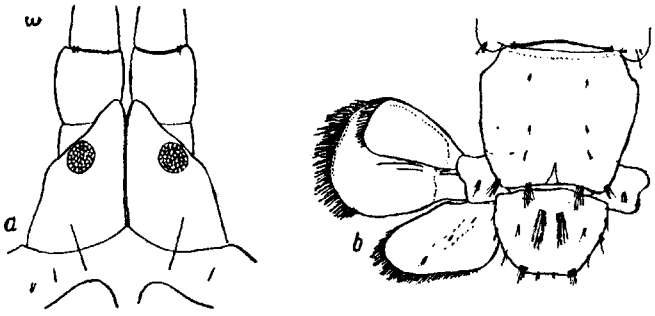

Figure 27. Callianassa pontica (Czerniavsky)

a–frontal edge of carapace and eyestalks; b–sixth abdominal segment and caudal fan (From de Man, 1928)

Coloration: white, with a transition toward bluish or pinkish red (Heller), or whitish, with a pink or light-blue tint (Pesta).

Dimensions

Total length (from end of rostrum to end of telson)	52.0 mm
Length of ischium of large cheliped	8.0 mm
Length of merus of large cheliped	9.0 mm
Length of carpus of large cheliped	10.0 mm
Width of carpus of large cheliped	8.5 mm

Length of chela of large cheliped	15.5 mm
Length of movable dactylus of large cheliped	8.0 mm
Length of merus of small cheliped	5.5 mm
Length of carpus of small cheliped	7.5 mm
Width of carpus of small cheliped	2.5 mm
Length of chela of small cheliped	8.0 mm
Width of chela of small cheliped	2.5 mm
Length of telson	4.0 mm
Width of telson	6.0 mm

Distribution. Mediterranean (Naples, Sicily); Adriatic Sea (Venice, Rovigno, Pizano, Lesina); western shores of France (St. Malo); Black Sea.

This species is found at depths down to 10 meters. It usually burrows in sand, or hides under the roots of Zostera (Zernov, 1913). Young specimens are quite often encountered swimming at night at the surface; larger specimens are seen at the surface only during heavy storms. According to Czerniavsky (1884), the mature and semimature individuals are very rapacious; in aquarium conditions they attack other animals or one another.

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3. Genus CTENOCHELES Kishinouye

Ctenocheles Kishinouye, 1926:63.

Type species: Ctenocheles balssi Kishinouye.

The rostrum is small. The first pair of pereiopods are asymmetrical and unequal, with well-developed chelae. The second pair of pereiopods are small and chelate. Podobranchiae and mastigobranchiae are lacking. The first pleopods of the second abdominal segment are similar to those of the three subsequent segments.

The genus Ctenocheles is on the one hand related to Callianassa, but differs from it in that the pleopods of the second segment have the same form as those of the subsequent pleopods; on the other hand it is related to Callianidea, but differs from it by the lack of mastigobranchiae. Unfortunately, Kishinouye (1926) does not specify whether the branchial filaments observed in Callianidea are found in this genus or not; if the lack of mastigobranchiae remains the only difference, this highly variable character will hardly be sufficient to justify the creation of a separate genus.

1. Ctenocheles balssi Kishinouye (Figure 29).

Pentacheles sp. Balss, 1914:75, Figure 43 – Ctenocheles balssi Kishinouye, 1926:63, Figure 1; Yokoya, 1933:55.

[Original description of Kishinouye, 1926]

"Carapace is nearly one fourth the total length of the body, not long enough to cover the whole length of the cephalothorax, leaving the segment of the last pereiopoda uncovered. It is more or less laterally compressed,

and its margin ciliated. Rostrum very short, laterally compressed, and continues to a low median keel behind with a row of about ten minute teeth. Ophthalmopoda are horizontally compressed at the anterior end, and the visual organ lacking. They are nearly equal in length to the first joint of the first antennae. First antennae subequally biramous, flagellae longer than the peduncle, and situated just below the ophthalmopoda. Second antennae have neither scaphocerite, nor spine, being situated on the external side of the ophthalmopoda. Two proximal joints of the peduncle of the second antennae are nearly equal in length to the peduncle of the first antennae. Mandibles have a very sharp cutting edge, and carry a synaphipod of three joints, of which the ultimate one is the longest, and is furnished with stiff hairs. Second maxillipeds carry a pediform endopodite of five joints, the distal joint of which is armed with thick bristles. Third maxillipeds are pediform and long, consisting of six joints. Fourth joint is very thick with a sharp, serrated inner edge.

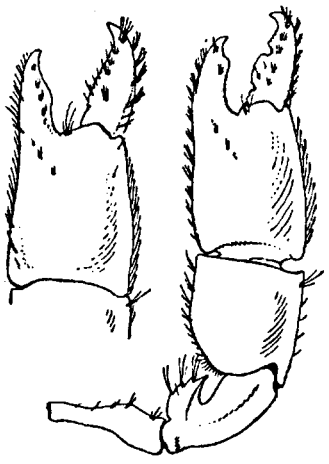

Figure 28. Large cheliped of Callianassa pontica (Czerniavsky); two types of dactyli.

"First pair of pereiopoda unequal in size and form, with well-developed chelae. Right chela is larger than the left, and resembles the right chela of Thaumastocheles more or less; but in this species the carpos is very short, and it seems as if fused to the propodus. Dactylus as well as the prolonged process of the propodus are armed with long, sharp teeth, alternating with same number of smaller teeth. Dactylus is turned outward. Merus is robust, having a rounded appearance at the proximal end. Ischium is nearly as long as the merus, but much more slender. Left chela is also well developed, but smaller, its dactylus being nearly half the length of that of the right chela. Inner side of the chela is serrated. Propodus is nearly the same in length with that of the right one, but about half in breadth. Carpus is longer, but both the merus and ischium are shorter, as compared with those of the right chela. First pair of pereiopoda is very poorly haired, and its surface is nearly smooth.

"Second pair of pereiopoda is chelate and compressed, with long hairs on the trenchant edges of the dactylus, propodus and carpos, and on the inner margin of the merus and ischium. In the propodus and carpos we find some groups of a few short hairs.

"Third pair of pereiopoda is a little longer than the second. Propodus and the distal portion of the carpos are broad, and their trenchant sides are ciliated. In the carpos and merus we find small groups of short hairs as in the preceding pair.

"Fourth pair of pereiopoda is a little longer and more slender than the preceding pair. Carpos is elongated and club-shaped. Ischium is rather short in the third to fifth pereiopoda.

"Fifth pair of pereiopoda is not subchelate. Propodus is thickly haired at the posterior inner margin.

"Coxal joint of pereiopoda on both sides meet with each other at the ventral median line of the cephalothorax, except the last two pairs which are separated by the thelycum.

"Abdomen is much elongated. Its segments are nearly smooth and the pleuron is little developed. Pleopoda are well developed. First pair of pleopoda, however, is small, narrow, and consists of two joints. Second to fifth pairs are quite similar to each other, consisting of two broad leaf-like plates at the end of a short basal joint. Inner margin of the endopodite is thickly ciliated, while the distal and outer margin of the exopodile [sic] is furnished with short hairs. Sixth pleopoda form the lateral plates of the rhipidura. Exopodite is broader than the endopodite, and is notched at the middle of the posterior margin. Telson is also nearly as broad as long, and has three radiating grooves from the middle of the anterior margin.

"Branchial system is very simple, arthrobranchiae only being developed. They are found two in every segment, from that of the third maxilliped to that of the fourth pereiopoda.

"The animal seems to have been caught from a deep water, as it is blind (Kishinouye)".

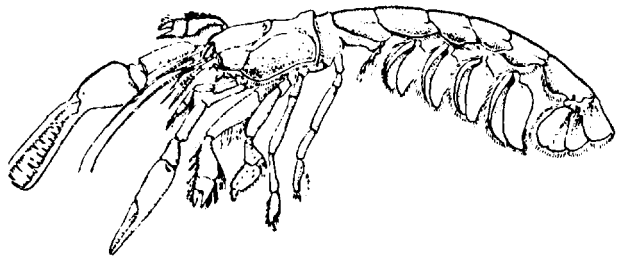

Figure 29. Ctenocheles balssi Kishinouye (From Kishinouye, 1926)

Distribution. Japan: the western shores of Honshu, Ohsu area, near Kashiwasaki, Niigata Prefecture (Kishinouye); Wakasa Gulf, 119 m (Yokoya). H. Balss described only a right cheliped of this species (from Doflein's collection, precise location not indicated).

Superfamily GALATHEIDEA

The carapace is well developed, generally with distinct lateral edges and a marked linea anomurica. The rostrum is also well developed. The carapace is not fused with the epistome. The eyestalks are short and stout. The basal joint of the antennules is more or less protuberant, and frequently bears one or more stylocerites. The antennal stalk is four-jointed (the second and third joints are fused), in a few cases five-jointed (genus Aeglea); in rare cases spiniform scaphocerites can be found (genus Uroptychus),

but they are, as a rule, lacking; the flagella are long and slender. The last maxillipeds are pediform or somewhat broadened. The first pair of pereiopods are chelate and almost symmetrical. The three subsequent pairs are well developed and simple. The fifth pair is smaller and bears small chelae; they are partly hidden in the branchial cavity. The thoracic sternites are broad. The gills are of the phyllobranchiate type (with the exception of Aeglea, in which they are of the trichobranchiate type), as a rule 14 in all, viz., ten arthrobranchiae and four pleurobranchiae; the fifth pereiopods always bear pleurobranchiae. Sometimes, mastigobranchiae still appear on some of the pereiopods; there are no podobranchiae. The abdomen is well developed and symmetrical; it is made up of seven segments, the first of which is hidden under the carapace; the abdomen is more or less completely hidden under the thorax; the epimera of the abdomen are well developed; the first epimera are small and the next ones are oriented obliquely outward and are almost horizontal. Uropods are always present and together with the telson form a broad caudal fan; the telson often has a transverse suture. The abdominal appendages are generally present in the male on the first two abdominal segments, while on the other segments they may be present or lacking. The first pair of pleopods are modified into gonopods. According to Boas (1880, Figure 169) every appendage has a single wide branch (the external plate)
79 and its very thin anterior edge (the internal plate), together with the external plate, forms a kind of tube. Each appendage of the second pair bears a rudimentary outer branch (ibid. Figure 170), while the inner branch bears an appendix masculina at its tip. If present, the three subsequent pairs of appendages on segments four and five, and often on two and three are each composed of a simple, narrow, three-jointed branch; Boas contends that the terminal joint is an appendix interna and that the penultimate joint is a reduced internal branch bearing the appendix interna at its distal end.

Boas, who created this superfamily (which consequently ought to bear his name and not that of Henderson, as used), noted some resemblance between Galatheidea and Paguridea. Ortmann (1892) states, "The Galatheidea are in fact Thalassinidea characterized by a specific habitus–as a consequence of the flattening of the body–and also by the modification undergone by the last pair of pereiopods; unlike the Paguridea, the abdomen in this group shows a close relationship to the Thalassinidea".

The species of this superfamily are marine forms, living in the littoral zone, as well as at great depths. The Aegleidae, which are aberrant in many respects, are represented monotypically by a single genus with a single species, viz., Aeglea laevis (Latreille), which inhabits the fresh waters of South America. Two families belong to the Soviet fauna.

Key to the Families

1 (2). Abdomen bent, but not hidden under thorax. Third maxillipeds with mastigobranchiae. First pereiopods usually slender and long. Shrimplike habitus . . . . . 3. Family Galatheidae.

2 (1). Abdomen hidden under thorax. Third maxillipeds without mastigobranchiae. First pereiopods usually of moderate length, strong. Crablike habitus . . . . . 4. Family Porcellanidae.

3. Family **GALATHEIDAE**

Galatheidae Dana, 1852: 1431; Ortmann, 1892: 244; 1901: 1150; Benedict, 1903: 244; Schmitt, 1921: 162.

Body shrimplike, carapace elongated, with well-defined areas, as a rule with transverse wrinkles; the lateral edges and the linea anomurica are distinct. The rostrum is well developed, triangular, and spiniform. The
80 antennules are not protected. The antennal stalk is four-jointed (the second and third joints are fused), very seldom having a scaphocerite, and as a rule without it; the flagellum is long. The third maxillipeds are imperfectly pediform, the ischium and the merus being narrow and frequently spinulated on the inner side; epipodites are always present. The first pereiopods are chelate, as a rule, long and slender. On each side, there are 14 gills of the phyllobranchiate type, namely four pleurobranchiae and ten arthrobranchiae, disposed as follows: one pleurobranchia on each of the second to fourth pereiopods, and two mastigobranchiae on each of the second to fifth pereiopods, and also on the third maxillipeds. The abdomen is curved ventrally, but is not bent under the thorax: the bend is at the level of the fourth segment, and not the third segment as in the true shrimps. The caudal fan is a well-developed natatory organ. In the male, genital appendages are found on the first two abdominal segments (on the first segment they may be rudimentary, but they are always present on the second); the three subsequent segments bear two-jointed pleopods, with broadened basal parts; these appendages may, however, be rudimentary. The females bear simple three-jointed pleopods on the second to fifth segments (on the second to fourth they may be rudimentary); pleopods are always lacking on the first segment.

The species of this family are chiefly known from the tropical seas, from both the abyssal and the littoral zones. Most of the Galatheidae are benthic and do not seem able to swim freely for great distances. The genus Uroptychus is well adapted to commensalism with sponges, hydroids corals, etc. The abyssal forms are usually blind. Benedict (1903) observed differences in the number of eggs between the littoral and the abyssal forms; the first have numerous small eggs, while the abyssal forms have few large eggs.

Henderson (1888) divided the family into two groups of genera according to the degree to which the abdomen is bent. To the first group belong the genera with a simply curved abdomen (this group in turn is divided into two subgroups: the littoral genera with pigmented eyes and the abyssal genera with unpigmented eyes); in the genera of the second group, the distal part of the abdomen is markedly bent under the proximal part, but not under the thorax; the genera of this group are all abyssal.

A. Milne-Edwards and Bouvier (1894) divided the genera of the Galatheidae into two groups: the "Galathéens flagellés", and the "Galathéens non flagellés". The first group is more primitive, and is characterized by the presence of a nonsegmented flagellum on the exopodite of the first maxillipeds (see name of this group). In addition, the pleopods on segments three to five in the males of this group are foliaceous. The adaptation to the abyssal life is very incipient within this group: the eyestalks are still free and bear pigmented eyes; the ocular segment is also free. The ciliary stripes on the

carapace are well developed; the carapace itself is slender. The anterolateral angle of the carapace always bears a spine. The larvae always hatch during the zoëa stage. In the genera of the second group, the exopodite of the first maxillipeds has no flagellum; the last pleopods of the male lose their foliaceous form and become filiform; the ocular segment is frequently fused with the adjacent areas, and the eyes are atrophied; the carapace becomes firmly calcified, thick and hard; the anterolateral angle of the carapace has no spine; the ciliary stripes gradually disappear. The larvae hatch during the metazoëa stage. "The following characters prove that this is the primitive group of the Galatheidae from which the other higher forms gradually evolved: the reduction of the flagellum on the exopodites of the first maxillipeds, the almost permanent absence of epipodites on the pereiopods, and the modifica-
81 tion and reduction undergone by the pleopods, which have no copulatory function. At the same time we observe an increasing and specific adaptation of these animals to abyssal life: the carapace becomes thick, the eyes cease to be functional organs, and become immovable, fused with their stalk and the rostrum. As may be expected, the antennular setae are strongly developed within this group, which became adapted to great depths" (A. Milne-Edwards and Bouvier).

On the basis of the same characters Ortmann (1901) created the subfamilies Galatheinae (="Galathéens flagellés" A. Milne-Edwards and Bouvier) and Munidopsinae (="Galathéens non flagellés" A. Milne-Edwards and Bouvier).

Key to the Subfamilies

1 (2). Eyestalks free, with well-developed eyes. Exopodite of first maxillipeds ending in a simple flagellum . . . . . 1. Subfamily Galatheinae Ortmann.

2 (1). Eyestalks free or fused with the ocular segment, which is itself frequently fused with the adjacent areas; eyes reduced. Exopodite of first maxilliped without flagellum . . . . . 2. Subfamily Munidopsinae Ortmann.

Key to the Genera

1 (2).* Corneas pigmented. Exopodite of first maxilliped with flagellum (Subfamily Galatheinae).

2 (5). Rostrum neither curved nor laterally compressed.

3 (4). Rostrum triangular and dorsoventrally flattened, with denticulated lateral edges. Supraorbital spines lacking or reduced. . . . . .1. Galathea Fabricius.

82 4 (3). Rostrum spiniform, smooth. Strong supraorbital spines on sides of rostrum. . . . . 2. Munida Leach.

5 (2). Rostrum curved and laterally compressed; edges, particularly the superior one, denticulated. . . 4. Cervimunida Benedict.

6 (1). Corneas not pigmented. Exopodite of first maxilliped without flagellum (Subfamily Munidopsinae). . 3. Munidopsis Whiteaves.

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* [Presumably (6).]

Subfamily **GALATHEINAE**

Galatheinae Ortmann, 1901: 1150.

The eyestalks are free, the eyes well developed. The exopodite of the first maxillipeds has a simple one-jointed flagellum.

1. Genus GALATHEA Fabricius

Galathea Fabricius, 1793: 414; Leach, 1815; Milne-Edwards, 1837: 273; Dana, 1852: 478; Bell, 1853: 195; Heller, 1863: 188; Henderson, 1888: 117; Ortmann, 1892: 248; Benedict, 1903: 246; Stimpson, 1907: 230; Balss, 1913: 1.

Type species: Galathea strigosa (Linné).

The length of the carapace exceeds its width; it is slightly protuberant, and its surface is covered with numerous transverse hairy lines. The carapace is usually smooth except for the anterior part of the gastric area. The lateral edges bear spines or denticles. The cervical groove is deep and distinct. The cardiac area is not protuberant. The rostrum is triangular and dorsoventrally flattened, frequently bearing a longitudinal furrow on its superior surface; the lateral edges of the rostrum are, as a rule, denticulated; of these denticles, two are situated above the eyes and are evidently homologous to the supraorbital spines of Munida. The first joint of the antennular stalk is large and bears a number of distal spines; the two subsequent joints of the stalk are slender and subequal in length as the first joint; the flagella are very short. The antennal stalk has three stout proximal joints; the first two joints bear strong spines; the flagellum is long. The eyestalks are short, strong, somewhat broadened distally, and partly hidden under the rostrum; the orbit is delimited ventrally by a denticulated crest. The third maxillipeds are straight, their two distal joints being neither foliaceous nor broadened. The second joint has a minute denticulation on the interior part of the posterior edge and is spinulated on its anterior edge. The third joint is generally shorter than the second and bears one or two spines on its inner edge. The first pair of pereiopods are chelate, moderately long and spinulose: the dactyli are distally spoonlike and convex. The second to fourth pereiopods are simple. The fifth pair of pereiopods are small; they are partly bent under the carapace and bear small chelae. The abdomen is almost as wide as the carapace, but is slightly longer. The anterior edges of the segments are smooth; the caudal fan is broad.

83 The species of this subfamily are mostly littoral, but some of them are also found at considerable depths. They prefer rocky bottoms and are especially abundant in the tropical seas among sponges and coral reefs.

Key to the Species

1 (4). Anterior part of gastric area with only two spines.
2 (3). Basal spines of rostrum small. Superior edge of meri of second pair of pereiopods with minute spines. . . . 1. G. strigosa (Linné).
3 (2). Basal spines of rostrum fairly strong. Superior edge of meri of second pair of pereiopods with 11 or 12 strong pointed denticles . . . . . 2. G. acanthomera Stimpson.
4 (1). Anterior part of gastric area with more than two spines.
5 (6). Lateral edges of rostrum smooth and unarmed beyond the basal spines. Broad gap remains open between chelae when closed. Each abdominal segment with a transverse furrow. Body moderately pubescent . . . . . 3. G. integra Benedict.
6 (5). Lateral edges of rostrum bear three or four spines on each side beyond basal spines. When closed, chelae approximate closely. Each abdominal segment with four transverse furrows. Body highly pubescent. . . . . 4. G. pubescens Stimpson.

1. Galathea strigosa (Linné) (Figure 30)

Cancer strigosus Linné, 1766: 1053. – Galathea strigosa Risso, 1826: 47; Milne-Edwards, 1837: 273; Bell, 1853: 200; Heller, 1863: 189, Pl. 6. Figures 1-2 (literature) Ortmann, 1892: 250, Pl. 11, Figure 6 i.

The surface of the carapace has transverse furrows, of which the four deeper ones are located beyond the cervical groove; on the anterior edge of each furrow are short hairs, directed forward. The rostrum is triangular, with a pointed tip, and bears three spines on each side (more correctly, four spines, since, under the inferolateral spine, an additional small one is usually found). The dorsal surface of the rostrum has a slight dorsal furrow at its base. The gastric area bears a pair of spines near the base of the rostrum and a lateral spine on each side. The hepatic area bears a spine in its anterior half. The lateral edge of the carapace usually bears eight spines. In front of the strong spine at the anterolateral corner, another very small spine is found; below it are two or three more spinules. The eyes are fairly large, with short eyestalks. The first joint of the antennular stalk is broad and bears three strong spines. The other joints, articulated between the internal spine and the median spines, are long and cylindrical, while the flagella are very short. The second joint of the antennal stalk
84 bears spines at the distal end of the internal and external edges. The third joint bears a spine at the distal end of the internal edge. The third maxillipeds are short; the merus is longer than the carpus and bears a spine at the distal end of the inferior edge; the internal edge has a minute denticulation; the carpus bears two strong spines on its inferior edge. The chelipeds are fairly long, spinulose, and pubescent. The ischium has one or two spines on its internal edge, which becomes sharp toward the distal end. The merus bears three strong spines on the distal half of its internal edge and two spines on its superior surface; it also bears a row of smaller spines on the external edge; on the inferior part of the interior side there is a row of spines, which starts from the end of the ischium. The carpus is shorter

than the merus; it bears two strong spines on its internal edge and two rows of spines on its superior surface; these rows are situated near the margins, so that the middle of the joint remains smooth or bears two or three tiny spinules; on the inferior part of the internal surface two spines are found. The propodus is fairly long, becoming somewhat broader distally, and it is rounded at the insertion of the dactyli. The superior surface of the propodus and of the dactylus is flat. The lateral edges of the propodus and the external edges of the dactyli bear strong spines. In the proximal half of the propodus, below the internal row of marginal spines, another row is found; it is usually made up of three spines. A row of small spines extends somewhat diagonally from the external proximal angle of the superior surface of the propodus to the gap between the dactyli. There is a row of similar spines at the middle of the superior surface of the immovable dactylus. The base of the movable dactylus bears a spine on its superior side and one on the inferior side. The inferior surface of the propodus is convex and has no spines. Both dactyli are identical in form and thickness; the prehensile edges bear pointed tubercles, which become gradually longer distally. The ends of the dactyli are concave and spoonlike; when closed, the tubercles of one dactylus correspond to the spaces between the tubercles of the other dactylus. The three subsequent pairs of pereiopods have somewhat flattened joints; the meral and carpal joints have spinulated anterior edges; the meral joints have a strong spine at the distal inferoposterior end, and two smaller spines. The anterior edge of the propodus bears small spines in the proximal half and on the posterior edge; the dactyli are short and wide, and almost straight at the base. The abdominal segments are smooth and have the same hairy transverse furrows as the carapace. The telson tapers distally and has a deep incision on its posterior edge, which consequently appears bilobate. The superior surface bears flat granules, surrounded by a crown of cilia directed backward. The plates of the uropods have broad carinae situated nearer to the external edge, and bear transverse rows of short movable spinules.

Coloration: reddish, with a number of blue transverse stripes and spots (Bell, Heller); the body is dark red, with blue stripes and red hairs (Risso); the specimens preserved in alcohol have a pale yellowish coloration.

86

Dimensions

Total length	44.0 mm
Length of rostrum	7.0 mm
Length of merus of cheliped	12.5 mm
Lengh of carpus of cheliped	8.0 mm
Length of chela of cheliped	17.0 mm
Width of chela of cheliped	5.5 mm
Length of dactyli of cheliped	7.5 mm
Length of second pereiopods	31.0 mm

Distribution. Adriatic Sea and Mediterranean Sea; shores of England, Ireland, Belgium, Denmark, Sweden and Norway (up to Varanger Fjord). Yarzhinskii (1870) recorded this species from the West Murman coast without

indicating the exact locality; after this author, nobody found G. strigosa in Soviet seas, but the possibility of a chance appearance of this species, owing to Atlantic streams, should not be overlooked; therefore we include it in the present work.

(85)

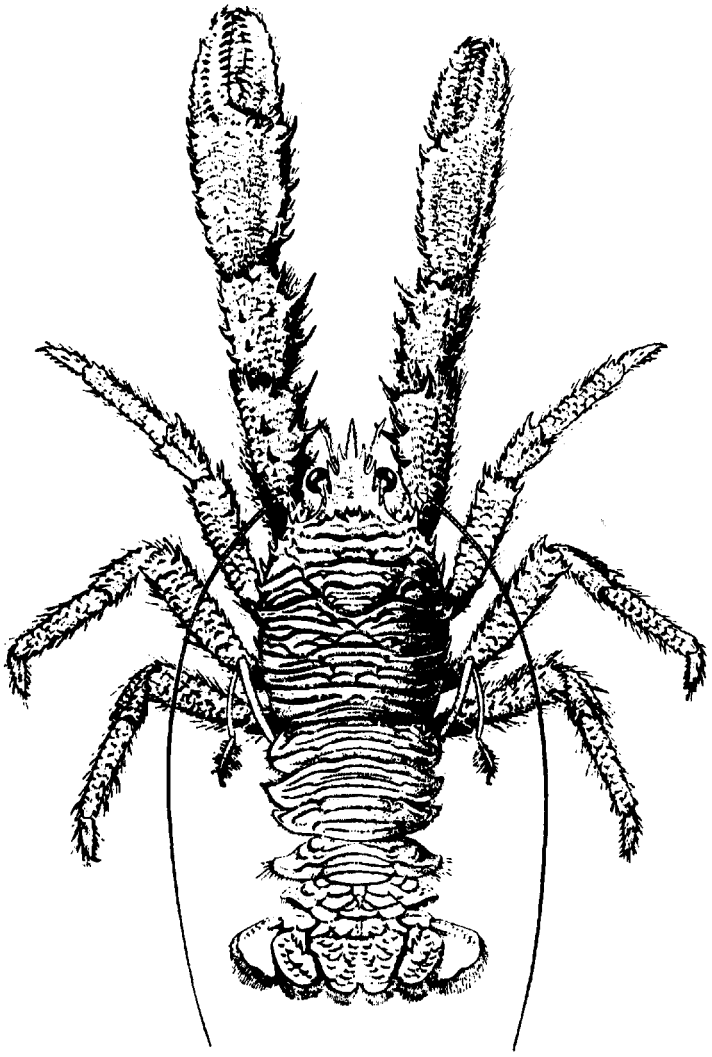

Figure 30. Galathea strigosa (Linné)

G. strigosa is found from the limit of the tidal zone to depths of about 65 meters; it prefers rocky and sandy bottoms.

[From Bell, 1853]

"It frequents pools between tide-marks, where there are loose stones and sand. It is, generally speaking, very slow in its motions, though it

will frequently move with very great activity, especially when alarmed. From the great length of its first pair of legs, its motions are always retrograde. In walking its pace is tardy; but in swimming it darts from spot to spot with the rapidity of an arrow. It is never seen in any exposed part of the pool, but always seeks the shelter of stones, or some hole in the rock, so that it can retire on the least alarm. It is very remarkable to witness the accuracy with which they will dart backward, for several feet, into a hole very little larger than themselves; this I have often seen them do, and always with precision."

2. Galathea acanthomera Stimpson

Galathea acanthomera Stimpson, 1858: 252; 1907: 232, de Man, 1907: 402; Balss 1913: 2; Figure 1; Yokoya, 1933: 55. – Galathea orientalis Ortmann, 1892: 252, Pl. 11, Figure 10 (nec Stimpson).

The length of the rostrum and its relative width vary. The lateral spines of the rostrum are pointed; the basal spine of the rostrum, the first of these spines, is directed straight forward or outward; the second spine curves slightly inward or is directed straight forward. The terminal spine, which is about two fifths of the total length of the rostrum, bears on its lateral edges four to six microscopic spinules and a few hairs. The length and form of the rostral spines is somewhat variable. Immediately behind the
87 transverse line, which extends between the bases of the first and second lateral spines, are two median spines situated close together. The superior surface of the rostrum is partly covered by a median pubescence, made up of short hairs, disposed in parallel arcuated rows on both sides and near the median line. At the level of the base of the fourth lateral spine, a long median hair is found, and there are two more hairs almost in the middle of the rostrum, one on each side of the median line. The lateral edges of the carapace bear nine spines. The first spine is situated at the outer angle of the orbit, and slants outward. The second spine has a less definite outward slant and is nearer to the first spine than to the cervical groove. The third spine is smaller than the second, and is situated on the superior surface near the cervical groove, some distance from the lateral edge. The fourth spine is found below the lateral edge and is the same length as the second spine. Beyond the cervical groove, the lateral edge bears five more spines of equal length and disposed at equal distances. Their length is the same as that of the second spine, with the exception of the last one, which is sometimes shorter. Behind the two spines, the surface of the carapace bears about seven transverse crests; the hairs on the crests are 0.3 to 0.35 mm long. On the superior surface of the carapace, the rostrum, and the abdomen there is a rough, dense sculpture of small hollows. The anterior edges of the abdominal segments are pubescent and bear a few additional moderately long hairs. Similar scattered hairs are also found on the lateral parts of the superior surface of the carapace. The third joint, considered from the end of the antennal stalk, has a strong spine on its superior surface

and a similar one on the inferior surface. The penultimate joint bears a smaller spine on its superior surface. The ischium of the third maxillipeds is somewhat longer than the merus, its external edge ending distally in a visible tooth which is bent slightly inward, while its internal edge ends in a shorter but thicker cylindrical tooth. The two pointed teeth on the internal edge of the merus are stronger than the teeth of the external edge; the anterior spine on the external edge is sometimes curved inward and is situated at the distal end; near the middle of the edge, another spine is found. The external edge of the carpus bears two or three pointed spines, and in front of these another small pointed denticle is found. The slender stalk of the exopodite is slightly longer than the merus. The chelipeds are not quite even; the movable dactylus of the large chela bears a fairly strong, moderately pointed tooth a third of the way along it, and from this tooth to the end of the prehensile edge are 25 blunt denticles; the immovable dactylus, as well as the dactyli of the small chela, bear only minute denticles on their prehensile edge; in the large male specimens, the dactyli, when closed, show open gaps. The merus of the second pair of legs bear along the entire length of its superior edge 11 or 12 strong, pointed denticles of almost equal length; the inferior edge is also slightly denticulated and ends at the distal end in a pointed spine, which extends slightly beyond the rounded end of the
88 merus. The external edge of the carpus bears four to six pointed spines of about the same length as the spines of the merus; the apical spine is somewhat longer than the others. The propodus bears in the proximal half of its superior edge three or four spines, slightly smaller than those of the merus, while the inferior edge bears six movable spines, which are almost the same length as the spines on the superior edge. The dactylus is slightly more than half the length of the propodus; it ends in a curved claw, and its inferior edge bears six movable spinules, which become gradually longer in a distal direction. The superior edge of the merus is covered with hairs, which are partly pinnate. The posterior surface bears transverse rows of short hairs, and, near the inferior edge, long hairs. The subsequent joints are also hairy. The third and fourth pairs of legs are identical with those described above, but the spines on the superior edge of the merus of the fourth pair are relatively smaller. The chelipeds and the walking legs have no epipodites.

The color is pale yellowish red. The rostrum is whitish, as are the lateral spines of the carapace. The hairy crests on the carapace and the abdominal segments are dotted with small red spots. The merus and the propodus of the second to fourth pereiopods each bear two dark-red transverse stripes (de Man). According to Stimpson, their color is grayish.

Dimensions

Length of carapace	7.2 mm
Width of carapace	5.0 mm
Length of rostrum	2.7 mm
Width of rostrum (at its base)	1.5 mm
Length of ischium of third maxillipeds	1.5 mm
Length of merus of third maxillipeds	1.2 mm
Length of large cheliped	20.0 mm
Length of small cheliped	18.0 mm

Galathea orientalis Stimpson (1858), described from Hong Kong, is doubtless a different species; its carapace is covered with short hairs; the lateral edges of the carapace bear six spines; the first lateral spine of the rostrum is small; the chelipeds are fairly thick; the movable dactylus has two denticles; the superior edges of the meri of the walking legs are densely covered with small regular spines.

Distribution. Bonin Islands; South Japan, near Tottori, on the western shore of Japan. Littoral, and to depths of 200 m.

3. Galathea integra Benedict (Figure 31).

Galathea integra Benedict, 1903: 248; Balss, 1913: 7, Figures 4-5; Yokoya, 1933: 55.

The rostrum has the form of a broad membranous leaf, with perfectly
89 smooth edges; its tip is pointed, bearing on either side of the base two small spines, situated in the internal angle of the orbits. The surface of the rostrum is smooth and sometimes concave between the eyes. The external corners of the orbits bear spines. A short distance behind these spines are the smaller spines at the anterolateral angles of the carapace. On the surface of the carapace are a few transverse stripes bearing long hairs. On the gastric area is a transverse row of four spines. The lateral edges of the carapace bear six or seven spines, which are often missing. The merus of the third maxillipeds is much shorter than the ischium and looks like a broad almost square plate, terminating in a pointed tooth at the internal edge; the external edge bears a spine. The chelipeds are long and slender; the merus bears sparse, short, thick spines; the carpus
90 bears a row of four spines on its superior surface, and a row of five or six spines on its internal edge, but the most prominent is a very large spine situated a little below the internal row; the propodus bears three rows of spines, the spines on the crest being the most numerous and the strongest; the dactyli are shorter than the propodus; they bear a minute denticulation on their prehensile edges, and when they are closed, a wide gap is left open; all the joints are covered with fine hairs. The meral joints of the pereiopods bear a few spines on the superior edge.

91

Dimensions

Length of carapace and rostrum.	7.0 mm
Width of carapace	4.0 mm
Length of cheliped.	17.0 mm

Distribution. South Japan (Yokoya, 1933). In the Sea of Japan it is found north of Noto; it has also been recorded in Tsugaru Strait and from Aomori. At depths ranging from 71 to 307 m.

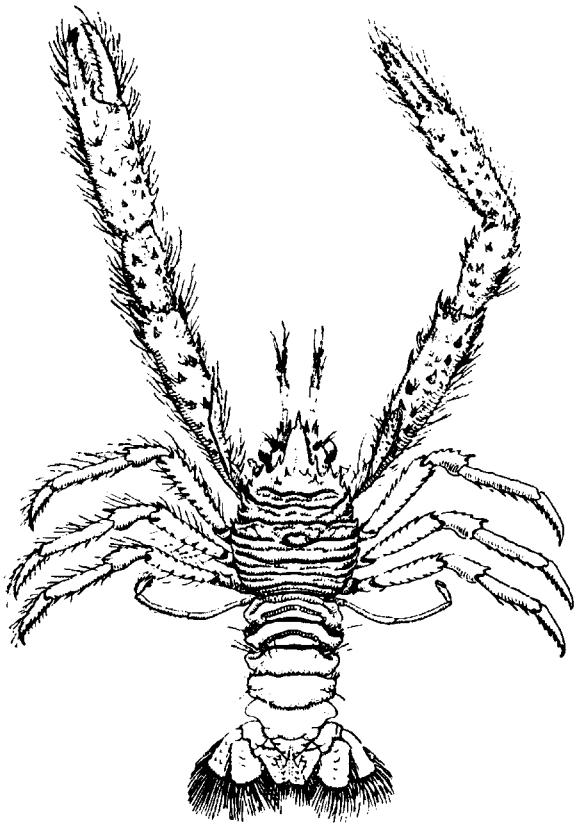

Figure 31. Galathea integra Benedict (From Balss, 1913)

4. Galathea pubescens Stimpson (Figures 32, 33).

Galathea pubescens Stimpson, 1858: 252; 1907: 233; Balss, 1913: 11, Figures 11-12; Yokoya, 1933: 57.

The carapace is regularly and evenly protuberant, tapering somewhat anteriorly. The superior surface bears many transverse furrows, only a few of which cross the whole cephalothorax; the whole surface is markedly pubescent, the hairs of every row being fairly long and reaching the following row. The gastric area is indistinctly defined and, near the center, bears three small spinules, the median one situated slightly behind the other two (according to Balss, the gastric area bears a row of six to eight spines). The lateral edges of the carapace bear six to eight spines. The rostrum is

large, triangular, very pointed, with dense hairs on its superior surface and four spines on each edge. The spines are very pointed and are directed forward; sometimes, an additional spine is found between the basal spine and the second one. The basal joint of the antennules bears two spines, directed forward. The merus of the third maxillipeds bears three inner and two outer spines. The chelipeds are long, slender and cylindrical, with scattered hairs and spines; sometimes, however, a strong spine is found on the carpus (according to Balss, the chelipeds are thickly covered with small scales, disposed in straight rows, from which long slender hairs arise); the dactyli are flat and parallel; they close perfectly, and are shorter than the propodus. The pereiopods are moderately long and very pubescent. The superior edge of the meri bears from seven to nine very
92 slender spines; the dactyli correspond to about half the length of the propodus. Epipodites are found only on the chelipeds. The abdomen is pubescent; each of its segments bears four furrows, the median ones being the deepest. Its coloration is reddish, sometimes with darker spots, and with a white dorsal median stripe.

Distribution. Japan, on the eastern shore of Oshima, Hakodate area; Uraga Strait; Sagami; western Muroto Cape. At depths to 234 m.

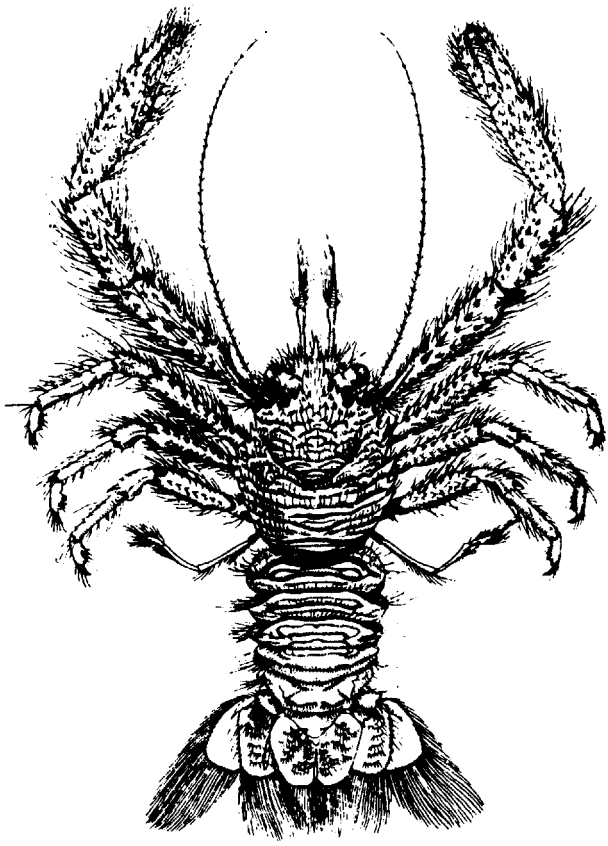

Figure 32. Galathea pubescens Stimpson (From Balss, 1913)

2. Genus MUNIDA Leach

Munida Leach, 1820: 52; Bell, 1853: 206; Heller, 1863: 192; Henderson, 1888: 123; Holmes, 1900: 111, Benedict, 1903: 251; Stimpson 1907: 235; Balss, 1913: 15.

Figure 33. Galathea pubescens Stimpson, third maxilliped (From Balss, 1913)

Type species: Munida bamffica (Pennant).

The length of the carapace exceeds its width. The transverse folds bear dense short hairs on their anterior edges, and are more numerous and more marked than in the genus Galathea; the cervical groove is always well marked; the cardiac area is distinct; the subbranchial areas are not protuberant and are separated from the dorsal surface by well-marked lateral edges, less curved than in the previous genus; the spines on these lateral edges are longer and more pointed, and the two spines situated in the antero-lateral angle are stronger than the others. The rostrum is long, slender, and awl-shaped; on both its sides, well-developed supraorbital spines are found. The vertical part of the frontal area does not form an external orbital crest, or at best it forms a rudimentary one, always lacking denticles; instead of this crest, a rather small spine may sometimes be observed; in some species of the subfamily Munidopsinae, this spine is more developed. The eyestalks are short, and become much broader distally; the eyes are large and well pigmented. The antennular stalks are longer than in the genus Galathea; the same is true for the third maxillipeds. The first pereiopods are very long, slender, and spinulose. The three subsequent pairs of pereiopods are also fairly long; the dactyli are long, straight, and slightly curved; they lack visible denticles on their inferior edge, but bear numerous minute corneous spinules. The abdomen bears transverse raised lines; the anterior edges of some of the first segments bear spines or are smooth. The telson is broad, almost square.

The species of this genus are always more spiniferous than those of the genus Galathea. According to Milne-Edwards and Bouvier (1894) they are more distantly related to the Macrura than are the species of Galathea. Moreover, the genus Munida differs from Galathea in that its species live at greater depths. Thus, in this genus littoral species are completely unknown and none of them are found at depths less than 20 to 40 meters; the
93 closest to the littoral is M. bamffica (found at a depth of 20 m), but it nevertheless descends to great depths. In our work, we deal with the

European species M. bamffica and with the Far Eastern species M. japonica, the western shore of Japan.

Key to the Species

1 (2). Gastric area of carapace lacks transverse row of spines. Dactyli of first pereiopods longer than propodus. Second abdominal segment (in large specimens also segments three and four) armed with spinules on anterior edge . . . . . †1. M. bamffica (Pennant).

2 (1). Anterior transverse row of 13 spines on gastric area. Dactyli of first pereiopods same length as propodus or shorter. All abdominal segments smooth . . . . . 2. M. japonica Stimpson.

†1. Munida bamffica (Pennant) (Figure 34)

Astacus bamfficus Pennant, 1777: 17, Pl. 13, Figure 25 (quoted from Hansen, 1908). – Galathea rugosa Leach, 1815, Table 29; Risso, 1826: 46; Milne-Edwards, 1837: 274. – Munida rugosa Heller, 1863: 192, Pl. 6, Figures 5-6; Ortmann, 1899: 253. – Munida rondeletti Bell, 1853: 208. – Munida bamffica Ortmann, 1892: 253; Milne-Edwards and Bouvier, 1894: 83, Pl. 7, Figures 1-7; Hansen, 1908: 32, Pl. 2, Figure 3a.

The rostrum has the form of a long, almost straight spine. The supraocular spines extend almost to the middle of the rostrum. Behind them, on the superior surface of the carapace, are two small spines. A pair of spines are also found on each of the branchial areas. The lateral margins of the carapace are spinose (usually with seven spines); the first spine, which is situated below the base of the antennae, is the strongest. There are two spines behind the cervical groove. The entire surface of the carapace is crossed by transverse hairy wrinkles. The posterior edge of the carapace bears spines which are directed forward, viz., two median and two to five lateral ones near the posterolateral angle of the carapace (the number of these lateral spines varies). The eyes are large. A ciliated border, which extends over the cornea, is situated on the boundary between the cornea and the eyestalks, chiefly on the dorsal surface. The first joint of the antennular stalk is very long, reaching the tip of the eyes, or extending slightly beyond. The third maxillipeds, when stretched, almost reach the end of the rostrum; the merus is longer than the carpus; the posterior edge has a minute denticulation; the anterior one has long hairs and a long apical spine; there is another spine on the internal surface of the carpus a short distance before the middle. The first pereiopods are very long; all the joints are almost the same width, and are not excessively pubescent. The internal edges of the merus, the carpus and the propodus bear
94 strong spines, those at the distal ends of the first two joints being the strongest. Above and below these marginal spines, smaller spines are found, disposed in a not quite regular longitudinal row. The superior surface of these three joints bears a median longitudinal row of spines, which continues

from one joint to the next, but the distal spines on each joint are larger than the others; on the propodus, the distal spine of this median row is situated above the base of the movable dactylus. The external edges of the merus and of the carpus do not bear visible spines; on the propodus, however, a row of minute spines is observed. On the inferior side of the propodus there is a large spine over the base of the movable dactylus. On the base of the movable dactylus–on the superior as well as on the inferior surface–spiniform outgrowths are found; they adhere to the above-mentioned spines, and rub against them during the movement of the dactylus. In addition, a fairly large, forward-directed basal spine is found on the external edge of the movable dactylus. The propodus is narrow. The dactyli are slightly longer than the propodus, and have numerous small tubercles on their prehensile edges, larger tubercles alternating with some (three to five) smaller ones; the tips of the dactyli are curved, and the tip of the immovable dactylus is bifurcated, so that the tip of the movable dactylus enters this incision when the chela is closed. The three subsequent pairs of pereiopods are somewhat compressed, with spinulose edges, especially those of the meral and the short carpal joints; the distal spines of these– both on the superior and the inferior edges– are stronger and less pubescent. The anterior edge of the second abdominal segment bears six spines directed forward (one pair of median and two pairs of lateral spines); the anterior edge of the third segment bears four spinules (two median and two lateral ones), while the anterior edge of the fourth segment bears two spinules (one median pair). The telson is broad, with an incision half way along the posterior edge. The superior surfaces of the second to fourth abdominal segments each bear one deep transverse furrow, with short hairs directed forward. Similar hairs are found on the anterior edges of these segments, the rest of their surface having transverse wrinkles, forming on the epimera a peculiar pattern resembling watered silk. The superior surface of the telson and of the uropods is covered with low prominences, which bear short hairs oriented backward; some of them also bear spines. The posterior edges of the uropods and of the telson have a minute denticulation and bear two rows of long hairs: the superior row, which is composed of simple, slender, shorter hairs, and the inferior one, of longer, thicker, pinnate hairs.

Dimensions	♀	♂
Total length (from end of rostrum) . .	48.0 mm	76.0 mm
Length of rostrum	9.5 mm	15.0 mm
Length of supraocular spine	5.0 mm	9.5 mm
Total length of cheliped.	55.0 mm	133.0 mm
Length of merus of cheliped.	20.0 mm	48.0 mm
96 Length*of merus of cheliped	8.0 mm	18.0 mm
Length of chela of cheliped	26.5 mm	62.0 mm
Width of chela of cheliped.	3.5 mm	6.5 mm
Length of dactyli of cheliped.	15.0 mm	35.0 mm
Total length of second pereiopod . . .	39.0 mm	87.0 mm

The synonymy of this species is somewhat unclear. Some authors consider M. rugosa Sars to be an independent species. Ortmann (1892) enumerates the following characters which in his opinion distinguish M. rugosa from M. bamffica: 1) the eyes have a ciliate border, which is lacking in

* [Obvious error in Russian text: should be width.]

M. bamffica; 2) the supraocular spines are hardly divergent and almost parallel with the rostral spine; the three spines are on almost the same plane, while in M. bamffica the supraocular spines are above the rostral spine; 3) on the posterior edge of the carapace are four to six spines directed forward, viz., two median ones and one or two on each side; 4) three abdominal segments bear spines (in M. bamffica only two), i. e., the first bears six, the second bears four, and the third bears two.

(95)

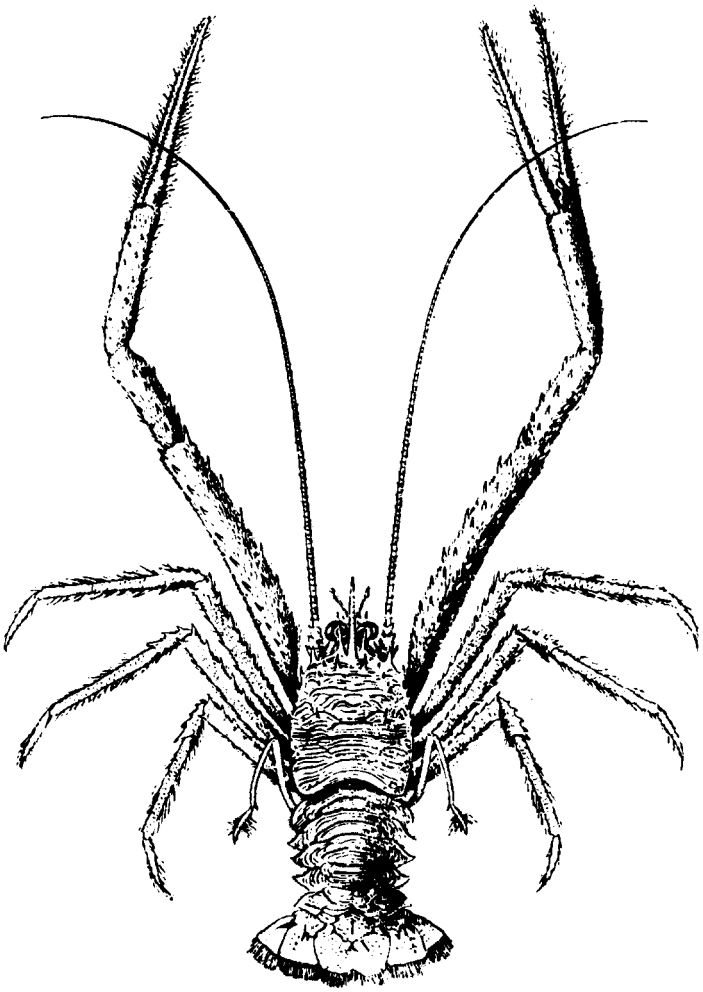

Figure 34. Munida bamffica (Pennant)

In the collections of the Zoological Institute of the Academy of Sciences of the USSR, there is a large male specimen from Nice labeled M. bamffica. A thorough study of this specimen revealed that the armature of the abdominal segments corresponds almost entirely to Ortmann's indications: six spines on the second segment, four on the third, but none at all on the fourth. At the edge of the cornea there is a distinct border, which is, however, formed by shorter cilia. The chelipeds are more pubescent than in small specimens. The two median spines on the posterior edge of the carapace are missing. There is one lateral spine on the left side, and two spines on the right. In the specimens labeled M. rugosa from western Norway, the variability of the number of lateral spines on the posterior edge of the carapace must be noted. In seven small specimens from collections on board "Andrei Pervozvannyi", the armature of the anterior edges of the second to fourth abdominal segments was found to be highly significant; thus, in one of the specimens, the second segment had four distinct spines; on the third segment there were only tubercles, which may have been primordia of spines (as they were in the places where the spines ought to have been); on the fourth segment, not even tubercles were found. In the other specimens, on the second segment there were four spines, on the third segment the two median spines were well developed, and the two lateral pairs were in the form of tubercles, and the fourth segment also lacked spines.

The above indicates that the differences between M. rugosa and M. bamffica are merely age differences within the same species. In fact, Ortmann's first item is incorrect: cilia are found also in M. bamffica, but they may become shorter with age. The second item may also be easily explained by modifications due to age: as the rostrum grows and becomes
97 longer, its tip curves slightly downward, thus leaving the plane of the supraocular spines. The third character usually varies considerably and thus cannot serve as a differential character. Finally, the fourth item proves beyond doubt that these modifications are due to age. The succession in the appearance of spines, firstly on the second segment, then on the third, and finally-in the largest specimens-on the fourth, is quite obvious. The identity of M. rondeletii Bell with M. bamffica is also obvious.

Coloration: reddish brown (Heller), dark reddish yellow, with spots of a deeper red (Bell), reddish with yellow hairs (Milne-Edwards), rust-red with violet spots and streaks; the six abdominal segments are traversed by violet stripes (Risso).

Distribution. Shetland Islands. Shores of England, Ireland, and France, to Madeira and past Cape Boyador, up to 25° 41'N. lat.; Mediterranean and Adriatic Seas; shores of Sweden and Norway to the West Murman coast (72° 34'N, 17° 20'E long.). In the collections of the Zoological Institute of the Academy of Sciences, there are numerous specimens of this species, captured by the "Andrei Pervozvannyi" on 28 July 1899, 69° 50'30"N, 47° 09' E, 75 m. In addition, this species is noted by K. M. Deryugin (1924) from Kola Bay: 70° 00'N, 33° 30'E, 146 m. Finally, N. Tanasiichuk (1927) tells of the capture of this species between the Sedlovatyi and Bol'shoi Olenii Islands, and south of Sal'nyi Island.

The locations listed above indicate that - owing to the warm Atlantic waters- M. bamffica penetrates somewhat farther east than A. A. Birulya thought (72° 34'N, 17° 20'E). Nevertheless, this species is relatively scarce

in the Murman waters, this being the easternmost limit of its range. It lives at depths ranging from 23 to 1, 244 m.

2. Munida japonica Stimpson (Figure 35)

Munida japonica Stimpson, 1858: 252; 1907: 235; Miers, 1879: 51: Ortmann, 1892: 254, Pl. 11, Figure 11; de Man, 1902: 724; Balss, 1913: 15, Figure 4; Yokoya, 1933: 58. – Munida heteracantha Ortmann, 1892: 255, Pl. 11, Figure 12.

The carapace is elongated. The rostrum is less than half as long as the carapace and more than twice the length of the supraocular spines. The eyes are large, and covered with long hairs. The lateral edge of the carapace bears five median spines, and its anterior angles bear three spines, the anterior one being the largest. The superior surface of the carapace is richly sculptured, most of the furrows traversing its entire surface in unbroken lines. The anterior part of the gastric area bears a transverse row of 13 spinules. Of these, the one found on the median line is somewhat displaced backward; the spines of this row, which are situated behind the supraocular spines are the strongest; on their lateral sides, four spines are found, and between them and the median spine is one small spine. The lateral parts of the cephalothorax bear three additional pairs of spines: one pair on the gastric area, another on the portion delimited by the bifurcation of the cervical groove, and the third immediately behind
98 the cervical groove. The chelipeds are long, straight, subcylindrical and squamate, with a few scattered spines. The dactyli are straight and slender; in the male they are shorter than the propodus, and have a basal gap; in the female they are the same length as the propodus, and the basal gap is almost absent. The ischium of the second [sic] maxillipeds is longer than the merus, which bears three spines on its internal surface. The abdominal segments are smooth.

H. Balss, who has a rich collection of this species, considers that Ortmann's species Munida heteracantha is merely a variety of M. japonica, and he presents the following table of comparison between the maximum deviation of the characters of these forms.

M. japonica typica Stimp.	M. japonica heteracantha (Ortm.)
Rostrum twice as long as supraocular spines. Carapace fairly wide (ratio of length to width – 11 : 9.5).	Rostrum three or four times as long as supraocular spines. Carapace long (ratio of length to width-12:9).
Superior surface of carapace richly sculptured; most furrows cross its entire width in uninterrupted lines.	Superior surface of carapace less furrowed; furrows usually interrupted.
Lateral parts of carapace with three spines.	Lateral parts of carapace with only two spines; the spine usually found between bifurcation of cervical groove is missing.

Second and third abdominal segments without spines.	Second abdominal segment with eight to eleven spines; the third with three spines.
Each abdominal segment with four to six adjacent furrows.	Each abdominal segment with only two furrows.
Surface of walking legs richly sculptured, with scales and hairs.	Surface of walking legs slightly sculptured, but more pubescent. Marked denticulation on inferior side.
Chelipeds relatively short and broad.	Chelipeds long and narrow.

From the comparison of the diagnoses of the two species, two additional items may be noted:

Eyes large, flattened, and with long cilia.	Eyes smaller, less flattened, and with short cilia.
Merus of second maxillipeds with three spines on internal surface.	Merus of second maxillipeds with two spines on internal surface.

100 H. Balss notes, morever, that all these characters are not segregated and that there is a perfect intergradation between these extreme forms; so for instance, specimens belonging to the forma typica bore spines on their abdominal segments, while specimens belonging to forma heterachantha had a smooth third segment. Munida sagamiensis Doflein is such an intermediate form, closer to forma heteracantha as well as M. honsuensis. According to Balss, the variety heteracantha prefers deeper waters.

Distribution. South Japan, up to Tsugaru Strait. On the western shores of Japan, at Noto, in the Toyama-Niigata Bay, Sado Island; in addition, it has been recorded fromTsugaru Strait and Aomori. At depths to 543 m.

Subfamily **MUNIDOPSINAE**

Munidopsinae Ortmann, 1901: 1151.

The eyestalks are either free or fused with the ocular segment. The ocular segment is often fused with the adjacent areas. The eyes are rudimentary. The exopodite of the first maxillipeds has no flagellum.

3. Genus MUNIDOPSIS Whiteaves

Munidopsis Whiteaves, 1874: 212; Henderson, 1888: 148; Milne-Edwards and Bouvier, 1894: 271; Schmitt, 1921: 167.

Type species: Munidopsis curvirostra Whiteaves.

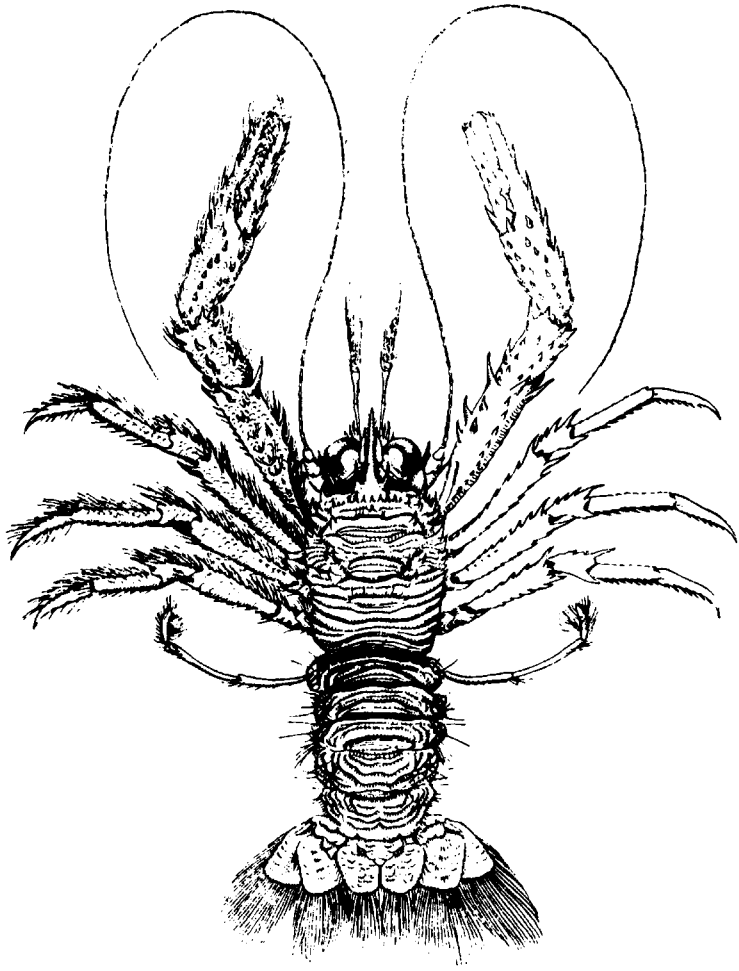

Figure 35. Munida japonica Stimpson (From Balss, 1913)

The carapace is more or less flattened, mostly with a rectangular outline; the dorsal surface bears transverse wrinkles, but these are usually short, and sometimes divided into sections having the form of scales; the surface is sometimes spinulose; sometimes it completely lacks hairs, and is covered with more or less marked tubercles; the areas are very well defined when the carapace has the above-described armature (wrinkles, spines, hairs), but they become indistinct as this armature disappears; the lateral edges of the carapace are arcuate or straight. The rostrum is well developed and spiniform. Sometimes, small supra-antennal spines are found, but never long supraocular ones as in Munida.

In some species, the eyestalks are still quite long, free, and slightly broadened distally, but most often they are short and bear a spine on the border of the cornea; in some species the eyestalks are fused with the orbit and are immovable; the corneas are not pigmented. The antennular flagella are well developed, and in most cases they bear a great number
101 of hairs. The chelipeds and the walking legs are of variable lengths and bear numerous spines. The integument is well calcified. The eggs are few, but large.

The reduction of the eyes and the parallel development of the antennal and the antennular flagella shows that this is undoubtedly an abyssal genus. Most of the species were described following deep-sea expeditions. This genus has a wide distribution, chiefly in tropical seas, and inhabits depths ranging from 1, 000 to 2, 500 m; a few species have been found at depths below 4, 000 m (e. g., M. reynoldsi, at about 4, 300 m, near the Antilles Islands, West Indies). This genus is represented by one species in the Soviet fauna.

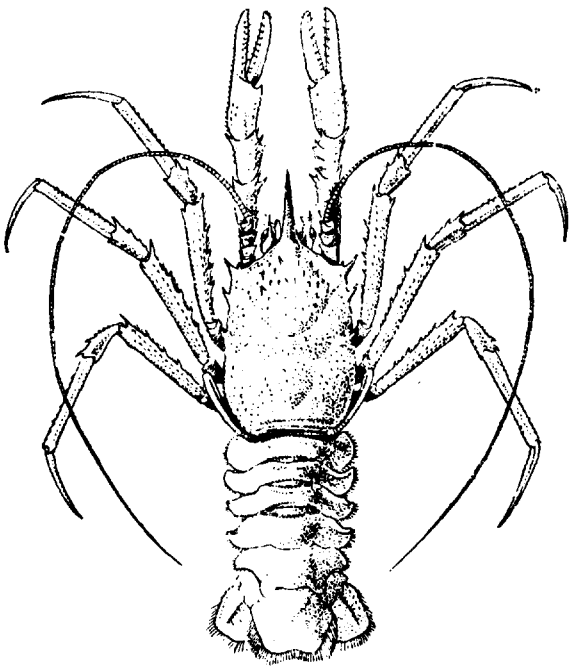

Figure 36. Munidopsis beringana Benedict

†1. Munidopsis beringana Benedict (Figure 36)

Munidopsis beringana Benedict, 1903: 279, Figure 23; Rathbun, 1904: 167.

The length of the carapace exceeds its width and is thickly covered with papillae and crowns of
102 hairs; the papillae on the posterior part of the carapace are often fused in short transverse rows. The anterolateral angle of the carapace bears a strong spine, with a second one behind it; in the middle of the lateral edge are two small spines; the posterior edge of the carapace is straight. The rostrum is long and awl-shaped; it is curved and directed forward. Two thirds of the distance between the rostrum and the spine at the anterolateral angle the frontal edge is markedly thickened. The gastric area bears two fairly strong spines behind the rostrum; a group of less distinct spines is found on the remaining surface of the gastric area; according to Benedict, their number fluctuates between 15 and 20. The cervical groove is broad and

visible, owing to the lack of pubescent granules on it; the triangular cardiac area is also bounded by smooth furrows. The eyestalk bears a long pointed spine on the superointernal surface of the unsegmented cornea. The chelipeds are relatively short, and – like the walking legs – are covered with short hairs. The merus has two strong spines on its superoanterior edge. The carpus bears a row of spines (usually four) on the internal edge, and an irregular row of smaller spines on the external edge, the anterior one being the strongest. The propodus bears spines on its internal edge, the basal spine being the strongest; the superior surface and the external edge have small scattered spines. The dactyli have a uniform thickness; they are somewhat longer than the propodus, their prehensile edges having a slight denticulation; the dactyli adhere closely when closed, and the movable dactylus extends slightly beyond the tip of the immovable one. The meral joints of the three subsequent pairs of pereiopods have a spine at the superodistal end, and strong spines on the superior edge. The carpi each bear two spines on their superior edge; the propodi lack spines; the dactyli are long, curved and smooth on their superior part; their inferior edge has a minute denticulation, and each of the lateral surfaces bears a row of thick hairs on the carina. The fifth pereiopod, when extended, only just exceeds the distal end of the merus of the fourth pereiopod. The superior surface of the abdominal segments is covered with granules and hairs similar to those on the carapace. The curved form of the rostrum is the main character distinguishing it from the related species M. antonii A. M.-Edw.; in the latter, the rostrum is also directed forward, but it is perfectly straight.

Dimensions

Total length	45.0 mm
Length of rostrum	8.0 mm
Length of merus of cheliped	12.0 mm
Length of carpus of cheliped	5.0 mm
Length of chela of cheliped	16.0 mm
Width of chela of cheliped	4.5 mm
Length of movable dactylus of cheliped	9.0 mm

Distribution. Benedict's three specimens were caught by the "Albatross" in the Bering Sea, southwest of the Pribilof Islands, at a
103 depth of 3, 188 m. In the collection of the Hydrobiological Laboratory of the State University of Leningrad, there is a single specimen of this species, caught in the Sea of Okhotsk, 46° 41'5"N. lat., 147° 28' E. long., 3, 500 m ("Gagara", 1932).

4. Genus CERVIMUNIDA Benedict

Cervimunida Benedict, 1903: 249; Balss, 1913: 18.

Type species: Cervimunida princeps Benedict.

This genus resembles Munida, but the rostrum is laterally compressed, and as curved as the free movement of the eyes allows; the inferior edge of the rostrum, and, even more so, the superior one, is spinulose. Of the few species of this genus, we shall deal here with only one species, recorded from the Sea of Japan, on the western shores of Japan.

1. Cervimunida princeps Benedict (Figure 37)

Cervimunida princeps Benedict, 1903: 249, Figure 3; Bouvier, 1906: 480; Balss, 1913: 18, Figure 15, Pl. 1, Figure 1; Yokoya, 1933: 65.

The eyes are very large. The rostrum is provided with three pointed, triangular spines: two on the superior edge, in front of the eyes, and one on the inferior edge in front of the superior spines. Between the tip of the rostrum and the first spine of the superior edge, some small spinules are usually found. The rostrum is horizontal, but at the level of the eyes, it is arcuate, becoming horizontal again, however. In cross section the rostrum is triangular, the base being the shortest side, and the inferior edges bearing crests which extend to the supraocular spines. The length of the rostrum, from its tip to the base of the free part of the supraocular spine, is equal to the distance from the last point to the posterior edge of the gastric area. The supraocular spines reach the middle of the eyes;
104 their free part is the same length as the anterolateral spines. The spines of the gastric pair are strong and pointed; at the same level, laterally, a small paired spine is found, and in some specimens, a much smaller additional one; the marked spine on the gastric area is situated at the intersection of the first ciliary line with the median line of the carapace; at the end of the ciliary lines, the usual spines are found. A paired spine is found at the bifurcation of the suture, and another in the usual place behind the suture. As to the sculpture of the carapace, it should be noted that between the straight lines which cross the whole surface, rows of scales, which are especially marked in the posterior half, are also found in most cases. The surface, particularly in the lateral parts, is iridescent. The merus of the last maxillipeds bears two strong spines on its internal edge and three spines on its external side. The ischium bears a masticatory lobe with a minute denticulation. The chelipeds are long and strong, covered with hairs over the whole surface, and with spines disposed in longitudinal rows; the spines on the internal edges of the joints are the strongest; the dactyli are longer than the propodus; their prehensile edges bear a slight denticulation, and meet closely. Numerous small spines are scattered over the entire surface of the propodus, with the exception of the inferior surface. The walking legs are densely covered with scales and hairs; the superior surface of the merus bears about ten spines; there are no exopodites on the walking legs. The armature of the abdomen consists as a rule of eight spines on the second and fourth segments, and six to eight (usually six) spines on the third segment. On the other segments the number of spines is also variable, but not so frequently.

Dimensions

Length of carapace (excluding rostrum)	40.0 mm
Length of rostrum	22.0 mm
Length of cheliped	190.0 mm
Length of merus of cheliped	70.0 mm
Length of carpus of cheliped	19.0 mm
Length of propodus of cheliped	91.0 mm
Width of propodus of cheliped	17.0 mm
Length of dactylus of cheliped	51.0 mm

Distribution. Southern Japan. On the western shores of Japan, north of Sado Island, and near Yamagata Prefecture. At depths from 76 to 452 m.

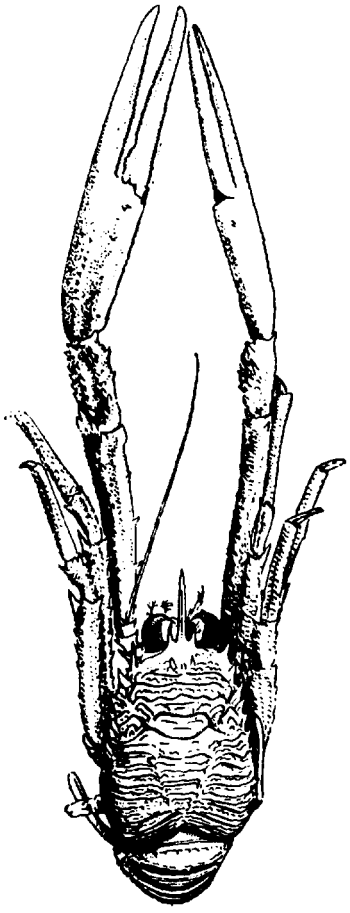

Figure 37. Cervimunida princeps Benedict (From Balss, 1913)

4. Family **PORCELLANIDAE**

Porcellanidae Henderson, 1888: 103; Ortmann, 1892: 245, 1901: 1151.

105

The carapace is broad and oval, with poorly defined areas. The frontal edge is broad, often divided into three lobes which, however, never become long; the median lobe or rostrum is usually broad and short. The lateral edges of the carapace are clear; the linea anomurica is distinct. The antennules are hidden; the basal joint of the stalk is wide. The antennal stalk is four-jointed, usually directed backward and having no scaphocerite. The eyes are pigmented and partly hidden in the orbits. The ischium of the third maxillipeds is broad, and the merus bears on its internal side a prominent lobe. The chelipeds are broad and often compressed; the walking legs are strong and of medium length. The gills are as in the Galatheidae; the mastigobranchiae on the pereiopods are missing. The abdomen is bent under the thorax, so that the animal has a crablike form. In the male, pleopods are present only on the second segment, and they have the function of gonopods; on the third to fifth segments they are reduced to the dimensions of small wartlike prominences; the female has slender

uniramous pleopods on the fourth and fifth segments, and sometimes on the third segment.

105 Henderson (1888) considers the Porcellanidae as being highly specialized Galatheidae which have developed a crablike habitus owing to a different way of life (by reduction of the abdomen, and the almost complete loss of its motor functions). Stimpson (1858) divided the genera of this family into two groups on the basis of the character of the antennal stalk: in the genera of the first group the basal joint of the antennal stalk is short, often hidden in the orbit and not reaching the superior edge of the carapace or the posterior angle of the superior edge of the orbit; therefore, the subsequent joints are near to the eyes. In the genera of the second group, this joint is elongated and bears a sharp-sometimes flat-outgrowth which almost reaches the posterior angle of the superior edge of the orbit; therefore, the subsequent joints are situated at some distance from the orbits. The two genera represented in our fauna belong to the second group.

The species of this family live chiefly in tropical areas, especially in the tidal zone, under stones (the carapace and the chelipeds are therefore flattened), or they are found at greater depths in the sublittoral zone, among coral, sponges and rocks.

Key to the Genera

1 (2). Frontal edge of carapace triangular and denticulated. Subbranchial (lateral) areas of carapace flat and not divided by a membranous space. . . . . 1. Porcellana Lamarck.

2 (1). Frontal edge of carapace triangular but not denticulated. Subbranchial areas of carapace divided by a membranous space into a large anterior part and a smaller posterior one . . . . . 2. Pachycheles Stimpson.

106 1. Genus PORCELLANA Lamarck

Porcellana Lamarck, 1801: 153; Milne-Edwards, 1837: 247; Bell, 1853: 188; Heller, 1863: 181; Henderson, 1888: 109; Stimpson, 1907: 187–Pisidia Leach, 1820: 53.–Porcellanides Czerniavsky, 1884: 109.

Type species: Porcellana platycheles (Pennant).

The length of the carapace usually exceeds its width; it is sometimes almost round, usually flat. The frontal edge is triangular and denticulated. The orbits are deep, bounded in their superior part by the edges of the carapace on their internal and external side by the antennular and antennal stalks, and in their inferior part, by a short, slightly prominent edge; from this edge a spinulose crest extends outward, and between it and the edge of the carapace a deep furrow is formed. The linea anomurica is distinct. The eyes are small. The second joint of the antennal stalk is the longest. The oral area is square. The third maxillipeds are large; they

are approximated, reaching the frontal edge of the carapace and partially covering the antennules. The merus is large, with a widened lateral edge, and with a denticle at the anteroexternal angle. The carpus is small, of an irregular triangular form. The subsequent joints become gradually smaller, and are covered by thick hairs, as is the carpus. The exognath has a many-jointed flagellum; the epignath is missing. The anterior pereiopods are fairly large, more or less flattened; the merus is short; the carpus is elongated, and has a denticulated, sharpened internal edge; the propodus is narrow at the base, and becomes slightly broader distally. The three subsequent pairs of legs are moderately long. They are cylindrical and have short dactyli. The last pair of legs are slender, situated above the base of the preceding pair, it is bent at the meralo-carpal articulation, and bears a small chela at its distal end. The abdomen is broad and lamellar. It is made up of seven segments and is bent under the thorax. The last segment (the telson) is broad, crossed by several furrows, and thus appears to be made up of five plates. The sixth segment bears a pair of uropods, the oval, lamellar parts of which are bent under the telson. The abdomen of the male bears a pair of short, slender pleopods on its second segment. On the third to fifth segments wartlike prominences (rudimentary pleopods) are found. The abdomen of the female bears a pair of pleopods on the fourth segment and one on the fifth. According to Milne-Edwards, there is also a third pair on the third segment in some species; the second segment has the same wartlike prominences as in the male. According to Milne-Edwards, there are seven gills on each side, viz., one pair on the third maxillipeds, one pair on the first pair of legs, and one branchia on each of the three subsequent pairs.

V. Czerniavsky (1884) created the new genus Porcellanides which, according to this author, has an intermediate position between Porcellana Lam. and Porcellanella White. However, this author failed to show by what
107 characters his genus differs from the two above-mentioned genera. Comparing the description of this new genus with that of the genus Porcellana (quoted, incidentally, by V. Czerniavsky, from Stimpson, in a footnote), no differences whatsoever may be observed, and therefore we consider Porcellanides to be synonymous with Porcellana.

The species of this genus are chiefly littoral, widespread mostly in the tropical zone. In the Soviet fauna, this genus is represented by two species.

Key to the Species

1 (2). Propodus of large chela more or less flattened, with a rounded, longitudinal, median carina. Dactyli fairly long. Prehensile edges of dactyli of small chela not hairy . . †1. P. longicornis (Pennant).

2 (1). Propodus of large chela protuberant, with no trace of a longitudinal median carina; dactyli short. Dactyli of small chela with dense hairs on the concave prehensile edges (pubescence is particularly noticeable on the inferior side). . 2. P. longimana Risso.

† 1. Porcellana longicornis (Pennant) (Figures 38, 39b)

Cancer longicornis Pennant 1777, Pl. 1, Figure 3 (quoted from Heller, 1863). Porcellana longicornis Leach, 1815, Plate 27, Figures 4-7; Milne-Edwards, 1837: 257; Bell, 1853: 193; Heller, 1863: 186. - Porcellanides rissoi Czerniavsky, 1884: 112.

The carapace is almost round, its length slightly exceeding its width; it is not very protuberant, sometimes even flat. The surface is smooth, and under a strong magnifying glass or on drying it shows small granules and wrinkles, the latter chiefly on the posterior part. The lateral edges are sharply outlined, with slight crests. The areas of the carapace are fairly distinct. The frontal edge is divided into three triangular lobes: the median lobe has strongly denticulated edges (seven to eleven denticles), and a rather deep longitudinal furrow, so that its surface appears concave; the lateral lobes are somewhat shorter than the median one; their edges are less denticulated and at the tip they bear a visible spinule directed forward and inward; the lateral lobes are separated from the median one by rounded hollows which, however, may sometimes be angular. The distance between the tips of the lateral lobes is less than half the maximum width of the carapace. Slightly beyond the anterolateral corner, and just above the base of the antennal stalk, the lateral edge of the carapace bears a spine, which in larger specimens may be replaced by a tubercle. The lateral edge of the carapace bears two to four spines above the base of the first walking leg; in addition, each hepatic area bears in its superior half, and near the edge of the carapace, two small spines, which may sometimes be entirely missing.
108 The eyes are fairly large, with small pigmented corneas. The first joint of the antennal stalk extends beyond the edge of the carapace and bears on its internal part a distally curved spine; the second joint is elongated and becomes slightly broader distally; the third joint is short. The first three basal joints of the last maxillipeds are fairly broad; the narrow terminal joints are densely covered with long pennate hairs. The exognath reaches the middle of the second segment of the endognath. The chelipeds are unequal, one usually slightly longer and broader than the other. The inner distal angle of the short merus bears a small lobe with two to four spines, and in large specimens, only one; the superodistal edge bears minute spinules; the protuberant inferior side bears a terminal spine, directed forward. The carpus is elongated and bears from two to six spines on the internal edge; the external edge bears five spines with tufts of short hairs at their bases; the inferior surface is smooth, concave on the internal side. The large chela is elongated and narrow, and is much longer than the carpus; the superior surface is smooth, with a soft, rounded, longitudinal median carina; the external edge is spinulose and pubescent, the internal edge of the propodus smooth. The dactyli are rather slender, with strongly bent tips. The external edge of the movable dactylus is less spinulated than the external edge of the immovable one. The prehensile edge of the movable dactylus has a longitudinal furrow in its distal half; the edges of this furrow have a minute denticulation. There is a distinct tubercle near the base. On the smaller chela, the dactyli are more compressed; their external edges are more spinulose. The prehensile edges of the dactyli have a minute denticulation, which extends over the entire length of the superior side, but only on the distal third of
109 the inferior side. The dactyli meet closely, while in the large chela, a small gap remains open between them. The first three pairs of walking legs

are slender. The meral joints are fairly broad compared with the other joints. All the joints are very slightly pubescent. The dactyli are short, almost straight, with long, curved claws. The fourth walking legs (the fifth pair of pereiopods) are slender and long, usually bent under the carapace, but when extended, they reach the proximal third of the preceding legs. The presence of the larger and the smaller chelipeds cannot be considered as a sexual dimorphism; however, on the basis of the material studied, it may be asserted that in all probability the larger cheliped is more frequently found on the right side in females, and on the left in males.

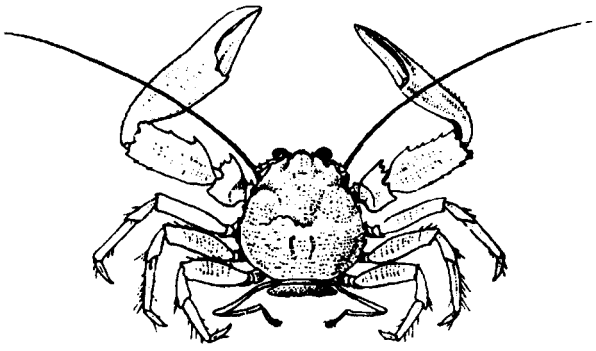

Figure 38. Porcellana longicornis (Pennant)

Dimensions

Length of carapace	5.0 mm
Width of carapace	4.5 mm
Length of carpus of large cheliped	3.5 mm
Length of propodus of large cheliped	5.0 mm
Length of dactyli of large cheliped	2.5 mm

This species usually has very small dimensions.

Coloration: whitish, yellow-brown or red-brown, sometimes light reddish, with darker irregular spots.

Distribution. Frequently encountered in the Black Sea, among rocks in the littoral zone, and under stones; it reaches depths of 1.5 to 3 m, and is often found among groups of mussels. Mediterranean and Adriatic Seas; East Atlantic: coasts of Norway and Sweden, Kattegat, North Sea, coasts of England, France and Spain, southward to Morocco; it reaches depths to 70 m, usually on sandy and rocky bottoms; it often lives in holes, chiefly of Pholas, in tubes of Sabellidae, in driftwood, etc. In the collections of the Zoological Institute of the Academy of Sciences there were two specimens of P. longicornis from Kil'din Island. This capture was probably accidental

(transported by driftwood?) as this species has not until now been known on the Murman Coast.

There is no reason to consider the Pontic form as a separate species, as was done by V. Czerniavsky (1884); for one reason or another this author compares the Black Sea form with Porcellana kriczagini, which he himself described from Singapore, without ever mentioning the existence of P. longicornis. The comparison of this species with the Pontic form shows that they are but one single species. Porcellana longicornis is no doubt a very polymorphic species. The variations are related chiefly to the armature of the lateral edges of the carapace and of the hepatic areas, and to the pattern of the lateral edges of the propodi of the chelipeds. It is difficult to assess the degree of variability in the Mediterranean specimens (we had no possibility of consulting the works of Pesta and Parisi, and the older works do not elucidate this question), but in the Black Sea, the polymorphism is quite obvious, as already shown by V. Czerniavsky.

110 † 2. Porcellana longimana Risso (Figure 39 a)

Porcellana longimana Risso, 1815: 68; 1826: 50. – Porcellanides longimana Czerniavsky, 1884: 118.

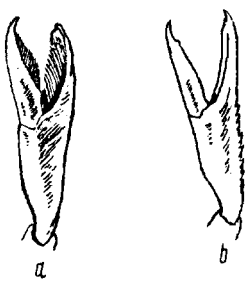

Figure 39. Chela of small cheliped:
a — Porcellana longimana;
b — Porcellana longicornis.

This species is closely related to P. longicornis. The carapace is rounded and smooth; its lateral edges bear three pointed spines. The frontal edge is divided into three lobes, the median one bearing eight spinules; the lateral lobes are pointed and bear small spines; the hepatic spines may be either present or missing. The chelipeds are long, naked and smooth, and in the male they are stronger. The chela of the large cheliped is exceptionally long and protuberant; both its edges are smooth; the dactyli are short. The small chela is medium in size; it is flattened. Its superior surface bears a slightly marked crest; the lateral crests of both sides are smooth; the dactyli are long, no shorter than the propodus, and have dense hairs on the curved prehensile edges.

Thus, this species differs very little from P. longicornis and it is possible that the authors who consider it synonymous with the former species are right.

Distribution. Black Sea and Mediterranean.

2. Genus PACHYCHELES Stimpson

Pachycheles Stimpson, 1858: 66; 1907: 186; Henderson, 1888: 113.

Type species: Pachycheles grossimanus (Guérin).

The carapace is round and ovate, its width being at least equal to its length; the lateral edges are marked by a prominent line. The frontal side of the carapace is sometimes inclined ventrally; it is slightly prominent in the middle and forms a wide, triangular, moderately pointed rostrum, never denticulated, but having a pubescent tip. The subbranchial areas of the carapace are not continuous, the smaller posterior part being separated from the larger anterior one by a membranous or soft space. The basal joint of the antennal stalk is elongated and touches the edge of the carapace; the second joint is some distance from the orbit; the chelipeds are unequal, strong, and more or less rough because of their granules; the carpus is short. The shape of the dactyli of the walking legs is normal.

The species of this genus are chiefly littoral, and are encountered in the temperate and tropical zones of the Pacific and Indian Oceans. In the Soviet fauna this genus is represented by one species.

111 † 1. Pachycheles stevensii Stimpson (Figure 40)

Pachycheles stevensii Stimpson, 1858: 242; 1907: 187, Pl. 23, Figure 6; Miers, 1879: 47; Ortmann, 1892: 267; Balss, 1913: 32; Yokoya, 1928: 760.

The carapace is almost round, the frontal edge projecting slightly to form a triangular rostrum, covered on its superior surface with dense, short, soft hairs; the tip of the rostrum is blunt. The lateral edges of the carapace are smooth and slightly raised, clearly separating the superior surface of the carapace from the lateral, subbranchial areas. These areas are subdivided by a membranous space characteristic of this genus; this space is merely an unusually broad linea anomurica, beginning at the base of the antenna and forming a narrow stripe, which gradually broadens posteriorly. Its superior border is parallel with the lateral edge of the carapace, while the inferior border deviates abruptly at the level of the base of the first walking legs, thus forming a triangular membranous space in the posterior half of the subbranchial area; the inferoanterior angle of this triangle is occupied by a large calcified plate; along the supero-posterior edge of this plate is a row of three or four very small plates. The central part of the superior surface of the carapace bears small granules, elongated transversely and increasing in size toward the lateral edges. From
112 each granule a few very short hairs rise in an anterior direction. These granules are almost completely missing on the cardiac area; on the postero-lateral parts, however, they become large, and resemble short transverse crests, which impart to this part of the carapace a wrinkled appearance, Observed with the naked eye, the carapace appears almost smooth, with indistinct areas; the posterior edge of the carapace is concave. The

outer ocular spines are short. The eyestalks are short and stout. The ischium of the third maxillipeds is short, with an outgrowth at the supero-external angle. The merus is narrower, with a large rounded lobe on the internal edge; the carpus widens proximally, and on the inferior side it forms a peculiar hollow, in which the proximal end of the propodus lies when the maxilliped is bent. The dactylus is short. The slightly curved, fairly broad exognath reaches the middle of the merus, and terminates in a rather long flagellum. The chelipeds are strong compared with the carapace; they are naked and markedly flattened, the right one being much larger than the left. The merus of the right cheliped has a wide, flat surface, turned toward the carapace; it continues at almost a right angle on the narrow superior surface; on its internal edge this narrow surface forms a triangular outgrowth; the inferointernal surface is concave, while the inferoexternal surface is convex. The superior surface of the carpus is covered with granules, which increase in size toward the edges. Around the granules is a crown of short hairs. The flattened internal edge bears three denticles, sometimes irregular in form, which are also covered with granules; when they touch, the inferointernal and inferoexternal surfaces form a fairly distinct crest. The chela, which is rather narrow at the articulation with the carpus, reaches its greatest width at the base of the movable dactylus. The external edge of the propodus forms a straight line with the external edge of the immovable dactylus; like the carpus, the superior surface of the propodus is covered with granules, which are largest near the external edge. Along the external edge of the propodus there is a pronounced hollow, which becomes deeper near the base of the immovable dactylus, often extending along this dactylus and becoming shallower. In the middle of the propodus there is a second, less marked groove, and finally a third insignificant groove, begins at the base of the movable dactylus. The entire superior surface of the propodus thus has a generally uneven character. The protuberant inferior surface of the propodus is covered with dense, low, flat granules. The dactyli are slightly curved at their ends; the prehensile edges are smooth, their base covered with dense, soft hairs, particularly on their inferior surface. When the chela is closed, a broad slit remains open (according to Stimpson's description, the dactyli close without leaving a gap; Balss notes that the large chela often remains open). The smaller cheliped generally has the same form, with the exception of the grooves on the superior surface of the propodus, which are perhaps more marked; the dactyli are adjacent when closed, and
113 their base lacks a hair cover. The walking legs are relatively small, and, unlike the chelipeds, they are very pubescent on their carpal and propodal joints; the dactyli are short, with curved claws. The pereiopods of the fifth pair are slender, and usually bent at the level of the mero-carpal articulation, so that, viewed from outside, only the merus is visible, together with the long carpus bent under it, while the small, elongated, pubescent chela is hidden in the gill chamber beneath the edge of the carapace. When extended, the fifth leg reaches the distal end of the preceding leg, or even extends slightly beyond it. The abdomen is relatively broad; the telson has the structure characteristic of this family. In the female, the external branch of the uropod is much longer and broader than in the male. The color of the specimens preserved in alcohol is pale orange-red.

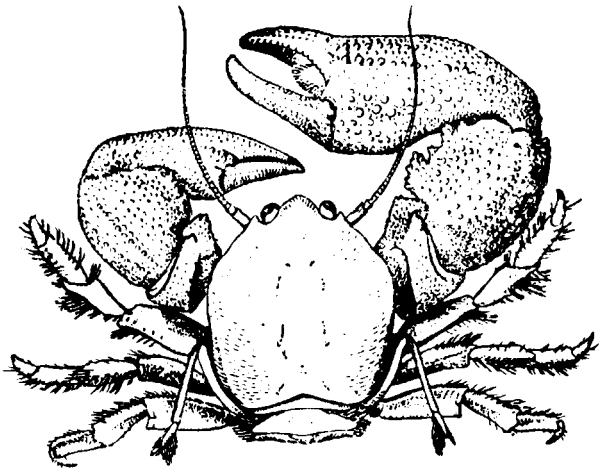

Figure 40. Pachycheles stevensii Stimpson

Dimensions

Length of carapace	17.0 mm
Width of carapace	17.0 mm
Length of merus of right cheliped	12.0 mm
Length of chela of right cheliped	26.5 mm
Width of chela of right cheliped	14.0 mm
Length of first walking leg	21.0 mm

Distribution. West coasts of Japan, from Hokkaido to Nagasaki; Tokyo Bay. On the Soviet coast of the Sea of Japan, from Gorshkov Bay to the Gulf of Strelok.

Superfamily HIPPIDEA

The carapace is oval or square, relatively smooth, with well-marked lateral edges; the frontal edge is broad and not fused with the epistome. The rostrum is either small or entirely missing. The eyes do not have distinct orbits; the corneas are small. The antennules are well developed. One of the flagella is long; the second is of moderate size or is absent. The antennae have a five-jointed stalk and a short flagellum; the scaphocerite is generally missing. The third maxillipeds are pediform or foliaceous, with no mastigobranchiae. The first pair of pereiopods are simple or with subchelae; the fifth pair is small, hidden in the branchial cavity; the other pairs of pereiopods have flattened and curved dactyli. The gills are of the phyllobranchiate type and the number is very reduced (nine or ten, sometimes with a number of rudimentary gills). There are no mastigobranchiae

on the pereiopods. The abdomen is bent under the thorax, and the epimera are partly reduced; uropods are always present, the telson has a normal size, its length exceeding its width. The males have no pleopods (except, of course, the uropods); the pleopods of the females are simple and three-jointed; the genital openings of the male are on the coxae of the fifth pereiopods, and those of the female on the coxae of the third pereiopods.

114 Miers (1877) relates the Hippidea – through the Raninidae Dana – to the Brachyura Oxystomata of de Haan, taking into account the habitus, the form of the chelipeds, and the development of the second to fourth pereiopods. All these characters, however, are merely convergent ones and do not indicate any true relationship; it suffices to recall the presence of uropods in the Hippidea, and that of the scaphocerites (though these are not always present), in order to realize that the resemblance to the Raninidae is but a superficial one. Ortmann (1892) considers the Hippidea as being a rather isolated group, and notes only a remote relationship to the Galatheidea. The species of the Hippidea are almost exclusively tropical; they inhabit the littoral or shallow waters, and burrow in sand.

5. Family **ALBUNEIDAE**

Albuneidae Stimpson, 1858: 230; Henderson, 1888: 39; Holmes, 1900: 103; Ortmann, 1892: 534; 1901: 1153.

The carapace is compressed, with no aliform lateral expansions covering the legs. The antennal stalk usually has a marked scaphocerite on its second joint. The last maxillipeds are narrow and have an exognath. The first pair of pereiopods is subchelate and flattened. Abdominal segments two to four (in Blepharipoda, also segment five) have well-developed epimera; the telson is oval and foliaceous. The females bear pleopods on segments two to five.

1. Genus BLEPHARIPODA Randall

Blepharipoda Randall, 1839: 130; Holmes, 1900: 103; Balss, 1914: 92.

Type species: Blepharipoda occidentalis Randall.

The carapace has an elongated oval form, with an incision on the posterior edge. The antennules and the antennae are long. The antennal stalk bears a scaphocerite*. The eyestalks are long, slender and cylindrical, with a median articulation. The third maxillipeds are pediform and

* In the diagnosis of the genus, Randall (1893, p 130) states: "Antennae four, unequal, the external being much the greatest, with one long revolute appendage, which is ciliate on the outer side". Some authors (Holmes, 1900; Ortmann, 1901) assert that the antennae lack scaphocerites. Bouvier (1898) states: "The antennal and the antennular stalks are unarmed". It is very possible that the type species of the genus B. occidentalis Randall has scaphocerites, while the species mentioned below has not.

do not cover the mouth; the ischium is very stout, the merus almost cylindrical, narrow, and resembling the carpus, which has no prominence in its
115 anteroexternal angle. The exognath is fairly strong, and almost reaches the end of the merus. The pereiopods are strong and hairy, their bases close together; the dactyli are sickle-shaped; the first pair of pereiopods bear pincers of the subchelate type.

†1. Blepharipoda japonica Duruflé (Figure 41)

Blepharipoda japonica Duruflé, 1889:92. – Blepharipoda fauriana Bouvier, 1898:566; 1893a; 339, Figures 1-5.

The length of the carapace exceeds its width. The superior surface is protuberant, with a slight median crest. The lateral edge bears three spines: a strong one at the anterolateral angle, a small one on the posterior end of the hepatic area (which may also be missing, as, for instance, in the specimen studied by us), and finally a small spine which is situated in the anteroexternal angle of the branchial area. The rostrum resembles a broad triangular tooth, with much larger lateral triangular teeth on its sides; these are separated from the rostrum by the concave frontal edge, which bears a minute denticulation; the lateral edges of the rostrum and of the lateral spines are also denticulated. Directly behind the frontal edge is a flat transverse line, and on the anterior edge of the gastric area there is another line, shallower, arcuate, bent abruptly at the level of the median line of the carapace, and fused with the first line at the sides, thus forming an angular hollow. Between these lines, the surface of the carapace is lower, has a darker color (in the specimens preserved in alcohol), and is covered with wrinkles and nodules. The remaining surface of the carapace, particularly the gastric area, is covered with small crescent-shaped hollows, in the concave side of which is a low papilla with a denticulated anterior edge. Two deep converging furrows bound the anterior branchial area on each side. The cervical groove is slightly curved; it crosses almost the entire carapace without fusing with any of the above-mentioned furrows. The posterior edges of the furrows bear short hairs,
116 directed forward, which may disappear owing to friction (in the specimen studied by us, they were retained only on that sector of the cervical groove which is the place of contact with the cardiac area). The lateral limits of the cardiac area are quite distinct in their anterior part and indistinct in the posterior one. The posterior edge of the carapace has a broad incision. The rounded posterolateral angles of the carapace bear a group of flat papillae which have denticulated anterior edges and often a very irregular form. The eyestalks are long, widening at their bases, but they become rather slender and scarcely widen at the level of the corneas. The corneas have a terminal position and a rounded sinus on their superointernal edge; the stalks are flat on their external surface, and slightly convex on their internal one, at the base of which are long dense hairs. The eyestalks are articulated, having narrow, but fairly long, ophthalmic scales, which almost touch one another on the median line. These stalks are bounded in their inferior part by a membranous surface, where a small triangular

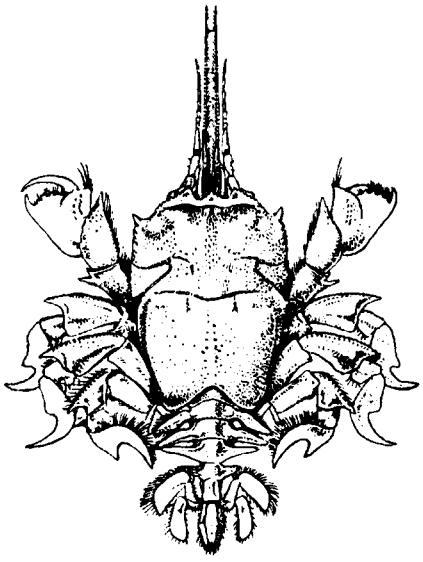

Figure 41. Blepharipoda japonica Duruflé

plate is found; this is the epistome. The antennular and antennal stalks are smooth; the first are covered with long dense hairs on both sides; similar hairs are also found on the superior surface of the large antennular flagellum, while on its inferior surface the hairs are much more sparse. The small flagellum is short, made up of only ten joints. The antennal flagella are somewhat longer. The exopodite of the third maxillipeds bears a flat one-jointed flagellum. The carpus bears small denticles on its inferior surface. The ischium bears seven fairly strong spines on its internal edge. The basipodite also has a spine on its internal edge. The epipoditic plate bears a rudimentary podobranchia at its free end. The first legs are relatively short, the merus having a strong spine at the inferodistal angle. The superoanterior angle of the carpus extends into a pointed denticle with pubescent edges, and the anterior edge is also spinulose. The superoexternal surface of the carpus is granulated; the subchela is broad, flat, and irregularly heart-shaped. The superoexternal surface of the propodus is granulated and parallel with the external edge. Some distance from it there is an irregular crest which extends onto the immovable dactylus; this crest bears hairs directed inward. Similar hairs are also found on the surface of the propodus; the inferointernal angle of the propodus bears a tuft of long hairs. The immovable dactylus is very broad at its base; it has a convex prehensile edge and a curved pointed tip; the prehensile edge bears four blunt denticles, and the spaces between them bear minute denticles and long hairs. When closed, the movable dactylus, curved at its base, meets the prehensile edge of the immovable dactylus, its tip extending beyond that of the immovable dactylus. Its superior and inferior surfaces are perfectly smooth, while the external edge bears a row of granules. The three subsequent pairs of pereiopods have flattened joints; the carpal and propodal joints have flat, blunt, triangular outgrowths
117 at their anterodistal ends; the dactyli have the form of curved plates, with perfectly smooth surfaces and pubescent edges. The fifth pereiopods are delicate and slender, ending in a hairy chela. The gills are (according to Bouvier): pleurobranchiae on the second to fourth pereiopods, two arthrobranchiae on each of the second to fourth pereiopods, and sometimes also on the first pereiopods and third maxillipeds, and podobranchiae on the

third maxillipeds. The first segment of the abdomen is long, with a membranous central part; the carapace overlaps a considerable part of it; this segment lacks epimera and appendages; the four subsequent segments are narrow, becoming gradually smaller, and have long blunt epimera. The female bears pairs of biramous pleopods on these segments; the male has only traces at the level of the articulation of these appendages. The sixth abdominal segment has an almost equal length and width. Both rami [branches] of the uropods are oval. The length of the telson somewhat exceeds its width; its central part is protuberant, strongly calcified, and separated from the lateral parts by a depression. The posterior edge bears a small incision.

Concerning the biology of B. japonica, Bouvier (1898) states: "These animals must burrow in the sand like other Hippidea, but they are less well adapted to this habitat, as their filtration mechanism is less perfect; in fact, their antennular flagella are shorter and less regularly ciliated, and the flagellum of the exopodite of the first maxillipeds has a much reduced surface.

Distribution. Coasts of Japan. In Soviet waters, this species is known from the Vladivostok area, from Patrocles Bay and from Poset Bay.

Superfamily PAGURIDEA

The cephalothorax is not fused in its anterior part with the epistome. The form of the carapace is either cylindrical, with soft integument and indistinct lateral edges, or broadened, crablike, and well calcified, with distinct lateral edges. The rostrum is either small, triangular, and sometimes completely reduced–or well developed and spiniform or of a different shape. The eyes do not have marked orbits; the eyestalks are cylindrical, with or without opththalmic scales. The antennal stalk is five-jointed, the second joint bearing a spiniform scaphocerite (which is reduced in the Coenobitidae). The flagella of the exopodites of the second and third maxillipeds are jointed. The third maxillipeds are pediform. All the pereiopods are six-jointed. The first pereiopods are chelate, and in most cases unequal; the last two pairs of legs are short and bear wartlike prominences;
118 in other cases, only the last pair of legs is reduced, and in this case it bears at its end a small chela, which is usually hidden in the gill chamber. In more primitive forms, the gills are of the phyllobranchiate type, but in most cases they are of the trichobranchiate type, at most 14 on each side. There are no epipodites on the pereiopods. The genital openings are found on the coxae. The abdomen is either specifically modified and soft, with relatively well-developed or poorly-developed tergal plates, or bent under the cephalothorax as in the Brachyura, and more or less covered with calcified plates and nodules. The males sometimes have gonopods. In most cases the pleopods are developed only on one side. The uropods may either be present or missing.

The species which belong to this superfamily either live in shells of Gastropoda and in other hollow bodies, or more freely on the bottom; in both cases, the abdomen is asymmetrical; only in the most primitive

forms is it symmetrical, although it shelters in worm holes, sponges, etc. A few species have adapted themselves to a free amphibious mode of life (Coenobitidae), but the asymmetry of the body has nevertheless been retained.

Key to the Families

1 (4). Abdomen straight or spirally coiled, not flexed below carapace. Carapace cylindrical, generally hard in its anterior part, while the posterior part is more or less soft. Fourth pereiopods unlike the third. Rostrum rudimentary or entirely missing. Uropods present.

2 (3). Abdomen symmetrical, with well-calcified segments on its dorsal surface. Paired pleopods on all abdominal segments. Gills of the trichobranchiate type . . . . 1. Family Pylochelidae.

3 (2). Abdomen usually asymmetrical, coiled spirally, soft, not segmented, with small, slightly calcified plates on left side. In rare cases, the first abdominal segment bears paired pleopods, but pleopods usually found only on left side, at level of second to fifth segments. Gills usually of the phyllobranchiate type. . . . . 2. Family Paguridae.

4 (1). Abdomen only in rare cases soft, short and saclike; it is usually foliaceous and flexed below cephalothorax. Carapace broad, with all parts well calcified. The animal has a crablike habitus. Fourth pereiopods like third pereiopods. Rostrum in most cases well developed. Uropods missing. . . . . 3. Family Lithodidae.

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6. Family **PYLOCHELIDAE**

Pylochelidae Bate, 1888: 11; Ortmann, 1901: 1144.

The carapace is fairly well calcified; its lateral sides are flat and very high. The eyestalks are moderately long. The antennules end in two flagella. Small scaphocerites are observed. The madibles have palps. The bases of the third maxillipeds are close together. The first pair of pereiopods is chelate, the legs having almost equal lengths. The legs of the second and third pairs of legs are long, ending in acicular dactyli. The pereiopods of the fourth and fifth pair are short, ending in a small rudimentary dactylus. The gills are of the trichobranchiate type, the filaments long, cylindrical and slender; podobranchiae and mastigobranchiae are missing on all the thoracic appendages. There are 14 branchiae on each side: two arthrobranchiae on each of the first four pairs of pereiopods and on the third maxillipeds, and one pleurobranchia on each of the last four pereiopods. The abdomen is symmetrical, the dorsal side of the segments being well calcified. The caudal fan is symmetrical, with hard, tapering uropods, the outer ones being larger than the inner ones. The telson is hard in its anterior part, and elastic in the posterior part. All segments have paired pleopods; in the male the pleopods of the first segment are modified into gonopods.

By their habitus the species of this family resemble somewhat the species of the family of the Paguridae, differing, however, by the symmetry of the abdomen and of the pleopods, and also by the fact that their abdominal segments are articulated in the usual manner, and have a hard dorsal surface; the ventral surface also has hard plates, which are, however, divided in the middle. These species live in sponges, in submerged fragments of bamboo, on roots of mangroves, in shells of Dentalium, and in other hollow bodies. Boas (1926) considers that the Pylochelidae do not bear their shelter with them, but leave it when foraging for food, thus leading a partly free existence, a fact which also explains the symmetry of the abdomen. There is no doubt that the Pylochelidae is the most primitive family of the Paguridea. Of the five genera of this family, we shall deal with only one species which lives in the Sea of Japan.

1. Genus MIXTOPAGURUS A. Milne-Edwards

Mixtopagurus Milne-Edwards and Bouvier, 1893: 23; Balss, 1913: 34. – Pomatocheles Miers, 1879: 49.

Type species: Mixtopagurus paradoxus A. Milne-Edwards.

The species of this genus show a close relationship with the genus
120 Pylocheles; they have 28 filamentous tetraseriated gills, disposed in the same manner. The thorax is calcified at least on its dorsal side. The bases of the eyestalks are far apart. The bases of the third maxillipeds are close together. The thoracic sternites are very narrow. The ventral surface of the abdomen is membranous, with very slightly calcified sectors on segments one to six; the dorsal surface is made up of closely articulated segments calcified on their entire surface. All the abdominal segments have paired appendages; the first two pairs of pleopods in the males and the first one in the females have been modified into gonopods. The first maxillipeds each bear an epipodite, an exopodite, and a flagellum.

Mixtopagurus differs from Pylocheles by the following characters: the frontal edge bears a rostrum. The antennular stalks extend to the tip of the eyes or slightly beyond; the second joint of the antennal stalk does not show the strong dentiform outer projection; the antennal flagellum reaches the end of the chela; at most the chelae of the first pereiopods are equal or subequal, ending in corneous claws and not forming an operculum; the third maxillipeds have simple ends and are not chelate; the pereiopods of the fourth pair are subchelate and have a large spinulose sector (the "Raspel" of the German authors); the sixth abdominal segment is much more calcified than the others; the telson is not segmented; all the pleopods, with the exception of the first pair, are two-jointed in both sexes.

1. Mixtopagurus jeffreysii (Miers) (Figure 42)

Pomatocheles jeffreysii Miers, 1879: 49, Plate 3, Figure 2–Mixtopagurus jeffreysii Balss, 1913: 35, f. 25, Plate 2, Figure 1; Yokoya, 1933: 71.

[Miers' description, 1879]

"The animal is slender and elongated. The carapace is marked with a distinct postfrontal and lateral suture, besides two smaller and less distinct sutures on the sides towards the lateral margins. The median frontal lobe is broadly triangulate and rounded at apex. The first post-abdominal segment is very small, the five following subequal, with the lateral margins straight, the last small, transparent, and membranaceous in its distal half, and ciliated on its margins, the terminal median notch very small. The ocular peduncles are a little shorter than the frontal margin, and are furnished with very small scales at base. The corneae are of a red-brown colour. The antennules are half as long again as the eye-peduncles, the antennae about as long as the antennules; the aciculum at base very small, acute, not half as long as the eye-peduncles. The anterior legs are much as in Cancellus; the arms with a slight denticulated crest on their upper surface, the wrists very short and slightly denticulated above; the flattened upper surface of the palms is covered with thick short hair, the surface beneath being smooth, and the straight inner and arcuate outer margins very slightly denticulated. The slender and elongated legs of the second and third pairs have the antepenultimate joint short, the two following long and straight, the last in particular very long, slender, and acute. The truncated distal end of the last joint of the fourth leg is armed with a series of short stiff setae or spinules, and

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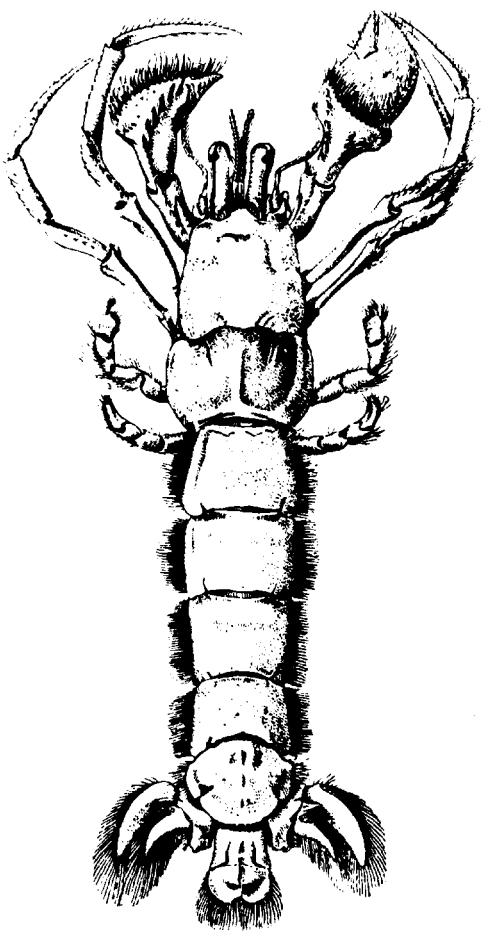

Figure 42. Mixtopagurus jeffreysii (Miers) (From Balss, 1913)

a small claw or spine; that of the fifth pair is densely ciliated. The basal portion of the uropoda is short and broad, and bears two unequal lamelliform rami, which are of spongy texture on the outer surface, and ciliated on the margins; the outer is twice as long as the inner. Length 5 lines* " (Miers).

"Concerning the biology of this form, it should be stressed that its telson has a perfect valvelike form, so that together with the sixth segment, which is lamellar, it closes the interior opening of the shell of Dentalium" (Balss).

122 The generic position of this species is somewhat debatable. This follows from the contradictions which arise when the above diagnosis of the genus as a whole is compared with the diagnosis of the species. Boas (1926) advocates the inclusion of this species in the genus Pylocheles. It is quite possible that Boas is right, but as we had at our disposal only the descriptions of this species, we confine ourselves to presenting it under the same generic name as it appears in the literature.

Distribution. Japan (Yokoya, 1933). In the Sea of Japan, it is known from the western Japanese shores, north of Nagato; Yamaguchi Prefecture, and near the Oki Archipelago. At depths from 64 to 350 m. Balss' specimens were found in shells of Dentalium intercostatum Boissevain, D. eburneum L. and D. usitatum Smith.

* [The old measure, a line, equals $\frac{1}{12}$ inch.]

Family PAGURIDAE

CHARACTERS OF THE FAMILY

Morphological outline*

123 The body of a hermit crab is made of a cephalothorax and an abdomen. Both these parts, and chiefly the abdomen, have morphological traits which are specific almost exclusively to this family.

CEPHALOTHORAX. The specific character of the cephalothorax is—with very few exceptions—the poor calcification of most of its surface. Only the cephalic area is well calcified and it is separated from the other areas by a marked cervical groove; in the taxonomic diagnoses this area will be called the anterior part of the carapace. As to the other areas, only the anterior part of the cardiac area is more calcified, the remainder of the carapace being membranous. The second characteristic of the cephalothorax of the hermit crabs is that its last two segments are free. The sternal plates of the fifth segment are narrow and are separated by an articular membrane, while the sternal plate of the fourth segment is displaced to the left in most of the species which have asymmetrical chelipeds. The free articulation of the last two segments allows the great mobility necessary to the hermit crabs, owing to the fact that they live in spiral shells.

In addition to the cervical groove (line C, according to Boas' terminology; branchial furrow or line C, according to Bouvier's terminology), the following additional furrows may be observed on the surface of the cephalothorax (Figure 43):

A longitudinal furrow, beginning at the anterior edge of the carapace, passing the cervical groove, and reaching the posterior edge of the carapace.
124 Borradaile considers this furrow as a whole to be the linea anomurica. In accordance with Bouvier's terminology, only that sector of this furrow which

* Before proceeding to the anatomical morphological part of our study we must mention that all data presented in this part refer in general to the genus Pagurus Fabricius. Owing to the size of our work we cannot deal in detail with the different morphological modifications shown by one genus or another. The genus Pagurus suits our purpose, since most of the species of this family occurring in the Soviet seas belong to this genus. Apart from this, most of the studies on the morphology of the Paguridae deal with this genus, the outstanding monograph of H. G. Jackson (1913) included. The various deviations will be mentioned in the systematic part, in which the different genera and species will be described.

extends from the anterior edge of the carapace to the cervical groove should be called the "linea anomurica". According to Boas' terminology, this sector of the furrow is called "line B", while the sector behind the cervical groove is designated by him as the linea anomurica.

At the level of the cervical groove, a slightly marked furrow runs vertically from the linea anomurica downward, and is considered by Boas to be a part of the linea anomurica.

Extending anteriorly from the cervical groove and parallel with the linea anomurica is a slightly marked furrow, called by Boas "line D"; together with its continuation beyond the cervical groove it is probably homologous with the linea thalassinica.

The surface of the carapace is often covered with tufts of hairs, particularly in its anterior part; it is sometimes richly sculptured. In most cases, the anterior or frontal edge of the carapace bears a triangular rostrum, called in the following taxonomic diagnoses "median prominence of the front"; lateral to the rostrum are supraorbital prominences, called "lateral prominences of the frons"; their form varies between a definitely triangular one and a rounded, hardly visible one; sometimes, the lateral prominences are entirely missing. Submarginal spines are often observed below the frontal edge of the carapace, at the level of the lateral prominences. The calficied folds of the cuticle (the so-called apodemes), found on the internal side of the cephalothorax, form the complex system of the endophragmal skeleton, which serves for the insertion of the muscles and for the protection of the internal organs.

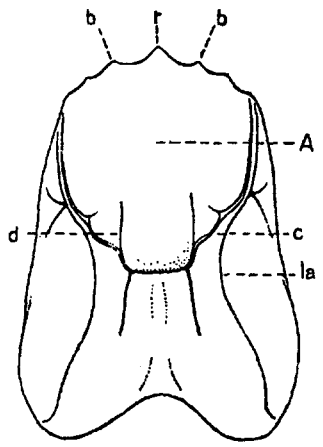

Figure 43. Surface of the carapace of Pagurus ochotensis subsp. aleuticus (Benedict). c - cervical groove; la - linea anomurica; d - line D (according to Boas); A - anterior part of carapace; r - rostrum, or median prominence of front; b - lateral prominences of front.

The histological structure of the carapace of the hermit crab differs very little from that of other crustaceans, the only exception being the degree of calcification. The following layers may be distinguished within the carapace: 1) a thin basal layer; 2) a chitinous layer, divided in its turn into four layers: a) a thin outer layer, composed of plates, b) a pigment layer, composed of plates parallel to the superior surface and containing a granular substance, c) a calcareous (fundamental) layer, also made up of plates covered with layers of calcium carbonate; the papillae of this layer may penetrate the pigment layer, d) a thin internal layer, not calcified, and composed of stratified plates ; 3) an epithelial layer (hypoderma), which produces chitin. These layers are pierced by porous spiral canals, which reach the basal layer; these canals are considered to be a continuation of the hypodermal cells, their function probably being the secretion of calcium. In addition, all

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the layers are also pierced by canals through which the sensory nerves reach hairs, cilia, etc.

THE ABDOMEN of the hermit crab has the appearance of a soft, sausage-like, membranous sac, usually coiled spirally; it is sometimes straight, though slightly bent ventrally at its posterior end. The walls of the abdomen are so thin and transparent that the digestive glands, the gonads, and the nephridial vesicles may often be seen. Only the first segment, the sixth segment with its appendages, and the telson are calcified (some authors do not consider the telson as being a separate segment). On the rest of the surface of the abdomen hardly any division into segments is to be observed. On the dorsal surface, the remnants of the terga may be observed in the form of poorly calcified plates, situated over the pleopods on the left side and symmetrically on the right side (Figure 44); these plates are less marked in young specimens and males than in females. At the level of the third segment, on the ventral side of the abdomen, a prominence of irregular form is found–the so-called columellar muscle. The function of this muscle has not been completely elucidated, but it is probably related to a better fixation of the animal in the shell it inhabits.

In its time Przibram's study (1907) on the form of the abdomen raised many controversies. He asserted that the abdomen of a hermit crab removed from its shell would recover the macruroid form of its ancestors; this assertion proved incorrect, as shown not long ago by Brinkmann (1926).

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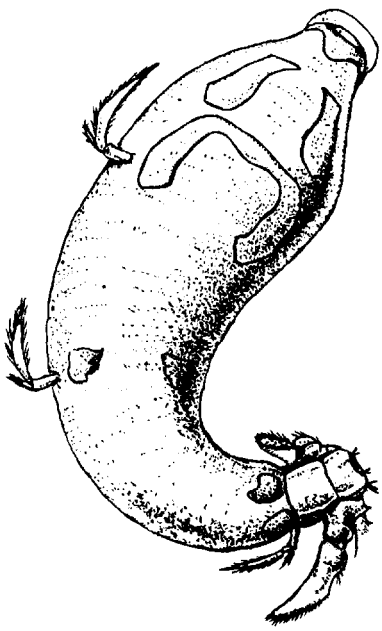

Figure 44. Abdomen of Pagurus ochotensis Brandt (dorsal view)

CEPHALIC APPENDAGES. Eyestalk (Figure 45). This is composed of two joints: a short basal one, and a longer distal one. The form of the stalk is cylindrical, often narrowing in the middle and widening again at its distal end. The basal joint bears a small appendage on its internal side–the so-called ophthalmic scale, which is usually oval with a pointed tip; below the tip a subterminal spine is often found; this is sometimes so prominent as to be visible from above (Figure 46). The distal joint bears the cornea, which has a terminal position, a round form and a small cavity on its supero-internal side.

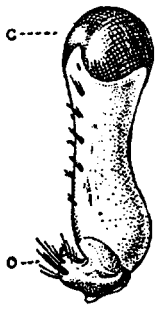

Figure 45. Eyestalk of Pagurus pubescens Kröyer: c – cornea; o – ocular scale.

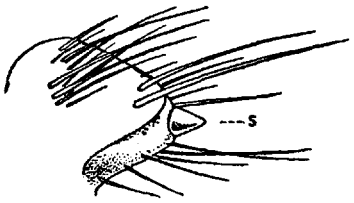

Figure 46. Ocular scale (dorsolateral view): s – subterminal spine (greatly magnified).

127 Antennules (first antennae) (Figure 47). The antennules are attached below the eyes, but owing to the curve of their joints, they seem to be situated between the eyes. The stalk of each antennule is made up of three segments: the coxopodite and a two-jointed basipodite*; the statocyst is situated in the coxopodite and it opens in a narrow slit on the dorsal side. At the end of the distal joint of the basipodite are the exopodite and the endopodite. The exopodite appears as a thick, longer flagellum, many-jointed and pennate, while the endopodite is shorter, more slender, and almost naked.

Antennae (second antennae) (Figure 48). The antennal stalk is made up of four joints: the coxopodite, the basipodite, and a two-jointed endopodite, from which extends a long many-jointed flagellum, almost without hairs in most cases. On the inferior side of the coxopodite is a tubercle bearing the excretory opening of the antennal gland. The basipodite, considered in taxonomic descriptions as being the basal joint of the antennal stalk, bears on its external side the exopodite, which is called here the "scaphocerite" (the "scale" of some authors). In hermit crabs, the scaphocerite has the appearance of a slender sickle-shaped appendage, almost cylindrical in form (sometimes, however, straight with sharp edges); inner [sic] edge is often denticulated and hairy.

128 Mandibles (Figure 49A). The mandible is composed of a gnathobase and a powerful apophysis, serving for the insertion of the masticatory muscles. The gnathobase is denticulated and furrowed on its internal side, but is not divided into a "pars incisiva" and a "pars molaris". There is a three-jointed palp (taster, synaphipod), its function being to clean the masticatory edge of the gnathobase and possible also to push through the food. From the comparative anatomical point of view, the body of the mandible corresponds to the coxopodite. There is a difference of opinion regarding the palp. Giesbrecht considers that it is an epipoditic appendage and a neoformation, while Hansen considers it to be a rudimentary endopodite. The mandibles are well calcified, and are the principal organs for the mastication of the food. The mandibles are situated between the epistome and the metastome, the palp as a rule adhering to the first.

Maxillules (first maxillae) (Figure 49 B). These are composed of a membranous coxopodite and basipodite, with edges bearing long setae.

* The coxopodite and the basipodite, taken together, are often called the protopodite.

The external appendage of the coxopodite corresponds to the exopodite (according to other authors, to the endopodite). The endopodite appears as a two-jointed palp. There are still controversies concerning the comparative anatomical interpretation of the coxopodite and the basipodite.

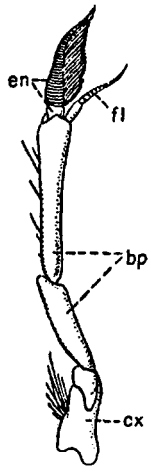

Figure 47. Right antennule of Pagurus pubescens Kröyer. cx – coxopodite; bp – basipodite; en – endopodite; fl – flagellum.

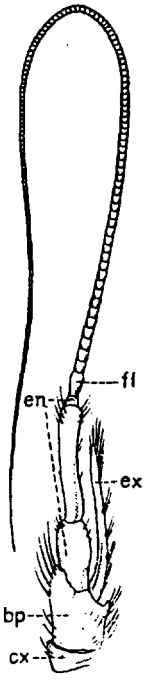

Figure 48. Right antenna of Pagurus pubescens Kröyer. cx – coxopodite; bp – basipodite; en – endopodite; ex – exopodite or scaphocerite; fl – flagellum.

Maxillae (second maxillae) (Figure 49 C). The coxopodite and the basipodite of the maxilla are each divided distally into two unequal lobes. There is a one-jointed palp (endopodite) and a broad epipodite. The exopodite has the form of a broad plate, bent in its anterior part, and thickly pubescent; it is called the scaphognathite (respiratory plate); by its movements, the scaphognathite produces the water flow which enters the branchial cavity.

THORACIC APPENDAGES (first maxillipeds) (Figure 49 D). In their external form they resemble the maxillules. They have a coxopodite, a basipodite, and an epipodite. The exopodite is small, with no flagellum; the endopodite is stronger, and bears a flagellum at its end.

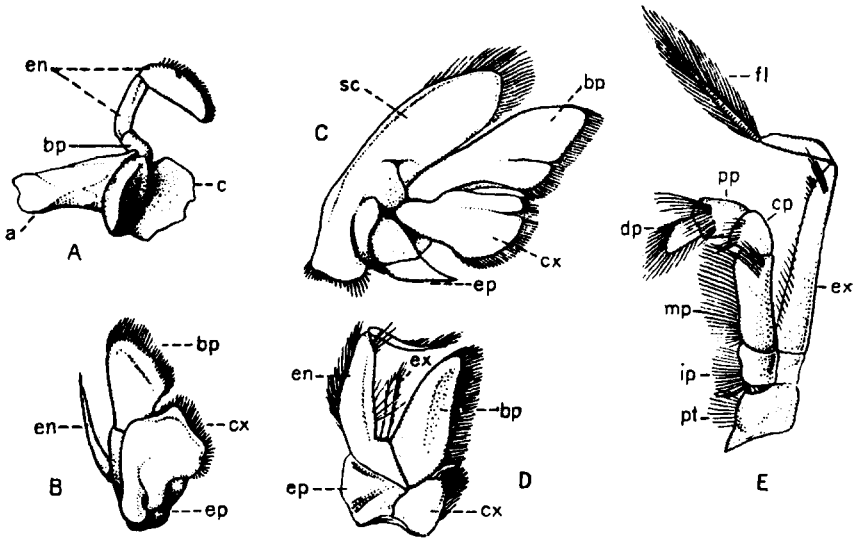

Figure 49. A – left mandible of Pagurus pubescens Kröyer. B – right maxillule of Pagurus pubescens Kröyer. C – right maxilla of Pagurus pubescens Kröyer (the endopodite is covered by the basipodite). D – left first maxilliped of Pagurus pubescens Kröyer. E. right second maxilliped of Pagurus pubescens Kröyer. cx – coxopodite; bp – basipodite; pt – protopodite; ep – epipodite; en – endopodite; ex – exopodite; fl – flagellum; ip – ischium; mp – merus; cp – carpus; pp – propodus; dp – dactylus; a – apophysis; c – gnathobase; sc – scaphognathite.

129 The second maxilliped (Figure 49 E) has the structure of a biramous appendage. The protopodite (coxa+basis) bears a five-jointed endopodite (made up of the following joints: ischium, merus, carpus, propodus and dactylus), and an exopodite (made up of a three-jointed stalk and a flagellum).

The third maxilliped (Figure 50) resembles the second maxilliped in structure, notwithstanding its relatively smaller exopodite. The ischium bears a row of denticles, which become larger proximally. The last two pairs of maxillipeds participate actively in the capturing of the prey. In addition, according to Brock's observations, the exopodite of the third maxilliped induces by its movements a water flow toward the antennules; the animal's sense of orientation depends on the stimuli received by the antennules from the various chemical compounds dissolved and carried by the water.

The first pereiopods or chelipeds (Figure 51) are made up of six joints; the basis and the ischium are fused to form one joint. The prolongation of the propodus forms the immovable dactylus (pollex). The part of the propodus extending from the articulation with the carpus to the base of the movable dactylus bears the name of 'palma'. The propodus together with the movable dactylus forms the 'manus'. The internal edges of the dactyli usually bear tubercles of various sizes, and are called prehensile edges. The size and form of the chelipeds vary considerably in the different genera and species; both cheliped may have the same length and structure, or one may be stronger than the other and of a different form. The surface of the joints may be smooth, but in most

cases it bears various armatures of granules, spiniform granules, spines,
130 denticles, tubercles, hairs, setae, etc. The size, form, and character of the chelipeds are the principal taxonomic character of the hermit crabs. If one of these appendages is missing or in an incipient stage of regeneration, the exact determination of the damaged specimen becomes difficult and often impossible.

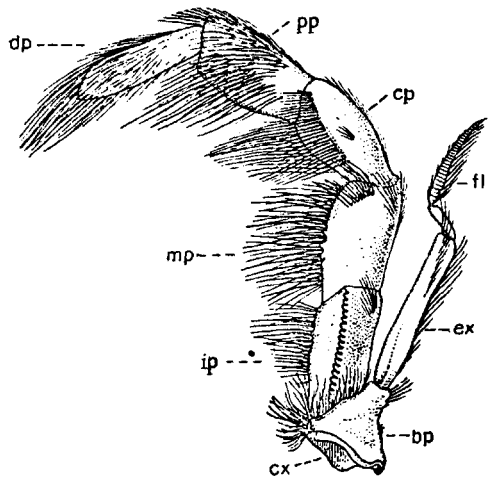

Figure 50. Right third maxilliped of Pagurus pubescens Kröyer (Captions as in Figure 49)

Second and third pair of pereiopods (first and second pair of walking legs) (Figure 52). The four pairs of legs following the chelipeds are called walking legs. The first two pairs of these legs have an identical structure and differ only in their length. In the taxonomic diagnoses, the term "walking legs" will refer only to these two pairs. Each leg is six-jointed; the dactylus is articulated at the distal end of the propodus, so that no pincers are formed. The dactylus is fairly long, straight or curved, and often more or less twisted around its longitudinal axis; at its distal end it usually bears a pointed corneous claw. The surfaces of all the joints (as a rule the outer one), as well as their edges, bears an armature like that of the chelipeds.

The fourth pair of pereiopods (third pair of walking legs) (Figure 53) is much shorter than the preceding pairs, each leg being six-jointed. The dactylus is articulated on the lateral edge of the propodus, so that a subchela is formed. The edge of the propodus opposite
131 the dactylus is covered with dense spinules, creating a rough surface like that of a file. The leg is usually bent in a right angle at the level of the meralo-carpal articulation.

The fifth pair of pereiopods (fourth pair of walking legs) (Figure 54) is also short, each leg being six-jointed. The propodus is very pubescent; the dactylus is very short and is articulated at the distal end of the propodus. The surface of the propodus and of the dactylus is covered with dense spinules. This appendage is introduced by the animal into the branchial cavity for cleaning the gills. In addition, the last two pairs of walking legs are pressed against the walls of the shell, serving for a good fixation of the animal within its shelter.

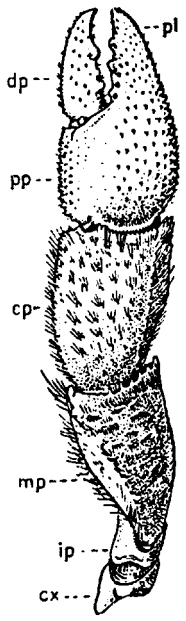

Figure 51. Right cheliped of Pagurus pubescens Kröyer: cx – coxa; ip – ischium; mp – merus; cp – carpus; pp – propodus; dp – movable dactylus; pl – immovable dactylus.

ABDOMINAL APPENDAGES. Pleopods. These (Figure 55) have a similar structure in both sexes. The short protopodite bears at its distal end an endopodite and an exopodite. The endopodite of all the pleopods of the male and the fourth pleopod of the female are small; in the other pleopods of the female, the endopodite is almost equal to the exopodite; both rami bear dense hairs; the pleopods bear the eggs. The pleopods of the hermit crabs are unpaired appendages, since on the right side of the abdomen, i.e., that adhering to the columella of the shell inhabited by the animal, the pleopods disappeared (an isolated exception is Paguropsis Hend., in which pleopods are, on the contrary, developed on the right side). The number of pleopods varies in the two sexes, the female bearing pleopods on abdominal segments two to five, and the male only on segments three to five. Thus, the presence or absence of pleopods on the second abdominal segment, as well as the size of the endopodites (with the exception of the pleopod on segment five), make it easy to distinguish between the sexes. Modifications undergone by the pleopods of some species of Paguridae will be mentioned under the diagnoses of the genera.

Uropods (Figure 56). The well-calcified sixth abdominal segment bears paired appendages, called uropods, which are also well calcified. Their structure is identical in both sexes. The protopodite bears a curved, sickle-shaped endopodite, and a stronger exopodite. The superoexternal surface of both the exopodite and the endopodite bears an area of dense spinules. As a rule, the uropod of the left side is stronger. Together with the telson – which is also calcified and bears pointed claw-like spinules on its distal edge – the uropods serve for a good fixation of the animal within the shell.

MUSCULATURE. With the exception of the abdominal muscles, the musculature of the hermit crabs differs very little from that of other Decapoda. The specific modification undergone by the abdomen owing to the way of life of the hermit crab left its mark also on the development of the abdominal muscles. The retractor muscles are much more developed than the extensors, the retractors of the right side being in their turn stronger than those of the left side. In the glaucothoë stage, the disposal of the muscles differs but slightly from the usual one; the extensors are still well developed, and are directed longitudinally; the retractors are composed of descending, transverse, longitudinal and ansiform fibers; the pleopods also still have independent retractors. Subsequently, the transverse fibers gradually disappear in the adult animal, and the lateral,

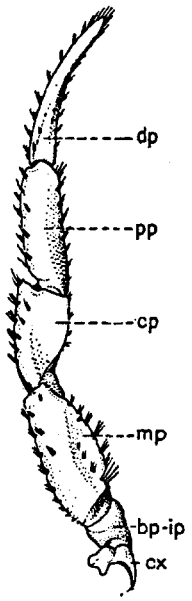

Figure 52. Left first walking leg of Pagurus pubescens Kröyer (Captions as in Figure 51)

longitudinal and descending fibers become rudimentary; the extensors become weak; the retractors are composed of strong, ventral, longitudinal and ansiform fibers. The muscles of the pleopods degenerate. The above-mentioned collumellar muscle derives from the ventral retractor of the third abdominal segment.

THE DIGESTIVE SYSTEM. The alimentary canal is divided into three sections: the fore-gut (esophagus and stomach), the mid-gut (the intestine) and the hind-gut (the rectum). The fore-gut and the hind-gut are lined with chitinous cuticle. The mouth is situated behind the maxillipeds, directed downward, and covered by a pair of mandibles. A fleshy three-lobed labrum (upper lip) is situated in front of and above the mouth; behind the mouth is the smaller lower lip (metastoma). The esophagus commences immediately behind the mouth, and appears as a tube with thick walls, the inner wall forming three large longitudinal folds in the lumen of the esophagus. The esophagus ends at the anterior end of the cardiac region of the stomach. At the proximal end of the esophagus three groups of stellate glands are found – two anterolateral groups and a posterior one; the efferent ducts of these glands open at the level of the internal wall of the esophagus. There are similar glands on the lips. The secretion of the glands probably serves as an emollient which facilitates the passage of the food mass without any enzymatic activity being carried out. The stomach (Figures 57 and 58) is composed of two sections: a large anterior one, known as the cardiac region, and a smaller posterior one, known as the pyloric region. The cuticle lining the stomach is impregnated with lime, and therefore the walls of the stomach never collapse. The small ossicles are products of this cuticle, and form the so-called gastric mill, a complex device for trituration, situated in the posterior part of the cardiac region and in the pyloric region; the structure of this device differs but little from that of Astacus, and we shall therefore not deal with it in detail, referring those interested to Huxley's monograph (1880). At the transition of the pyloric region of the stomach toward the mid-gut, five valves are found: a superomedian valve, a pair of superolateral valves, and a pair of smaller inferolateral valves; both pairs of valves are very pubescent. In addition, there is a pair of hairy crests on the superior wall of the pyloric region of the stomach; there is also a median hairy crest. The function of these valves and crests is to prevent the return
134 of the food from the intestine to the stomach, but they do not interfere

with the passage of the food to the intestine. Beyond the pyloric region of the stomach extends the longest part of the digestive tract, i. e., the mid-gut, which has no chiltinous cuticle. The length of the mid-gut differs in the various species. On the dorsal wall of the mid-gut, a little distance from the pyloric region of the stomach, two well-developed pyloric caeca (caeca anteriora dorsalia) are found. They extend in the form of thin tubes a little way along the superior wall of the stomach, subsequently bending abruptly downward; they descend along the lateral walls, then take a somewhat anterior direction, and terminate under the stomach in a small vesicle. On the dorsal side of the mid-gut, at the place of its transition to the hind-gut, is an unpaired pyloric caecum (caecum dorsale posterius), which extends anteriorly and ends in a small vesicle at the level of the third abdominal segment. In the male this caecum seems to be longer than in the female. Apart from this, its length varies in the various species according to the location of the transition from the mid-gut to the hind-gut. The short hind-gut (the rectum) resembles a muscular tube with thick walls lined inside with chitinous cuticle. The rectum has glands similar to those of the esophagus; the inner walls are strongly folded. The anal opening is found on the inferior surface of the telson, and has a sphincter. Thus, the anterior and posterior parts of the digestive tube are ectodermal in origin, while the median part, together with the pyloric caeca, is endodermal in origin. During molting, when the hermit crab first frees its cephalo-thorax, then its appendages, and lastly its abdomen, the chitinous cuticle of the fore-gut is eliminated through the mouth, and the cuticle of the hind-gut is eliminated through the anus.

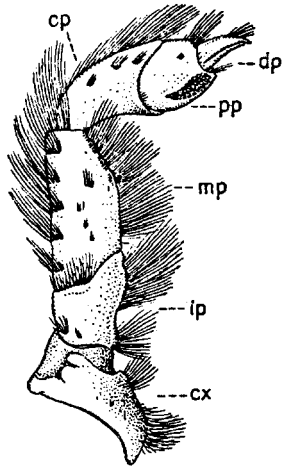

Figure 53. Right third walking leg of Pagurus pubescens Kröyer (Captions as in Figure 51)

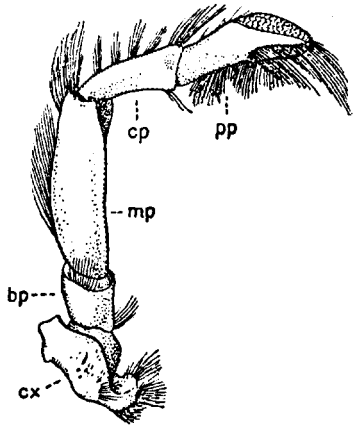

Figure 54. Right fourth walking leg of Pagurus pubescens Kröyer (Captions as in Figure 51)

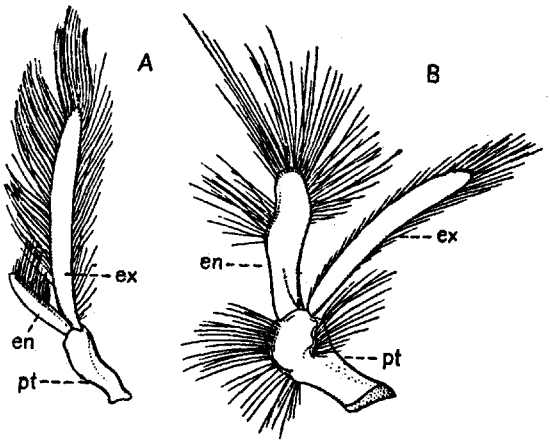

Figure 55. Pleopods of Pagurus pubescens Kröyer:
A – pleopod of male; B – pleopod of female.

The digestive gland (hepatopancreas), often called the liver, appears in the hermit crabs as a very long paired organ, extending very far within the abdomen. Each lobe is made up of a mass of ramified canaliculi, filling the abdominal cavity and finally being reunited in the axial ducts. The intestine passes either between the two lobes, or through the right lobe. The axial ducts extend along the retractors of the abdomen, but in the thorax they closely adhere to the ventrolateral walls of the intestine, and finally open on the inferior wall of the mesenteron, not far from the pyloric region of the stomach and in front of the anterior pyloric caeca. The hepatopancreas contains two kinds of cells; 1). high, cylindrical, alveolar cells, often having inclusions of lipoid droplets and glycogen, and 2). glandular cells, containing a large vacuole filled with a brown, liquid secretion, which penetrates the lumen of the canaliculus, either by the bursting of the vacuole, or by the elimination of the whole cell. It is very possible that besides their secretory function, these cells may also have an excretory function. At their distal ends, the glandular canaliculi have cells with large nuclei, and homogenous protoplasm; by mitotic divi-
135 sions these cells form the so-called fibrilar cells, which in their turn form the secretory cells.

The process of capturing food may be conceived as follows: as a rule, the left cheliped transmits the food to the maxillipeds; these then transmit it to the mouth parts, which carry out the first trituration of the food. The triturated food enters the stomach through the esophagus; here the gastric mill carries out the final trituration. The pasty mass passes through the pyloric region to the mid-gut, and the fragments which are unamenable to trituration are eliminated through the mouth. Immediately after leaving the stomach, the food paste is mixed with the secretion of the hepatopancreas. A part of this secretion may also enter the pyloric region of the stomach. In this case, digestion, which is carried out chiefly in the

mid-gut would begin while the food is still in the stomach. Absorption is carried out as the food passes along the mid-gut. The undigested remains are removed through the anus by the peristaltic movements of the rectum. It is not very clear how the feces are eliminated from the shell; they may be swept away by the water flow, and some of them are probably consumed by small Amphipoda which often inhabit the shells. The hermit crabs are omnivorous. According to Blegvad (1914), they feed on small mollusks, crustaceans, echinoderms, and possibly on fish and ground detritus. It has often been observed how hermit crabs wash out the sand between their mouth parts. M. T. Thompson explains the finding of diatoms and rhizopods in the digestive tract of Paguridae in this way. According to Hunt's studies (1925), Pagurus bernhardus and P. prideauxi feed on small lamellibranchs (Venus, Cultellus), echinoderms (Echinocyamus, small Echinocardium, ophiuroids), crustaceans (Amphipoda, Crangonidae, small Paguridae). Orton (1927) states that the hermit crab finds its food chiefly by plowing the detritus with the aid of the small cheliped and the third maxillipeds, and by the subsequent selecting of its organic particles (small polychaetes, crustaceans, algae, foraminifers, diatoms, etc). The hermit crab may also feed on larger food particles, but its mouth parts are less adapted for such food. Orton (1927) ascertained this by simultaneously feeding a hermit crab (Pagurus bernhardus) and true crabs (Carcinus moenas and Portunus ruber) with food particles of equal size. After an hour and a quarter the hermit crab had left untouched one fourth to one third of the food, while the true crabs ate the whole quantity of meat in only 4 to 11 minutes. Thus, the form of the third maxillipeds is wholly determined by the feeding habits of the animal. The feeding of the hermit crab on small detritic organisms also determines on the one hand the smaller size of the ossicles of the
136 gastric mill, and on the other hand the presence of crests on the lateral teeth of the stomach and the presence of hairs on the cardiopyloric valves, which serve for the filtration of the small food particles. A confirmation of this fact is found in the plankton-feeding crustaceans (e. g., Hapolocarcinus and Cryptochirus) in which the reduction of the ossicles of the gastric mill is even more pronounced.

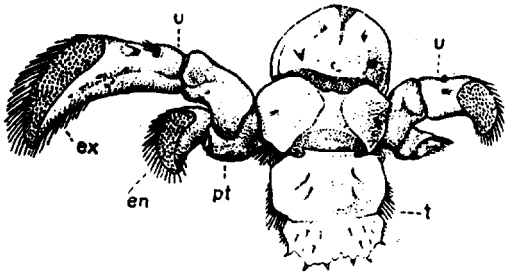

Figure 56. Sixth abdominal segment, uropods and telson of Pagurus pubescens Kröyer. u – uropods; t – telson; pt – protopodite; en – endopodite; ex – exopodite.

THE RESPIRATORY ORGANS are the gills, found in the branchial cavity; this cavity is protected laterally by the wall of the carapace, the so-called branchiostegite. According to their position the gills are arthrobranchiae, i.e., they are inserted on the articular membrane between the coxae and the body. On the twelfth segment a pleurobranchia is sometimes found, i.e., a gill inserted on the actual body wall. The usual branchial formula is as follows: segments eight to thirteen each have two arthrobranchiae (one anterior and one posterior); on segment twelve an additional pleurobranchia is sometimes found. According to their form, the gills of most hermit crabs belong to the phyllobranchiate type, i.e., they are composed of an axial stalk bearing biseriated leaflets. On the outer side of the branchial stalk is the afferent blood vessel, and on the inner side, the efferent vessel. The gills have so-called branchial glands, which produce a mucilaginous secretion. The first gills are smaller than the succeeding ones. The branchial cavity opens forward, downward and backward, so that water enters freely. The movements of the scaphognathite of the maxilla induce a permanent water flow which passes through the branchial cavity in a posteroanterior direction. The fourth pair of walking legs serve for the cleaning of the gills. From the point of view of comparative anatomy, the posterior arthrobranchiae and the pleurobranchiae are considered as being modified epipodites of the praecoxa, and the anterior arthrobranchiae as modified epipodites of the coxa.

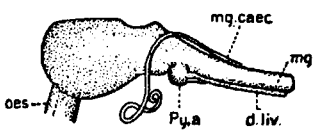

Figure 57. Stomach of Pagurus bernhardus (Linné) (view of left side). oes – esophagus; pya – pyloric ampullae; mg. caec – left anterior pyloric caecum; mg – midgut; d. liv – hepatic duct (From Jackson, 1913).

CIRCULATORY SYSTEM. The pericardial cavity in which the heart is housed extends from the cervical groove to the eighth thoracic segment. The mid-gut is located just below the pericardial cavity, and on its dorsal side; the pericardium adheres closely to the carapace. Thus, the heart is situated under the cardiac area of the carapace, and has — in dorsal view — an irregular pentagonal form, relatively strong muscular walls, and three pairs of ostia, through which the blood enters the heart from the pericardial cavity. One pair of ostia is situated anterodorsally, the second ventrally and somewhat laterally, and the third posterolaterally (Figure 59). Of the seven arteries that lead away from the heart, three are anterior (arteria mediana cephalica, and the paired arteriae laterales cephalicae), three go downward (the paired arteriae hepaticae and a. descendens), and one goes backward (aorta posterior). Let us follow schematically the track of these most important vessels.

1). Arteria mediana cephalica (a. ophthalmica) — or the median
137 paired aorta — passes above the stomach, then descends and divides into two branches which carry blood to the frontal area of the head. At the exit from the heart, this aorta forms a bulb, the so-called "cor frontale".

2). The paired arteriae laterales cephalicae (a. antennariae) lead away from the heart on both sides of the unpaired median aorta, curve

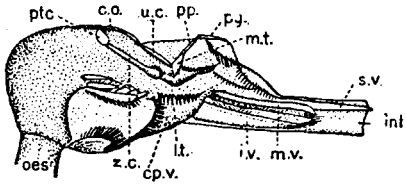

Figure 58. Sagittal section through the stomach of Pagurus bernhardus (Linnê), view to left side. ptc – pterocardiac ossicle; c.o. – cardiac ossicle; zc–zygocardiac ossicle; u.c. – urocardiac ossicle; m.t. – median tooth; l.t. – lateral tooth; pp. – prepyloric ossicle; py. – pyloric ossicle; cp.v – cardiopyloric valve; s.v. – superior valve; m.v. – median valve; i.v. – inferior valve; int – intestine (From Jackson, 1913).

hepaticae are poorly developed in the Paguridae; they do not carry blood to the digestive gland, which is housed in the abdomen, but terminate in small ramifications on the mid-gut.

3). The paired arteriae hepaticae are poorly developed in the Paguridae; they do mot carry blood to the digestive gland, which is housed in the abdomen, but terminate in small ramifications on the mid-gut.

4). The unpaired arteria descendens (a. sternalis) is the largest blood vessel leading away from the heart, and curves left and downward; it leaves the intestine at its right, then takes a horizontal forward direction in thoracic segments seven to five, subsequently again curves downward and passes through the central ganglionic mass, between the nerves of the second and third pereiopods; below the nerve chain it divides into an anterior branch, reaching the head, and a posterior branch, reaching the tail; these two branches bear a common name: a. subneuralis. The anterior branch carries the blood to the chelipeds and to the mouth parts, and also sends ramifications toward the inferior and anterior parts of the stomach, the pyloric caeca and the excretory organs. The posterior branch sends ramifications toward all the walking legs.

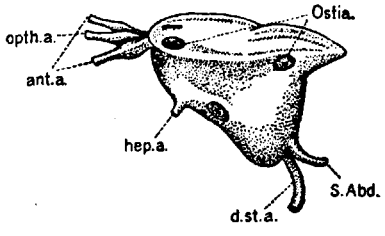

Figure 59. Heart of Pagurus bernhardus (Linnê) dorsolateral view. opth. a. – arteria mediana cephalica; ant. a. – arteriae laterales cephalicae; hep. a. – arteria hepatica; d.st. a. – arteria descendens; S. Abd. – aorta posterior (From Jackson, 1913).

5). The unpaired aorta posterior (arteria abdominalis dorsalis) carries the blood to the abdomen and the organs it contains. Corresponding to the specific modifications undergone by the abdomen, this vessel also undergoes changes peculiar to the Paguridae. After leaving the heart, above the aorta descendens, the aorta posterior extends as a strong trunk above the intestine, up to the first abdominal segment; here it is divided into two asymmetrical branches. One of the branches – the segmental artery – descends on the right side and reaches the end of the retractor muscles; at the level of the third abdominal segment, it is divided in turn into two branches: one

submuscular and one supramuscular; the first branch follows the nerve chain and ends in the vicinity of the last ganglion; the supramuscular branch sends ramifications to the gonads, the hepatopancreas, the rectum, the uropods and the telson. The second one of the two asymmetrical branches
138 is directed to the left, follows the surface of the hepatopancreas and sends ramifications to the gonads and the pleopods. It is interesting to note that in the female, each ovary receives blood from both branches, while in the male, the right testis receives blood from the left branch, and the left testis from the right branch.

The venous blood is concentrated in venous sinuses which are interconnected, and finally form a common sinus. The following venous sinuses are known: 1) the dorsal sinus, situated in front of and above the stomach; 2) the sternal (ventral) sinus, which extends ventrally along the whole thorax; 3) the abdominal sinus, which is the continuation in the abdomen of the sternal sinus; 4) the paired infrabranchial sinuses, situated on both sides of the thorax; they each communicate with the sternal sinus by five canaliculi; the lacunae of the thoracic appendages also open into these sinuses. From the infraorbital sinuses arise the afferent branchial vessels, which are found on the outer side of the stalk of every gill, and descend as efferent branchial vessels on the internal side of the stalk. The efferent vessels unite on each side in four branchiocardiac vessels (the so-called branchial veins), which open into the pericardial cavity by three slits on each side.

The blood appears as an almost transparent, slightly opalescent liquid, containing formed elements (amoebocytes, granulocytes and thrombocytes), carotenoids (which impart to the blood a pale-reddish shade), and hemocyanin, which fixes the oxygen; the hemocyanin contains not iron but copper, and if it remains for a long time in contact with the air, it becomes blue or rather violet (hemocyanin + carotenoids). Before molting takes place, the blood becomes considerably richer in calcium carbonate.

EXCRETORY SYSTEM (Figure 60). The excretory system of the hermit crabs has a much more complicated structure than in the other Decapoda; in addition to the paired antennal glands there is also a highly ramified pair of vesicular masses in the cephalothorax, as well as an unpaired abdominal bladder; the vesicular masses communicate directly with the antennal glands. Let us examine in detail each part of the excretory system:

1). The paired antennal glands (the "green glands" of Astacus) are found in the posterior part of the head behind the antennae. Each gland is composed of a mesodermal coelomic sacculus and an ectodermic nephridial canaliculus; the proximal part of this canaliculus is very ramified, and forms the so-called labyrinth (nephrostome), while its distal part broadens to form a collector bladder; out of this leads an efferent duct, lined with a chitinous cuticle and which — as already shown above — terminates in an opening (nephroporus) on the inferior side of the coxopodite of the antenna.

2). The anterior vesicular mass is found within the cephalothorax and communicates by anastomoses with the antennal glands. Each anastomosis
139 broadens to form a mass of ramified tubes, which in turn together form the epigastric lobe; from this lobe extends a narrow canal which leads to another mass of ramified tubes–the paragastric lobe–situated on the sides of the stomach; this mass communicates also with a small supragastric lobe; beneath the stomach is found the unpaired medioventral lobe, which by means of an anterior and a posterior branch is connected with the paragastric lobes.

3) The posterior vesicular mass. A pair of ramified tubes lead out of the paragastric lobes, extending along the intestine to the abdomen, where they unite to form an unpaired abdominal bladder (nephrosac) with thin walls, extending for about three quarters of the length of the abdomen.

In specimens preserved in alcohol, only rarely can all the parts of the system described above be observed; (as a rule, only the antennal glands and the nephrosac are visible; for a detailed study, a vital stain, such as a concentrated solution of methyl green or of acid fuchsin in sea water is recommended; 1-2 cm^3 of the solution are injected by means of a syringe into the articular membrane, under the thoracic appendages. After about 48 hours, the animal can be dissected; it is true that the antennal glands do not become colored, but all the other parts of the system become quite visible.

As the excretory system is completely embedded in the venous sinuses, it is probable that excretion is effectuated by direct diffusion through the wall. The cells of the vesicular masses project in the form of transparent vesicles in the lumen of the tubes; the excretory liquid contains such exfoliated vesicles, and sometimes even whole cells. An excretory function is also carried out by the glandular cells (nephrocytes) situated along the branchial stalks (these cells are also colored by the injected methyl green and acid fuchsin), as well as by the glandular cells of the hepatopancreas.

140 THE NERVOUS SYSTEM shows perhaps the least deviations in its structure as compared with the other systems; the principal modifications are related, as one could expect, to the abdominal part of the system.

The supraesophagial ganglion is situated at the level of the median line of the carapace, behind the eyestalks. The following nerves issue from the supraesophagial ganglion: 1) nervus opticus issues from the anterior part of the ganglion and enters the eyestalks; 2) n. oculomotorus — a small nerve, having a course parallel with that of n. opticus; it innervates the oculomotor muscles; 3) n. antennarius I (n. antennularis) issues from the inferior surface of the posterior half of the ganglion and is, in fact, made up of two branches–the nerve of the statocyst, and n. olfactorius; the latter innervates the sensory hairs and the antennular muscles; 4) n. tegumentarius, which by its ramifications innervates the teguments and the other tissues of the anterior part of the head; 5) n. antennarius II (n. antennalis) starts from the ganglion, behind n. tegumentarius, and innervates the antenna.

The supraesophagial ganglion is connected with the thoracic ganglionic mass by two peripharyngial commissures, commencing from the posterior half of the ganglion and extending onto the sides of the esophagus. Each commissure forms in its middle a parapharyngial ganglion, from which issue four nerves: two external and two internal ones; the anteroexternal one innervates the surrounding tissues, and the posterior one the mandibular muscles. The two internal nerves form the so-called somatogastric system; the two nerves start together. They then diverge, and at the anterior part of the esophagus, they again fuse to form the unpaired somatogastric nerve. This passes downward to the anterior part of the stomach, where it forms a somatogastric ganglion. From this issue ramifications to the muscles of the stomach. The somatogastric nerve then encircles the stomach, forms another ganglion on its dorsal side; it finally bifurcates and ends in the pyloric region of the stomach. The peripharyngial commissures are reunited about half way between the parapharyngial ganglia and the thoracic

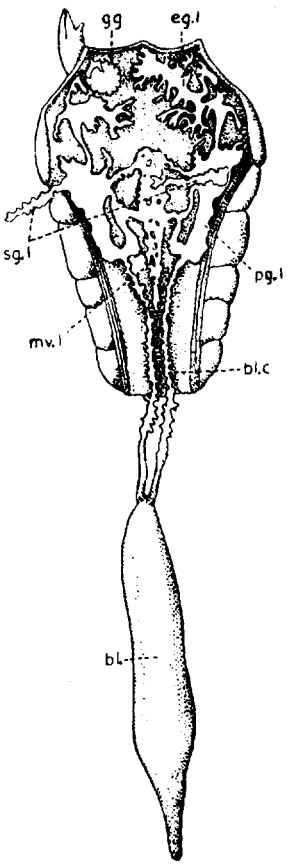

Figure 60. Excretory system of Pagurus bernhardus (Linné). The left epigastric lobe; all the other organs, the muscles and the abdomen have been removed (semischematic view).
gg – left antennal gland; eg.l – epigastric lobe; sg.l – supragastric lobe; pg.l – paragastric lobe; mv.l – medioventral lobe; bl.c – ducts between the anterior and posterior vesicular masses; bl. – nephrosac (From Jackson, 1913).

ganglionic mass, by means of a posteropharyngial commissure. The thoracic ganglionic mass, to which pass the peripharyngial commissures, is found at the level of the third to sixth thoracic segments, and is made up of three fused ganglionic masses. The degree of fusion of these masses is more advanced than in Macrura, but less so than in the Brachyura. At any rate, three sections, separated by narrow transitions, may be readily distinguished. Each section has an orifice through which arteries pass. From the first section, which is the result of the fusion of seven pairs of ganglia, issue seven pairs of nerves – the first pair to the mandibles, the second and third to the maxillae, the fourth, fifth and sixth to the maxillipeds, and the seventh to the chelipeds. The second section – the median one – results from the fusion of a single pair of ganglia, and sends a pair of nerves to the first walking legs. Three pairs of nerves directed toward the second, third, and fourth pairs of walking legs begin from the posterior section of the thoracic ganglionic mass. The first pair of abdominal ganglia are also fused with the thoracic mass, but are separated by a small groove.

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The thoracic ganglionic mass is connected to the abdominal chain by means of the abdominal commissure, which is unpaired at the beginning, but divides into two branches as it enters the abdomen. The abdominal chain is composed of five pairs of ganglia, each pair being almost fused in a common mass; the ganglia are interconnected by means of paired commissures. The whole chain is situated beneath the mass of retractor muscles and above the mass of tegumentary muscles. The ganglia are found within segments two to six. After entering the abdomen, the chain curves to the left, and after the fourth pair of ganglia, the chain achieves a median position. From every pair of ganglia, nerves issue to the muscles, to the pleopods and to the teguments. In addition, ramifications issue from the interganglionic

commissures. From the last pair of ganglia, nerves pass to the uropods, to the telson, and to the rectum.

SENSORY ORGANS. Eyes. The eye is composed of numerous so-called ommatidia; their number is fairly great, and increases as the animal grows. The cornea of the facets has a hexagonal form. Each facet represents the distal end of an ommatidium, and owing to the curve of the cornea, all ommatidia are disposed radially. An ommatidium is made up of the following parts (Figure 61): 1) the cornea, which is composed of three chitinous layers (the tegument layer, the pigment layer and the basilar layer, corresponding to the layers of the cuticle), shows no calcification, and is distinct from the two subjacent corneal cells (according
142 to Schneider, there are four such cells). The cells of the cornea have the form of right-angled triangles, adhering by their hypotenuses; these appear as diagonals when the cornea is seen from above. The nuclei of these cells are found in the right angle of these triangles; 2) the crystalline cone is composed of four conical cells (often called Semper's cells), each cell has a transparent and refractive body, which becomes narrower at its proximal end, forming a stalk which reaches the distal end of the rhabdome. The nuclei of the conical cells (the so-called nuclei of Semper) are found at their distal ends; 3) the two principal pigment cells are situated at the opposite ends of the conical cells; they contain an iridescent pigment, and modify their size in accordance with the intensity of light; 4) eight retinal cells are found, one of them sometimes rudimentary. The distal ends of these cells are swollen and contain a large nucleus, the proximal ends tapering and reaching the basilar membrane. The fibrils of the optic nerves pass on the external surface of the cells, partly surround their nuclei, then descend along the internal side and end in the transverse plates of the rhabdome. The latter appears as a complex formation, showing a general photosensitive rhabdite, surrounded by retinal cells. Every second retinal cell participates in its structure so that four groups of four cells, known as rhabdomeres, are formed. Each rhabdomere is made up of square transverse plates, starting on the internal longitudinal sides of the retinal cells (Figure 62), and then uniting with the plates of the opposite cells; as these "half-plates" form in their successive positions an angle of 90°, in longitudinal section one may observe a structure of light stripes (transversely sectioned fibrils) and dark stripes (longitudinally sectioned fibrils). At the distal end of the rhabdome, a cavity is found. The retinal cells, like the principal pigment cells; contain pigment; according to Parker, in the dark the pigment spreads in the retinal fibrils, penetrating beneath the basilar membrane; owing to this fact the rhabdome is penetrable by light from any direction. In the principal pigment cells, the pigment is concentrated at the distal ends in darkness, while in daylight it is concentrated at the proximal ends; 5) the complementary cells (Tapetumzellen, Hesse) are slightly pigmented; they are situated at the base of the rhabdome and on both sides of the basilar membrane, forming a reflecting surface. The basilar membrane is composed of anastomosed conjunctive fibers. The nerves which arise from each of the ommatidia pass through the basilar membrane toward the four optical ganglia (lobus opticus), situated one behind the other; these ganglia are called: lamina ganglionaris (first ganglion), medulla externa (second ganglion), medulla interna (third ganglion), and medulla

terminalis (fourth ganglion). The first ganglion is in direct contact with the ommatidia. Between the first and second ganglion lies a nerve chiasma, the
143 so-called chiasma externa; between the second and third ganglia lies a second chiasma—chiasma interna—and finally, between the third and fourth ganglia, is another chiasma which bears no special name. The fourth ganglion is connected to the supraesophagial ganglion by means of the pedunculus lobi optici (n. opticus). For a more detailed description of the structure of the eye, see the works of Parker (1890, 1895), Hesse (1901), and Trojan (1913).

There are studies on Clibanarius misanthropus (Risso) concerning phototropism. This hermit crab changes the type of its phototropism every fourteen days, adapting itself to the intensity of illumination specific to the level of the tide: at low tide, it shows a negative phototropism, while at high tide it shows a positive one; it is interesting to note that, when placed in an aquarium, the animal continues to show for a time this rhythmic change in phototropism.

Minkiewicz (1907) tried to find a chromotropism in the hermit crabs, i. e., the preference for a bottom of a certain color; he established the following succession of colors (in order of increasing preference): black-red-yellow-blue-violet-green-white. Cotte (1921), who repeated the experiments of Minkiewicz, could not confirm the exactness of this author's conclusions. Mikhailov's experiments (1920) indicate that the hermit crab may distinguish and memorize various colors. Dardanus arrosor (Herbst) shows a connection between tactile stimuli, to which it reacts by hiding in the shell, and an illumination of a certain color; after consolidating this conditioned reflex, the animal reacted to the respective color by withdrawing into its shell (even without any tactile stimulus); this reaction was maintained for 200 days; after the cessation of this reflex, it could be established again much more quickly than the first time.

The statocyst (otocyst, "auditory sac", of earlier authors) is found in the basal joint of the antennules. It appears as a simple invagination of the external tegument and has the form of a sac; it is consequently lined with chitinous cuticle. The statocyst is connected with the exterior by means of a narrow longitudinal slit, found on the dorsal surface of the joint; the orifice is protected against foreign bodies by means of two fringed hairs. From the posterior end of the statocyst and along the internal wall of the external part extends a small crest, while on the ventral side, within a small groove, is found the tract of the "acoustic" branch of the antennular nerve. The cuticle bears mobile sensory hairs, which, beginning at the posterior end of the statocyst, form two or three indistinct rows, most of the hairs being situated on the crest of the external part of the statocyst. Each hair is pennate and has an axial cavity; to every hair corresponds a bipolar, sensory cell, one of its ramifications entering the cavity of the hair, and the other ramification connected with the "acoustic" (static) nerve. Serving as statholiths are granules of sand, either free or stuck to the hairs by the secretion
44 of the glands at the base of the statocyst. The nerve enters the statocyst at its posterior end, and then divides into two branches; the larger branch extends along the external wall of the statocyst, and the smaller along the medial wall. During molting, the entire inner lining of the statocyst (which is ectodermal in origin) is eliminated and replaced by a new one; the statoliths are also replaced. The statocysts, which were considered by former

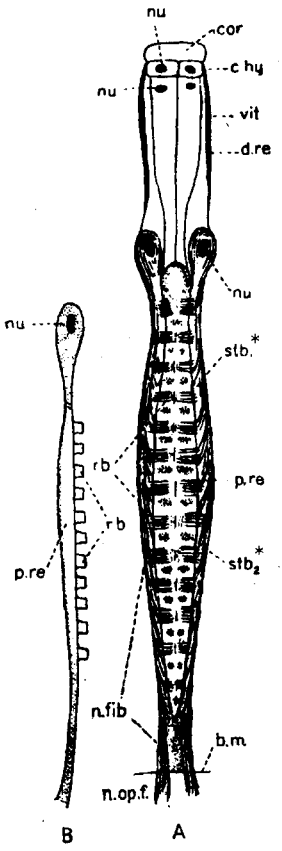

Figure 61. A longitudinal section through an ommatidium. B. An isolated proximal retinal cell (semischematic view, greatly magnified). nu - nucleus; cor - cornea; chy - corneal cells; vit - vitreous body; d.re - distal retinal cells (principal pigment cells); rb - rhabdome; p. re - proximal retinal cells; n. fib - unpaired fibrils; b. m. - basilar membrane; n. op. f. - the fiber of n. opticus (From Jackson, 1913).

* [Omitted in Russian text.]

authors as being auditory organs, have an exclusively static function, enabling the animal to find its correct orientation. A detailed description of the statocysts, and a survey of the different opinions as to their function may be found in C. W. Prentiss' work (1901).

Smell. Olfactory hairs (esthetascs) are found on the exopodites of the antennules. Each joint bears a number of such hairs, which appear as cavitary formations having about 24 joints each; the basal joint is broad and surrounded by a tuft of small hairs; each hair shows an innervation. By moving its antennules, the animal continually investigates its surroundings. There is a detailed study by Brock (1926) on Dardanus arrosor (Herbst) regarding the importance of the olfactory hairs; if in the vicinity of the animal a lure is suddenly introduced, it becomes restless and begins to move its antennules vigorously; it then turns and moves toward the lure; the time elapsing until the moment the animal begins to move is proportional to the distance between it and the lure; it also depends on temperature (in winter it takes twice as long as in summer). An important part is also played by the respiratory water flow, which, on leaving the branchial cavity, reaches the antennae, transporting various stimulating substances toward the sensory hairs.

Touch. Tactile hairs are scattered all over the body. Every hair represents a cavitary outgrowth of the cuticle; the canaliculi leading the nerves to the hairs penetrate all the tegumentary layers of the animal. Blind animals may, for instance, distinguish with the aid of their second and third pereiopods the surface of a shell from the smooth surface of a glass tube. The form of the objects may also-it seems-be discerned with the aid of the tactile sense. So, for instance, A. Drzewina succeeded in observing how Clibanarius misanthropus distinguished between a shell of Trochus, which it was not using, and one of Cerithium, which it preferred as a shelter. The antennae possess exceptional tactile sensibility, thus enabling the animal to follow the movements of fish and other animals approaching him.

Few data exist concerning the thermic sense. As to the Paguridae, Matisse has found that high and low temperatures bring about a thermic collapse of the animal.

REPRODUCTIVE ORGANS. The paired testes of the male are located between the lobes of the hepatopancreas, the left testis being larger and nearer the surface than the right one. The testis appears as a long, winding
145 tube, with ansae forming a flat elongated organ. The terminal section of the tube makes a number of convolutions, then straightens and is called the sperm duct (vas deferens); it reaches the abdominal cavity, then is directed abruptly downward and opens onto the coxa of the last pair of walking legs. The terminal section of the vas deferens is surrounded by strong muscles and is called the sperm-ejecting canal. In some genera, a tegumentary penis is observed (usually only on the left side) or paired genital appendages are found (in Paguristes and Parapagurus) which will be described when we deal with these genera. The spermatozoids possess three outgrowths, and while passing through the vas deferens, they are united into spermatophores.

The paired ovaries of the female have an elongated form and a granular external aspect; they extend along the whole abdomen, the left ovary at the anterior end being situated at a higher level than the right one. The oviducts are muscular tubes, opening on the coxa of the third pair of walking legs (only in Parapagurus is an unpaired opening found on the left coxa). On the inferior side of the abdomen of the female the so-called "cement" glands are found at the base of the pleopods. Their mucilaginous secretion serves for the fixation of the eggs to the pleopods. It is possible that in this mucus the fertilization of the eggs also occurs, since the mucus probably dissolves the membrane of the spermatophores. The entire process may be conceived thus. The male places the spermatophores in the space between the columellar muscle and the body of the female, where the oviducts open when the abdomen of the female is bent. The female bends her abdomen, fills the space with mucus, and there lays the eggs; by the movements of the pleopods, the eggs are mixed with the sperm, and the fertilized eggs are fixed by means of the mucus to the pleopods of the second, third and fourth segments. The whole process is probably carried out inside the shell. According to the studies of Brandes (1897) on Pagurus prideauxi (Leach), the spermatophores are fixed not to the body of the female but to the shell in which it lives. During copulation, the male holds with his left cheliped the right second pereiopod of the female, and the movements of the reduced fourth and fifth pereiopods facilitate the introduction of the spermatophores into the shell. The females of some genera (Paguristes, Paguropsis) have on the left side of their abdomen a tegumentary fold, which covers and protects the eggs carried by the pleopods. We have already dealt with sexual dimorphism when describing the pleopods. It may be added that the genital openings have a different position in the two sexes. Sometimes, the right chela of the male is stronger than that of the female.

The postembryonic development of the Paguridae comprises six larval stages, which may be briefly described as follows: 1) the first zoëa stage:
146 the first and second maxillipeds are developed and their exopodites bear four pinnate hairs. The thoracic appendages are still missing. Only six abdominal segments are distinguished, the sixth one being fused with the telson; 2) the second zoëa stage: there are three maxillipeds, and the primordia of the thoracic appendages appear. The exopodites of the maxillipeds bear six hairs. The primordia of the uropods appear; 3) the third zoëa stage: the exopodites of the maxillipeds bear seven or eight hairs. The sixth abdominal segment may be distinguished. Uropods are present. Primordial gills appear on the appendages; 4) the fourth zoëa stage (metazoëa); the thoracic

appendages are developed; the fifth pereiopod, bent under the body, is chelate; the first pereiopods are unequal. Primordial pleopods appear; 5) the glaucothoë stage (Figure 62), which corresponds to the megalopa of the Brachyura, represents the characteristic larval stage of the Paguridae, and was considered for a long time as an independent species. The carapace already has the form of the mature animal, but the branchiostegite is not yet bent downward at a right angle. The fourth and fifth pereiopods are reduced. The abdomen is made up of seven segments. The pleopods are symmetrical. The right uropod is less developed than the left. The statocysts appear. At the beginning of this stage, the larva swims freely near the bottom during the day, while at night it rises to the surface, where it can be easily caught with plankton nets. Next, the transition to a reptant life takes place. The animal begins to look for a shelter. This stage usually lasts from 4 to 5 days, and during this period, the hepatopancreas, the nephrosac and the gonads move to the abdomen, the pleopods on the right side disappear, while those of the left side degenerate. As shown by Thompson, the anatomical changes undergone during the glaucothoë stage do not depend on the presence or lack of the shell, or on its form. But, if there is no shell, the stage lasts from 6 to 8 days, and mortality increases greatly. Exceptions are known in which rudimentary pleopods are retained on the right side, although it is typical for these appendages to disappear on this side during this stage; 6) the juvenile stage is represented by a typical adult animal. The organs are definitely developed, and the sexes may be distinguished by the pleopods. Thompson considers that sexual maturity is reached one year or more after molting from the glaucothoë to the juvenile stage.

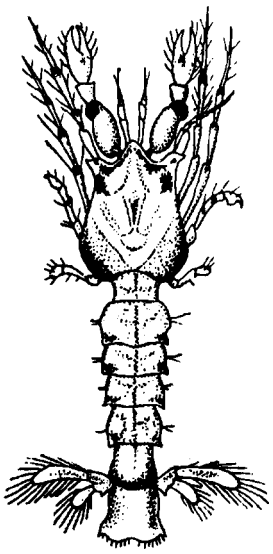

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Figure 62. Glaucothoë stage of Paguristes oculatus (Herbst): the abdomen is still segmented and symmetrical (From Balss, 1913, reproduced from Issel, 1910).

In his work on larval Decapoda of Plymouth Sound, Webb (1921) describes as follows the larval Paguridae found there: the rostrum is long and pointed, extending beyond the antennules. The eyes are large and oval. The carapace is relatively wide and short, concave in its posterior part, ending in a pointed prominence in each of the posterolateral corners, and lacking a spinose border on either side (as in the larvae of the Galatheidae). The telson is more or less spatulate, with an abrupt posterior edge. In the fourth stage, there are three pairs of setigerous exopodites (first to third maxillipeds). The author distinguishes only four larval stages (the fourth being the glaucothoë stage), characterized by the following features: first stage: the caudal plate is simple and bears 12 spines; uropods are missing; second stage: the caudal plate is simple and bears 14 spines; uropods are

missing; third stage: the telson and the outer uropods are well developed and spinulose; the inner uropods appear as small naked outgrowths at the base of the outer pair; the pereiopods are moderately developed; fourth stage: the telson and the uropods are as in the third stage; the pereiopods are more developed; they extend posteriorly, and cover all the pleopods except the last two pairs. Describing the larva of Pagurus bernhardus, Webb states that it is almost transparent, with a reddish-yellow chromatophore on the back. The mouth parts have dark crimson spots; an orange chromatophore is found on the developing chela of the first leg (most marked in the last larval stage). The eyes are dark with a pale-yellow luster.

One ought to stress the complete lack of monographic studies on the larvae of the Paguridae (which is, in fact, true for all Decapoda). In almost every work on the larvae, the specific determinations, and sometimes even the generic ones, are provisional. Webb also shows that only the larvae of Pagurus bernhardus and P. prideauxi can be reliably determined. In presenting the detailed description of three larvae of Paguridae, M. V. Lebour (1934) does not even succeed in determining exactly the genus to which they belong (possibly Clibanarius). Thus, this field is still very little studied and in need of further investigations.

THE HOUSE OF THE HERMIT CRAB. Stereotropism is well developed in the Paguridae, which all try to hide their soft abdomen in a hollow object of any kind. The spiral shells of the Gastropoda usually serve this purpose. Nevertheless, they also use tubes of various worms, sponges, corals, tubes of wood or of bamboo, etc. In experimental conditions, the animals, when deprived of shells, use glass tubes introduced into the aquariums. The way in which hermit crabs take possession of the shells is highly interesting. Swammerdam, one of the first students of the anatomy
148 of the Paguridae, tried to prove that the shell is secreted by the hermit crab itself. Bell was of the opinion that the hermit crab attacks a live mollusk, eats it, and then uses its shell as a shelter; this opinion was apparently confirmed by the observations of fishermen who caught hermit crabs which were in the process of eating mollusks. Jackson, however, doubts the ability of the hermit crab to overcome a live mollusk alone; therefore, without completely refuting Bell's opinion, he advances the hypothesis that the harder portions of the mollusk (foot and head) are eaten by fishes, and he tries to confirm his hypothesis by the fact that opercula of mollusks are often found in the stomachs of cod; the soft remains are then eaten by the hermit crab, which subsequently occupies the shell. Jackson does not deny the possibility of the occupation of empty shells, which, in fact, seems to happen in most cases. The hermit crabs deprived of any shelter did not develop, and perished. Taylor's description of the helplessness of the hermit crab deprived of a shell is extremely apt. He compared it to a bather whose clothes have been stolen. It is quite difficult to take a hermit crab out of its shell; it is fixed within the shell by the last two pairs of walking legs as well as the uropods. Even if the shell is opened and the abdomen subjected to irritation, the hermit crab, instead of leaving the shell, reacts by fixing itself even more firmly within it. The chela of one or both chelipeds, broadened like an operculum, often serves to close the opening of the shell; in the genus Cancellus, the broadened walking legs serve this purpose. The presence of the shell does not greatly hinder the animal in its movements;

(149)

Figure 63. Pagurus pubescens Krøyer. Moment of changing its shell. Original drawing by N. Kondakov.

thus, Jackson observed hermit crabs climbing sheer rocks with relative ease. The aeration of the interior of the shell is carried out by the movements of the pleopods; that the aeration is sufficient is shown by the fact that Anemia, Amphipoda, and other small animals are found even in the deepest convolutions of the shell inhabited by the hermit crab. Gray believed the hermit crabs to be capable of dissolving the shell they inhabited. It is, however, difficult to conceive of such a possibility. This author probably dealt with shells decomposed with time. As to the choice of shells belonging to a definite species, no detailed studies are at hand, but it seems that such selectivity does not as a rule exist, and that the animal uses the shell of any species available, taking into account only the dimensions of the shell. A peculiar shelter is that of Paguropsis typica Henderson, which holds over its body like a hood an actinia of the genus Mammilifera, to which purpose the uropods and the last pereiopods are specifically modified. Porcellanopagurus holds over its body a valve of a lamellibranch, thus covering its body entirely.

THE SYMBIOSES of the Paguridae form the majority of such cases among the Decapoda. The symbiosis of a hermit crab with an actinian is a classic case; the same actinian can be associated with different species of Paguridae, or with a single species. So, for instance, Adamsia palliata Bohadsch is associated only with Pagurus prideauxi (Leach), Epizoanthus sagamiensis Pax is found only together with Paguristes palythophilus Ortmann, and Epizoanthus paguriphilus Verrill, almost exclusively with Parapagurus pilosimanus Smith. When changing their shell, many hermit crabs also remove "their" actinian, transplanting it with the chelipeds to the new shell (this was observed by Brunelli in Dardanus arrosor Herbst). Pagurus bernhardus and P. excavatus are often found together with Sagartia parasitica. We must also mention here Sagartia paguri Verrill, which is borne by Diogenes edwardsii (de Haan) on the chela of its left cheliped. It is also interesting to note that the hermit crab becomes immune to the toxins and to the nematocysts of "its" actinian, which usually act strongly upon other Decapoda; the experiments of Cantacuzene and Cosmovici (1925) have shown that a normally fatal dose of actinian poison injected into the crab Carcinus maenas, together with blood of Pagurus prideauxi, does not cause death.

Sponges often settle on shells inhabited by hermit crabs. We note Suberites domuncular Nardo, in symbiotic relationship with Pagurus bernhardus, P. pubescens, P. pectinatus, P. undosus and Paguristes oculatus; Hymeniacidon suberea with Pagurus bernhardus and P. pubescens; and finally Ficulina ficus Esper with Paguristes oculatus, Pagurus pubescens and P. bernhardus. It is interesting to note that the sponge sometimes completely dissolves and absorbs the shell, so that the hermit crab is covered directly by the sponge. When opening such sponges, one can see that the cavity occupied by the hermit crab corresponds perfectly to the convolutions of the former shell. Arndt (1933) wrote a detailed study on the symbiotic relations between sponges and hermit crabs.

Hydractinia echinata Flemming and Podocoryne carnea M. Sars are among the hydroids encountered on shells of Pagurus bernhardus and P. pubescens; Hydrissa sodalis (Stimpson) is found on the shell of Pagurus constans (Stimpson).

Of the bryozoans, Conopeum commensale Kirkp. and Metz. covers the shell of P. granulimanus Miers, and Cellepora senegambiensis Carter – the shell of Diogenes pugilator Roux.

Generally known is the symbiotic relationship between the polychaete Nereilepas furcata inquilina Wirén and Pagurus prideauxi. The hermit crab does not disturb "its" worm (although it eats others), and when moving to another shell, it removes it also. It is possible that the worm eats the ectoparasites found on the posterior part of the body of the hermit crab. A similar symbiotic relationship is that between Nereis cyclurus Harrington and Pagurus ochotensis in California and in the Sea of Japan. Turbellaria are also found, as for instance Emprostopharynx opisthoporus Bock and Euprosthiostomum adhaerens Bock with Pagurus californiensis, or Stylochus zebra Verrill with P. pollicaris. A more detailed description of the symbiotic relationships of the hermit crabs can be found in H. Balss' study
151 (1924).

PARASITES OF THE HERMIT CRAB. Of the sporozoans some types of coccidians are found in the intestine of Pagurus. The greatest number of ectoparasites is furnished by the crustaceans. The copepod Sunaristes paguri Hesse (of the family Longipediidae) lives, as a rule, only on shells inhabited by hermit crabs. Of the Cirripedia, Peltogaster Rathke, Clistosaccus Lilljeborg and Apeltes Lilljeborg are often found on the abdomen of Pagurus and Anapagurus. There are studies showing that as a consequence of the infestation with certain species of Cirripedia, anatomic modifications appear. For instance, if Anapagurus chiroacanthus (Lilljeborg) is parasitized by Peltogaster sulcatus, the pleopods of the male become like those of the female, i.e., they develop long endopodites. If it is parasitized by Peltogaster paguri, the pleopods undergo almost no modification, but the penis is reduced; in addition, a parasitic castration appears, marked by the degeneration of the gonads. Of the isopods, we note the genus Bopyrus, found in the branchial cavity of the hermit crabs, and the genera Athelges, Phryxus and Pseudione, which are fixed on the abdomen of hermit crabs.

ZOOGEOGRAPHICAL OUTLINE

152 Most of the species belonging to the Paguridae are typical inhabitants of the littoral and sublittoral of the Tropical zone. The Boreal zone also has its pagurid species, but they are far less numerous; the Arctic zone completely lacks species of its own, although some boreal, more or less eurythermal species, reach relatively high latitudes in the Arctic Zone. At present, about 450 species of Paguridae are known. If the total number of Decapoda is considered to be about 6, 000 (this figure is no doubt somewhat exceeded now), then the hermit crabs form 7. 5 % of them. In the Soviet waters 25 species of hermit crabs are known, i.e., 5. 5% of the total number of species.

The present study deals with the fauna of the following waters: Black Sea; White Sea; Barents Sea, west [sic] of North Cape – Bear (Medvezhii) Island – Spitsbergen; the entire Sea of Japan, including Japan's western shores, Tsugaru Strait and La Perouse Strait; the Sea of Okhotsk, including the Kurile Islands; the eastern shores of Kamchatka; the whole

of the Bering Sea, including the Aleutian Range and Kodiak Island; the Chuckchee Sea east of the Point Barrow meridian.

Taking into account these geographical limits, the species number 42, belonging to 8 genera.

Let us now proceed to the survey of the distribution of the hermit crabs in the various waters.

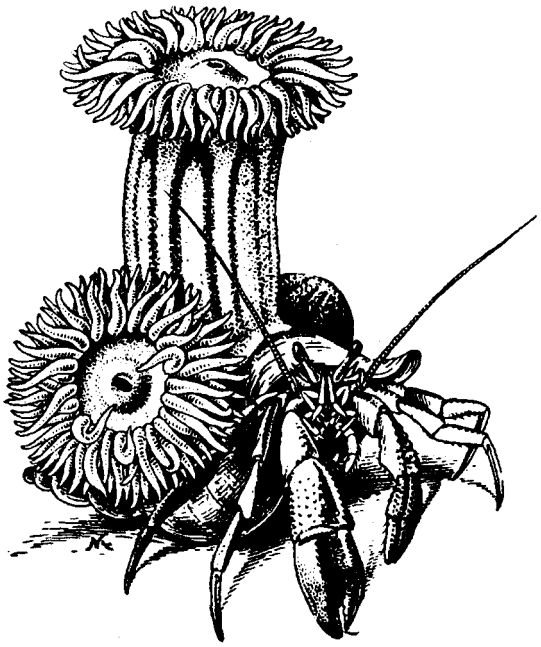

Figure 64. Pagurus bernhardus (L.) with Sagartia parasitica. Original drawing by N. Kondakov.

In the Black Sea, only two species of hermit crabs are known, namely, Diogenes varians and Clibanarius misanthropus, typical representatives of the Mediterranean fauna. The specific conditions of the Black Sea (probably chiefly the reduced salinity, which is 17 to 18% [sic]; in some regions only 10%), determined the nanism of these forms, which is very striking when compared with specimens from the Mediterranean. Clibanarius misanthropus is much more rare than Diogenes varians.

In the White Sea and the Barents Sea, only one species of hermit crab (Pagurus pubescens) is found. Another species - P. bernhardus — appears very seldom on the West Murman coast, which is the eastern limit of its range. P. pubescens occupies a special position among the hermit crabs of the Soviet waters, as it is a typically amphiboreal species.

The seas of the northern shores of Siberia have no hermit crabs in their fauna, not taking into account the sporadic appearance of Pagurus pubescens
153 in the Kara Sea; hermit crabs appear again only in the Far Eastern part of the Arctic Ocean, east of Kolyma River.

The fauna of the Soviet Far Eastern seas is the richest in hermit crabs, containing 84% of the species known in the the Soviet fauna. According to their distribution, this total amount of Far Eastern species may be divided into four main groups.

First group: species with a wide distribution, found in all three Far Eastern seas (Sea of Japan, Sea of Okhotsk and Bering Sea), as well as in the Chuckchee Sea; to this group belong Pagurus pubescens, P. rathbuni and P. capillatus.

Second group: species almost exclusively confined to the Sea of Japan, not taking into account the fact that they enter the Inland Sea of Japan and appear also on its southeastern coast: Pagurus gracilipes, P. dubius, P. anomalus, P. brachiomastus, P. lanuginosus, P. pectinatus, Diogenes penicillatus.

Third group: species found in the Sea of Japan and the Sea of Okhotsk, as well as on the western shores of North America; the connection is through the Aleutian Range; the species do not enter the Bering Sea, with only one exception. To this group belong Pagurus hirsutiusculus, P. middendorffi, P. undosus, P. ochotensis and P. gilli.

Fourth group: Species with a discontinuous distribution, found in the Sea of Japan and on the western shores of North America, but not encountered in the intervening region–Pagurus samuelis, Orthopagurus minimus, O. schmitti.

SEA OF JAPAN. Of the first group, only Pagurus pubescens is found on the shores of Japan proper; the other two species are known only from the Soviet shores of this sea, which is the southern limit of their range. All the members of the second group are found in Japan, and, with the exception of Pagurus anomalus and P. brachiomastus, they inhabit mainly the southern part of the Sea of Japan and the southeastern coast of Japan. The northern limit of their range is on the Soviet shores. Pagurus anomalus and P. brachiomastus, on the other hand, are confined to the Soviet waters of the Sea of Japan, the southern limit of their range being southern Japan. Of the third group, Pagurus undosus is found only in the Soviet waters, and is unknown in Japan. Of the fourth group, Pagurus samuelis is known also in the Japanese waters, while the two species of Orthopagurus were recorded only from the Soviet shores. A special group is that of species endemic to the Inland Sea and to the eastern shores of Japan, only entering part of the Sea of Japan proper, and not reaching the area north of Tsugaru Strait. These are: Pagurus obtusifrons and P. constans, Clibanarius japonicus and Paguristes digitalis. We also mention the group of the tropical species, whose northern limit is the southern Japanese coast, and which are found
154 but seldom in the Sea of Japan proper, namely Spiropagurus spiriger, Diogenes edwardsii, Dardanus arrosor and Paguristes setosus. Unfortunately, very few data exist on the fauna of the western Japanese coasts, from the Tsushima Strait as far as Niigata–one of the most interesting regions, at the gateway to the southern species entering the Sea of Japan. If this region is studied more comprehensively, the number of species known to the Sea of Japan will no doubt increase

Consequently, the Paguridae fauna of the Sea of Japan is fairly heterogeneous. As will be seen further, the same is also true–although to a lesser extent–for the Bering Sea, where the heterogeneity is caused by the Californian faunistic element. The Sea of Okhotsk and the Chuckchee Sea have, on the contrary, a very homogeneous fauna.

SEA OF OKHOTSK. The pagurid fauna of the Sea of Okhotsk is mainly composed of the members of the first and third groups. In addition, a frequent form is Pagurus splendescens, which is characteristic also of the Bering and Chuckchee Seas, and which does not extend beyond the Sea of Okhotsk, being replaced in the Sea of Japan by the closely related species P. anomalus. The distribution of Pagurus gilli is not very clear. On the basis of the very scarce data available, we are inclined to believe that this species may be included in the third group. It has not yet been found in the Sea of Okhotsk, but it is very probable that its range includes the arch formed by the Kurile Islands. What was shown with regard to the Sea of Okhotsk holds good also for the eastern shores of Kamchatka, down to the parallel of the Commander Islands.

BERING SEA. The fauna of this sea is composed of the species of the first and third groups (chiefly along the Aleutian Range), and of Pagurus splendescens. In addition, in the southeastern corner of the Bering Sea (Unalaska–Pribilof Islands–Matthew Island–Nunivak Island) a pagurid fauna different from that of the rest of this sea is encountered. This complex of species includes elements of the Californian fauna, which reach here the northern limit of their range (they do not extend beyond the parallel of Nunivak Island in the north. Such are Pagurus beringanus, P. tanneri, P. granosimanus, P. armatus, and P. setosus. The last three of these species advance northward beyond the Aleutian Range (Unalaska and Kodiak). The following group is comprised of species which are also specific to the western shores of North America but do not range southward farther than British Columbia, Washington or Oregon. To this group belong the following species of Pagurus: dalli, kennerlyi, ochotensis subsp. aleuticus, cavimanus (?), tenuimanus and cornutus. The last two species advance along the entire Aleutian Range, down to and including the Commander Islands. P. cornutus
155 ranges farther along the Soviet littoral to Cape Navarin. Parapagurus mertensii is not found in the Bering Sea, being an endemic Californian species. In this study, it is mentioned only because of an error of synonymy.

From the above indications it is apparent that the Aleutian Range is the bridge by means of which a limited faunal exchange is effected between the Paguridae of the two sides of the North Pacific. The various stages in this faunal exchange can be followed, as well as the direction it takes. The majority of the Californian species at present reaches the eastern end of the Aleutian Range and stops here. Pagurus tenuimanus and P. cornutus have succeeded in crossing the bridge of the Aleutian Range, the latter having advanced even farther northward. Pagurus hirsutiusculus and P. middendorffi, which belong to the third group of species, are examples of a complete faunal exchange between the two sides of the Pacific. As to Pagurus undosus, it may be assumed that its expansion was carried out in the opposite direction. The center of distribution of this species may be considered to have been the Sea of Okhotsk, whence the species partly penetrated into the Sea of Japan (only on the Soviet littoral), and partly

advanced along the eastern shores of Kamchatka up to the Aleutian Range. From here it diverged in two directions: one advancing along the Soviet littoral of the Bering Sea, up to the parallel of Cape Chaplin, and the second covering the entire Aleutian Range, not reaching the west coast of North America, however. The distribution of Pagurus ochotensis, probably followed the same route, its arcuate range, however, being discontinuous. This is shown by the relative scarcity of this species on the east coast of Kamchatka and the western part of the Aleutian Range (Commander Islands). If we assume that Pagurus ochotensis expanded in this way, then the position of P. ochotenis subsp. aleuticus is evidently that of a subspecies which originated from the typical species in the eastern half of the Aleutian Range, i.e., at the point furthest from the center of distribution. Pagurus gilli will have the same distributional pattern if it is proved that the Japanese species P. cavimanus is identical with P. gilli. In this case, an arcuate distributional pattern of P. cavimanus (Miers) (= P. gilli) and of P. cavimanus subsp. munitus (Benedict) will again appear in the eastern half of the Aleutian Range. Finally, the fourth group of species is an example of a break in a formerly continuous range, which in the past no doubt also included the Aleutian Range*.

156 CHUCKCHEE SEA. The first group is encountered in the Chuckchee Sea also (namely, Pagurus pubescens, P. rathbuni, P. capillatus) as well as Pagurus splendescens. This area being as yet insufficiently explored, it is still difficult to trace the northern, eastern and western limits of the range of these species.

In conclusion we must mention the widespread species Parapagurus pilosimanus, which, owing to its presence on the eastern littoral of Kamchatka, is included in the Soviet fauna.

SPECIAL SECTION

7. Family **PAGURIDAE**

Paguridae Dana, 1852:435; Stimpson, 1858:232; Henderson, 1888:52; Stebbing, 1893:159; Ortmann, 1892:269; 1901:1145; Alcock, 1901:215; 1905:21. – Parapaguridae Smith, 1883:20; Henderson, 1888:85; Stebbing, 1893:166.

* Pagurus samuelis, found according to H. Balss (1913) in Avachinskaya Gulf, may be considered as a relict of this formerly continuous range. Considering, however, comparatively rich material from Avachinskaya Gulf, we are bound to believe that this determination is wrong and that the two specimens of this author in fact belong to P. hirsutiusculus, a species whose habitus greatly resembles that of P. samuelis.

156 The rostrum is small, reduced or completely missing. The carapace has, as a rule, a hard anterior and a soft posterior part. The orbital segment is more or less free. The scaphocerites are well developed and spiniform. The abdomen is asymmetrical, soft, straight or in most cases spirally curved, the segmentation being hardly visible. The pleopods are reduced and found only on the left side; the paired uropods are adapted for the fixation of the animal within its shell, and bear warts on their surface. The fourth and fifth pereiopods are small, the fourth pair usually having a subchela. The gills are mostly of the phyllobranchiate type, their maximum number being 14, the minimum 11.

The family of the Paguridae is divided into two subfamilies*.

Key to the Genera

1 (8). Bases of third maxillipeds far apart (Subfamily Pagurinae).

2 (7). Abdomen flexed and spirally coiled. Uropods asymmetrical, the left larger than the right.

3 (4). No genital appendages on the coxae of the last pair of legs, nor on the first two abdominal segments. . . . . 5. Pagurus Fabricius.

157 4 (3). Genital appendages present.

5 (6). Paired appendages on first two abdominal segments in the male. Right cheliped much larger than the left . . . . . 6. Parapagurus Smith.

6 (5). Unpaired spiral genital appendage on coxal joint of the left fourth walking leg of the male. Chelipeds almost equal, or the right one slightly larger than the left . . . . . 8. Spiropagurus Stimpson.

7 (2). Abdomen slightly bent, but not spirally coiled. Uropods symmetrical, or the left very slightly larger than the right . . . . . 7. Orthopagurus Stevens.

8 (1). Bases of third maxillipeds close together (Subfamily Paguristinae).

9 (12). Left cheliped larger than right; dactyli move in a vertical plane.

10 (11). Frontal edge of carapace bears a blunt median spiniform prominence. Ocular rostrum between the eyestalks . . . . . 1. Diogenes Dana.

11 (10). Frontal edge of carapace has no median spiniform prominence. No ocular rostrum . . . . . 4. Dardanus Paulson.

12 (9). Chelipeds equal or subequal; in some cases, left cheliped very slightly longer than right one. Dactyli move in a horizontal plane.

13 (14). Fourth pair of pereiopods with subchelae. Abdomen without paired genital appendages on first segment in either sex . . . . . 2. Clibanarius Dana.

14 (13). Fourth pair of pereiopods simple, without subchelae. Abdomen with paired genital appendages on first segment in both sexes . . . . . 3. Paguristes Dana.

* Ortmann (1892) created also the subfamily Diogeninae for the single genus Diogenes, which has an ocular rostrum. But in all its other characters, Diogenes so closely resembles the genera of the Pagurinae that later authors include it in this subfamily.

Subfamily **PAGURISTINAE**, nom. nov.

Pagurinae Ortmann, 1892: 269. – Diogeninae Ortmann, ibid: 270.

The bases of the third pair of maxillipeds are close together; the chelipeds are equal, or the left is longer than the right.

1. Genus DIOGENES Dana

Diogenes Dana, 1852: 438; Stimpson, 1858: 232; 1907: 201; Heller, 1863: 169; Henderson, 1888: 53; Stebbing, 1893: 160; Alcock, 1905: 59; Balss, 1913: 44; Terao, 1913: 362.

Type species: Diogenes miles (Dana).

The frontal edge bears a blunt median spine. Between the eyestalks is a pointed movable outgrowth — the ocular rostrum. The scaphocerites have broad bases, and are often deeply two-lobed. The flagella of the an-
158 tennae are ciliated. The bases of the third maxillipeds are close together; their basal joints are broad. The chelipeds are unequal; the left is much stronger than the right, and has a broad propodus with a sloping outer surface. The propodus is articulated obliquely with the carpus; the dactyli move in a vertical plane and have calcified ends. The dactyli of the walking legs are long. The fourth pair of pereiopods have subchelae.

This genus is characteristic for the tropical Indo-Pacific region, but some species are also encountered in the eastern half of the Atlantic, in the Mediterranean and in southern Japan. In the Soviet seas, the genus is represented by two species (D. varians and D. penicillatus). D. edwardsii is included in this work as being found on the west coast of Japan (Niigata).

Key to the Species

1 (2). Ocular rostrum very small, hardly visible to the naked eye. On the external surface of the left chela is an oval area with upturned edges, to which an actinian is usually attached . . . . . 1. D. edwardsii (de Haan).

2 (1). Ocular rostrum larger, though not reaching the tips of the ocular scales. No oval area on external surface of left chela.

3 (4). Scaphocerites with six or seven spines on their internal edge. Walking legs of left side extend beyond left cheliped. . . . . †2. D. penicillatus Stimpson.

4 (3). Scaphocerites with four or five spines on their internal edge. Walking legs of left side reach tip of left cheliped . . . . . †3. D. varians (Costa).

1. Diogenes edwardsii (de Haan) (Table I, Figure 3)

Pagurus edwardsii de Haan, 1850: 211, Pl. 50, Figure 1. – Diogenes edwardsii Stimpson, 1858: 246; 1907: 202, Pl. 24, Figure 1; Ortmann, 1892: 295; Rathbun 1902: 36; Alcock, 1905: 165; Balss, 1913: 44; Terao, 1913: 362; Yokoya, 1933: 77.

The ocular rostrum is small and very narrow, scarcely visible to the naked eye. The scaphocerites are short and triangular, with small spinules. The dactyli of the walking legs are long and slender, one and a half times as long as their propodi. The external surface of the left chela has an oval area, which occupies about two thirds of its surface and has partly raised edges; an actinia (Sagartia paguri Verrill) is almost always attached to this area; during preservation the actinian often falls off. Some specimens of the same actinian are often found on the shell. Coloration of the live specimens: the carapace is light red; the legs have light reddish-brown transverse stripes; the left chela is white; the abdomen is yellow, with bright red sides.

159 Ortmann (1892) considers that Pagurus spinifrons de Haan is a young specimen of D. edwardsii.

Distribution: China Sea (Hong Kong). Southern Japan; Sea of Japan (Niigata Prefecture); at depths down to 97 m.

† 2. Diogenes penicillatus Stimpson

Diogenes penicillatus Stimpson, 1858: 245; 1907: 200; Terao, 1913: 364; Yokoya, 1933: 77.

The anterior part of the carapace is as wide as it is long; its median part is smooth but both sides are rough, with irregular scalelike dimples, the edges of which are denticulated and bear minute setae. The median outgrowth of the front is short and blunt; the lateral outgrowths are pointed and longer than the median one. The eyestalks are cylindrical, of medium length, slightly exceeding half the length of the anterior part of the carapace. The ocular scales are broad; their inner edge is straight and the outer one rounded; the scales bear two or three spines on their tip. The ocular rostrum is narrow and pointed, and does not reach the end of the apical spine of the ocular scale. The scaphocerites are shorter than the eyestalks; they have an elongated triangular form, and bear six or seven strong spines on the superointernal edge. The external outgrowth of the basal joint of the antennal stalk bears a strong spine, while the internal outgrowth bears a shorter one. The flagella of the antennae are short and bear long hairs on their inferior side. The chelipeds are unequal; the left leg is much stronger than the right. The merus of the left cheliped has a triangular cross section and is covered with granules, the largest being those on the internal edge of the inferior surface; the superior crest bears fairly long hairs. The carpus has an irregular triangular form; its interior edge is straight, while the external edge is angular; the external half of the

superior surface is covered with large granules and scattered hairs; the internal edge bears 10 to 12 spines which are directed forward; the inferior surface is almost naked and covered with flat granules. The external edge of the propodus is almost straight; the propodus itself is oblique and bears two parallel rows of denticles or spines on its distal part; one of the rows is marginal, while the other is disposed below the true margin; the external surface of the propodus is densely covered with small tufts of delicate, silky hairs; at its base are found a spiniferous transverse crest – which separates the hairy surface from the naked one – and a smooth furrow near the carpal articulation. The inferior surface is covered with flatter granules. The immovable dactylus is short, with a broad triangular form; the movable dactylus is curved, with three rows of granules on its superior surface; the prehensile edge of the immovable dactylus bears a white tubercle; the tips of the dactyli are calcified. The right cheliped extends somewhat beyond the distal end of the carpus of the left cheliped. The merus bears long hairs on the superior crest. The carpus is short and hairy, bearing two rows of spines on its superior surface. The chela is oval with long, curved dactyli; its superior surface is covered with spiniform granules and fairly
160 dense, long hairs; the tips of the dactyli are calcified. The walking legs of the left side extend slightly beyond the left chelipeds. The carpal joints are spinulose above; the superior side of all the joints are hairy, while the lateral sides are almost naked. The dactyli are long, slender and slightly curved, with corneous claws.

Dimensions

Length of anterior part of carapace	3.0 mm
Width of anterior part of carapace	3.0 mm
Length of eyestalks	2.0 mm
Length of merus of right cheliped	2.5 mm
Length of carpus of right cheliped	2.0 mm
Width of carpus of right cheliped	1.5 mm
Length of chela of right cheliped	3.0 mm
Width of chela of right cheliped	2.0 mm
Length of merus of left cheliped	3.0 mm
Length of carpus of left cheliped	3.5 mm
Width of carpus of left cheliped	2.5 mm
Length of chela of right cheliped	5.0 mm
Width of chela of right cheliped	4.0 mm
Length of left first walking leg	13.0 mm

Distribution. Japan (on the eastern shores of Honshu Island, 38° N. lat.; east of Miyagi Prefecture; north of Inubo Cape; Bungo Strait), at depths ranging from 33 to 88 m. A single specimen is known from the Soviet seas; it was obtained in Shamara Bay, Ussuri Bay.

†3. Diogenes varians (Costa) (Plate I, Figure 6)

Pagurus varians Costa, 1832-1862:9, Pl.2, Figure 2. – Pagurus pugilator Roux, 1828, Pl. 14, Figure 3 – Pagurus drenarius Lucas, 33, Pl. 3 Figure 7a; – Pagurus ponticus Kessler, 1861; Wagner, 1864. – Diogenes varians Heller, 1863:170, Pl. 5, Figures 13-14; Carus, 1884:493; Czerniavsky, 1884: 99; Ortmann, 1892:294; Kalishevskii, 1906.

The length of the anterior part of the carapace is almost the same as its width. The anterior edge has a sharp, triangular, lateral outgrowth. The lateral edges are almost parallel. The ocular scales are broad triangles with straight, smooth internal edges and oblique spiniferous outer edges; the spines become larger distally. The ocular rostrum is pointed, and does not reach the end of the apical spine of the ocular scale. The eyestalks are cylindrical in form and of medium length. The scaphocerites are short, reaching the distal end of the carpus of the left cheliped, and bearing long hairs. The chelipeds are very unequal; the right leg reaches only the distal third of the carpus of the left one. The merus of the left cheliped bears an irregular row of short spines on its superointernal crest; the outer surface is almost smooth, the inferior one granulated; the whole joint is slightly
161 hairy. The carpus bears spines on its internal edge; its superior surface is swollen and hairy with a gradual transition toward the lateral surface; the inferior surface is granulated and slightly pubescent. The superior and inferior surfaces of the propodus are granulated and slightly pubescent; the dactyli are short, with calcified ends. The right cheliped is very small, with hairs longer than those of the left. The carpus bears a longitudinal row of spines on its superior surface. The propodus is short; the movable dactylus is curved, so that when the chela is closed a broad slit is left open; the inferior surfaces of the propodus and of the carpus are smooth and almost naked. The walking legs of the left side reach the end of the left cheliped. All the joints are flat; the carpal joints are spinulose on their superior surface. The dactyli are fairly long, curved, but not twisted, with sparse hairs and pointed corneous claws. Coloration (according to Heller): the body is greenish or reddish white, with some darker red-brown spots on the carapace, or with longitudinal stripes of the same color on some of the joints of the legs. The eyestalks are reddish, the antennae light yellow. Color is as a rule very variable. Czerniavsky (1884) described a heterochromic variety from the region of Sukhumi: "The cephalothorax and the legs have a dirty grayish-yellow color; the spots are red-brown and whitish; the superior part of the abdomen is greenish brown with black stripes and spots; the lateral sides and the inferior surface of the abdomen are violet-blue, like the cephalothorax [sic]. The eyes are golden brown and the stalks are pink." It must be noted, however, that these colors cannot be perceived in specimens preserved in alcohol.

Dimensions

Length of anterior part of carapace	4.0 mm
Width of anterior part of carapace	4.5 mm
Length of eyestalks	2.0 mm
Length of merus of right cheliped	3.0 mm
Length of carpus of right cheliped	2.0 mm
Length of chela of right cheliped	3.0 mm
Width of chela of right cheliped	2.0 mm
Length of merus of left cheliped	4.0 mm
Length of carpus of left cheliped	4.5 mm
Length of chela of left cheliped	6.0 mm

Width of chela of left cheliped	3.0 mm
Length of left first walking leg	14.0 mm

The specimens do not attain a large size. As already noted by Kalishevskii (1906), the Black Sea specimens are half the size of those from the Mediterranean.

Distribution. Adriatic and Mediterranean Seas; Black Sea. Diogenes varians is the common hermit crab of the Soviet shores of the Black Sea; it lives in shallow water, chiefly on sandy bottoms; according to S. A. Zernov, it migrates in winter to greater depths.

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2. Genus CLIBANARIUS Dana

Clibanarius Dana, 1852: 461; Stimpson, 1858: 234; 1907: 208; Heller, 1863: 177; Miers, 1876: 67; Henderson, 1888: 60; Milne-Edwards and Bouvier, 1893: 156; Stebbing, 1893: 160; Ortmann, 1901: 1146; Alcock, 1905: 40; Balss, 1913: 40; Terao, 1913: 360.

Type species: Clibanarius depressus Dana.

The median prominence of the front is pointed. The eyestalks are long and slender. The ocular scales are very small. The scaphocerites are short. The bases of the third maxillipeds are close together. The chelipeds are short, almost equal in length and form; the dactyli of the chela move in a horizontal plane and have strong, spatulate, concave corneous tips. The fourth pair of pereiopods are subchelate.

The species belonging to this genus mainly inhabit the littoral of the tropical zone. In Soviet seas the genus is represented by one species.

Key to the Species

1 (2). Ocular scales with straight internal edges. Carpus of left cheliped without two rows of spines on its dorsal surface. Dactyli of walking legs much shorter than the propodi . . . . . †1. C. misanthropus (Risso).

2 (1). Ocular scales with suboval internal edges. Carpus of left cheliped with two rows of spines on its dorsal surface. Dactyli of walking legs longer than propodi . . 2. C. japonicus Rathbun.

†1. Clibanarius misanthropus (Risso) (Plate I, Figure 7)

Pagurus tubularis Risso, 1815: 56. – Pagurus misanthropus Risso, 1826: 40; Roux, 1828, Pl. 14, Figure 1; Guérin, 1836: 32; Milne-Edwards, 1836: 277; 1837: 228. – Pagurus nigritarsis Lucas, 1849: 30, Pl. 3, Figure 4 – Clibanarius misanthropus Heller, 1863: 177, Pl. 5, Figures 16-18; Carus, 1884: 495; Czerniavsky, 1884: 97; Ortmann, 1892: 291.

The transverse portion of the cervical groove is fairly broad, and the anterior part of the carapace consequently does not become much narrower posteriorly. The surface of the carapace is almost naked. The median outgrowth of the frons is pointed and triangular; behind it, a short longitudinal ridge is located. The frontal edge of the carapace is thickened. The lateral prominences of the frons are blunt and much less protuberant than the median one. The eyestalks are very long and slender. The ocular scales are triangular, their straight internal edges touching; their tip and their external edge are denticulated. The scaphocerites are very pubescent; they extend slightly beyond the fourth segment of the antennal stalk, and have pointed denticles on their internal edge. The antennules are somewhat longer than the eyes; the antennae are longer than the chelipeds. The chelipeds are of almost equal length. The merus extends slightly beyond the eyes;
163 it is flattened and is triangular in cross section; its superior edge is sharp and arcuated; the internal edge bears some tuberculiform denticles, and the external edge is blunt. The carpus is short, triangular in cross section and bears a group of spines at the distal end of its superior edge. The propodus is obliquely truncate on the external side, flattened on the internal side, and very protuberant at the base; the dactyli are short, slightly curved, with big black corneous, concave, spatulate tips; when the chela is closed, a broad gap is left open at the base. The surface of the propodus and the dactyli is covered with scattered pointed tubercles. All the joints have hairs, chiefly on their edges. The walking legs are longer than the chelipeds; the merus is flattened; the propodi and the dactyli are more rounded; all the joints have hairy edges. The dactyli are much shorter than the propodi, with pointed corneous claws, and with yellowish spines on their inferior edge. Coloration of live specimens: the carapace and the chelipeds are greenish, with brown or bluish spots; the spines on the chelae are bluish; the dactyli of the chelae have two reddish-brown, longitudinal, ventral stripes; the tips are black; the eyestalks and the antennae are reddish. The walking legs are yellowish brown; the dactyli are bluish, with longitudinal red stripes. The abdomen is brown, becoming reddish in the distal part. In young specimens, and in those preserved in alcohol, the coloration of the walking legs is more yellow, and on the dactyli four longitudinal red stripes and four whitish (originally blue) stripes can be easily perceived; the spines and spots on the chelipeds are grayish white.

V. Czerniavsky (1884) distinguished two forms of this species in the Black Sea: forma suchumica and forma jaltensis, but the differential characters given by this author are so insignificant and uncertain – as compared with the typical Mediterranean species – that the creation of the two forms is not justified.

The specimens of this species do not attain a large size. As a rule, they live near the shore, in shallow water.

Distribution: Mediterranean, Adriatic and Black Seas. This species is found in the Black Sea much less frequently than Diogenes varians (Costa).

2. Clibanarius japonicus Rathbun (Figure 65)

Clibanarius japonicus Rathbun, 1902: 35, Figures 2-5; Terao, 1913: 361.

The lateral and anterior parts of the carapace are wrinkled; there are about 19 tufts of hairs, 13 of which are disposed in a pyriform pattern. The median denticle of the anterior edge is more prominent than the lateral denticles, and bears a small spine almost hidden under a tuft of hairs. There is a small spine, directed outward below the true edge of the lateral denticle. The inner part of the ocular scales has a continuous, suboval contour; a small spine is found at its end, below the edge. The antennular stalk is longer than the eye; the third segment is somewhat longer than the second, reaching the end of the penultimate joint of the third maxillipeds. The antenn-
164 nal stalk is shorter than the eye; the scaphocerite is slender and sickle-shaped, reaching the middle of the last joint of the antennal stalk. The chelipeds are more unequal than in the other species of the genus. The left cheliped is the stronger one; the merus extends beyond the level of the eyes; its lower surface is bordered with spines on the outer and inner edges; the superior edge bears two distal spines, and two smaller subterminal ones. The length of the carpus exceeds its width; it bears two dorsal rows of spines, and its anterior edge is also spinulose. The external surface of this joint bears a short row of spines at the distal end. The propodus is spinulose on its superior side, the spines being disposed in seven unequal rows; this joint broadens distally to a considerable extent, and its internal edge is slightly longer than half the length of the dactylus; each dactylus has about three rows of spines on the superior side; the edges of the dactyli touch when closed, the tips crossing. The spines have corneous tips. The legs are covered with tufts of hairs situated near the bases of the spines. The right cheliped reaches the end of the propodus of the left cheliped*; the merus does not reach the end of the eyes. The spines are smaller and disposed in less marked rows; the propodus broadens very slightly distally; the dactylus is 1.3 times as long as the inner edge of the propodus. The first walking leg exceeds the left cheliped by half the length of its dactylus. The first and second pairs are stout; they are pubescent on the superior side, the dactyli being longer than the propodi. The inferior edge of the merus and the superior edge of the carpus of the first pair of walking legs bear a row of spines; the dactyli of both pairs bear a number of rows of dark spines on their internal surface. The legs are not striped, and when preserved in alcohol they do not show transverse colored stripes.

Dimensions

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Length of body	58.0 mm
Length of cephalothorax	26.2 mm
Distance between end of rostrum and cervical groove	16.0 mm
Width of anterior edge	11.1 mm
Length of eyestalks	9.0 mm
Length of propodus of right first walking leg	11.4 mm

* H. Balss (1913: 41) expressed the opinion that regeneration may have occurred here, since a smaller right cheliped is not characteristic of this genus as a whole. It is, however, possible that this is a case of sexual dimorphism; M. Rathbun studied only one female of this species, and no other specimen has subsequently been found.

Length of dactylus of right first walking leg . . 13.4 mm
Length of propodus of right second walking leg. 13.4 mm
Length of dactylus of right second walking leg . 16.6 mm

Distribution. Japan, Hokkaido (M. Rathbun).

3. Genus PAGURISTES Dana

Paguristes Dana, 1851: 269; 1852; 436; Stimpson, 1858: 236; 1907: 211; Heller, 1863: 172; Henderson, 1888: 77; Milne-Edwards and Bouvier, 1893: 32; Ortmann, 1901: 1146; Benedict, 1901: 143; Alcock, 1905: 30; Balss, 1913: 36; Terao, 1913: 373; Schmitt, 1921: 122; Stevens, 1925.

Type species: Paguristes hirtus Dana

The frontal edge of the carapace bears a pointed median projection. The eyestalks are long and slender. The scaphocerites are well developed. The antennae are short; the stalks are more or less pubescent, frequently bearing long cilia. The antennules are longer than in the other genera, the end of the second joint reaching the end of the eye. The bases of the third maxillipeds are close together. The chelipeds have a similar structure and are either equal or subequal in length; in only a few cases one of them — generally the left one — is somewhat longer than the other. The dactyli of the chela move in a horizontal plane. The fourth pair of pereiopods is simple, without subchelae. The males have paired genital appendages on the first two abdominal segments, while the females have them only on the first abdominal segment. The abdomen of the female forms on its left side a tegumentary fold which protects the eggs carried on the abdomen.

No species of this genus – which is widespread in the tropical and subtropical regions – is encountered in the Soviet waters. Stimpson found Paguristes digitalis at Hakodate, while P. setosus is reported by Yokoya from Aomori. Both species are therefore included in this work.

Key to the Species

1 (2). External side of movable dactylus of chela with seven oblique rows of brown granules . . . . . 1. P. digitalis Stimpson.
2 (1). External side of movable dactylus of chela without such rows of granules . . . . . 2. P. setosus (Milne-Edwards).

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1. Paguristes digitalis Stimpson (Figure 66)

Paguristes digitalis Stimpson, 1858: 247; 1907: 212, Pl. 25, Figure 1; Balss, 1913: 37, Figures 26, 27; Terao, 1913: 374; Yokoya, 1933: 73.

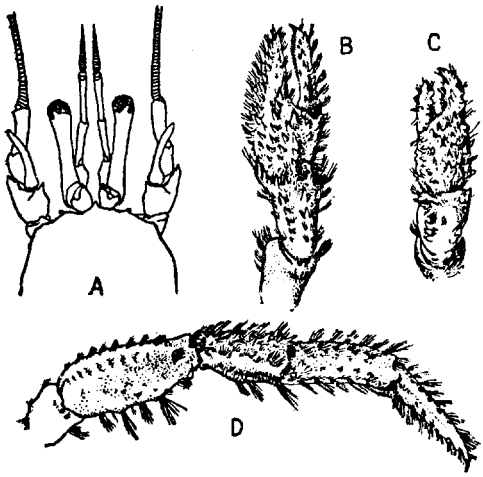

Figure 65. Clibanarius japonicus Rathbun. A – anterior part of body; B – left cheliped; C – right cheliped; D – right first walking leg – lateral view (From Rathbun, 1902).

The carapace is almost naked in the middle; it becomes narrower anteriorly and somewhat broader posteriorly. The cardiac scutellum – the hard median plate of the posterior part of the carapace – is shaped like a halberd, narrow in the middle and broadening slightly toward its pointed end. The margins of the anterior part of the carapace are more concave than in most other species. The rostrum-shaped outgrowth of the frons is elongated and very pointed, somewhat exceeding the base of the ocular scales; it has a median carina. The eyes are very long and slender, very slightly exceeding the front, and not quite reaching the end of the of the antennular stalk. The stalk is naked, except for a small tuft of hairs at the superior part of its base. The apex of the ocular scale is short and pointed, with a denticle on its exterior edge. The third maxillipeds are long and extend beyond the eyes. The chelipeds are equal and greatly resemble those of Paguristes hirtus, P. turgidus, etc; the carpus and the propodus are spinulose and hairy on the superior side; the spines are fairly numerous and have dark, corneous tips. The chela is fairly broad and has a flat superior side; the immovable dactylus has a hollowed surface; the inner edges of the dactyli are corneous on their terminal half; the movable dactylus is angular, with a flat external surface, beautifully and delicately ornamented with some seven oblique crests (Figure 66). The posterior legs are hairy; the second pair of legs are spinulose on their superior side; the dactyli are more than one and a half times as long as the propodi. The dorsal tegument of the abdomen is fairly hard in the male, forming on each segment a thin curved plate. The lobes of the terminal segment are almost symmetrical in both males and females. The horny areas, which form a "stridulating organ" on the inferior surface of the thorax and the legs, are less marked than in P. turgidus. The coloration of the specimens preserved

in alcohol is light brick red; whitish spots may also be observed; the eyestalks bear red transverse stripes (Stimpson).

167 Distribution. Southern Japan (Sagami Sea, near Siriyazaki; southeast of Tsushima Island). The northernmost location is Hakodate (Hokkaido- or Yezo-Island). At depths ranging from 20 to 150 m.

2. Paguristes setosus (Milne-Edwards) (Figure 67).

Pagurus setosus Milne-Edwards, 1848: 64. - Paguristes setosus Ortmann, 1892: 281, Pl. 12, Figure 9; Yokoya, 1933: 76.

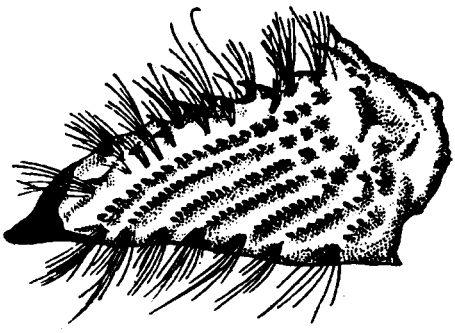

Figure 66. Paguristes digitalis Stimpson. External surface of movable dactylus of chela (From Balss, 1913)

This species is closely related to Paguristes pilosus, but the chelae are much less hairy and the third legs more slender. It has a yellowish-red coloration. It is about one inch long (Milne-Edwards). The eyestalks are shorter than the antennular stalks. The chelipeds are equal; their spines are the same color on both legs, and are without dark tips. No further details are available in the literature with regard to this species.

Distribution. New Guinea. Southern Japan; Sagami Sea; south of Inubo Cape; near Oma Cape; between Koti and Ashizuri Cape; east of Tsushima Island. The northernmost locality is a point west of Tubaki Cape in Aomori Prefecture. At depths ranging from 73 to 238 m.

4. Genus DARDANUS Paulson

Pagurus Fabricius, 1775: 410 (part.); Milne-Edwards, 1837: 213; de Haan, 1850: 202; Dana, 1852: 449; Stimpson, 1858: 233; 1907: 204; Heller, 1863: 174; Henderson, 1888: 55; Ortmann, 1901: 1146; Milne-Edwards and Bouvier, 1893: 161; Alcock, 1905: 78; Balss, 1913: 45; Terao, 1913: 375. - Dardanus Paulson, 1875: 90; Rathbun, 1902: 33; Schmitt, 1921: 126. - Pagurias Benedict, 1901: 141.

Type species: Dardanus depressus (Heller).

The median part of the frontal edge protrudes slightly, but the anterior edge of this protuberance is straight or rounded, and does not bear a rostrum; the lateral outgrowths are distinct. The eyestalks are short and

stout; the ocular scales have broad spinulose tips. The scaphocerites are short and stout. The antennal flagella are long and smooth. The bases of the third maxillipeds are close together. The chelipeds are unequal, the left leg being considerably larger than the right one. The dactyli move in a vertical plane, and have short, corneous, sometimes concave tips. The fourth pair of pereiopods have subchelae. The abdomen does not bear genital appendages (Paulson's indication that the ocular segment bears a median movable outgrowth, like Diogenes, must be considered erroneous).

Most species of this genus inhabit the tropical littorals, chiefly of the Western Hemisphere. This genus is never encountered in Soviet waters. Dardanus arrosor (Herbst) is described in the present work, since it is
168 known from the Sea of Japan, on the western shores of Japan (Niigata Prefecture), as well as from the northern part of the Sea of Japan (Yokoya).

1. Dardanus arrosor (Herbst). (Plate I, Figure 1)

Cancer arrosor Herbst, 1794: 170 Pl. 43, Figure 1. – Cancer strigosus Bosc. 1803: 77, Pl. 11, Figure 3. – Pagurus striatus Latreille, 1803: 163; Risso, 1815: 54; 1826: 38; Roux, 1828, Pl. 10; Costa, 1836: 7; Milne-Edwards, 1836: 270; 1837: 218; Lucas, 1849: 29; de Haan, 1850: 206; Pl. 49, Figure 1; Heller, 1863: 174; Miers 1881: 274; Studer, 1882: 23; Carus, 1884: 494; Henderson, 1888: 56; Ortmann, 1892: 283; Chevreux and Bouvier, 1892: 119; Whitelegge, 1900: 166; Doflein, 1902: 645; Stimpson, 1907: 206. – Pagurus incisus Olivier, 1811: 641. – Pagurus arrosor Milne-Edwards and Bouvier, 1900: 178; Moreira, 1901: 24, 85; Alcock, 1905: 168; Nobili, 1906: 121; Stebbing, 1908: 22; 1910: 350; Cunningham, 1910: 121; Balss, 1912: 95; 1913: 46; Terao, 1913: 375; Parisi, 1918: 112; Yokoya, 1933: 78.

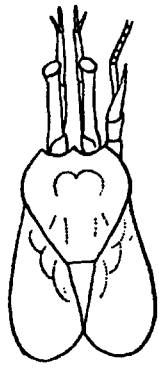

Figure 67. Cephalothorax of Paguristes setosus (M. Edw.) (From Ortmann, 1892)

The length of the anterior part of the carapace is equal to its width. The lateral outgrowths of the front are pointed and triangular. The eyestalks are stout. The ocular scales are broad, with straight internal edges and inflated external ones; the tips of the scales bear a bifid spine, and the swollen external edge bears pointed corneous spines. The scaphocerites do not reach the tips of the eyes; they have spines and hairs on their internal edge. The external and internal outgrowths of the basal joint of the antennal stalk bear strong spines, with small spinules at their bases; the spine of the external outgrowth is frequently bifid. The chelipeds have the same form and structure; the left leg, however, is larger than the right. The right cheliped extends only slightly beyond the base of the movable dactylus of the left one. The merus is triangular in cross section and bears strong, pointed spines on its inferointernal edge. The carpus also has spines on

its internal edge, and there are scattered spines on its sloping external surface. The inner edges of the propodus and of the stout movable dactylus bear short pointed spines. The superior surface of the carpus and of the chela (including the dactyli) are covered with stripes, which are, as a rule, diagonal; each stripe appears as a slight prominence which bears granules or small spines, chiefly near the internal edges of the joints. Rising from these prominences in an anterior direction are soft, pinnate hairs, closely appressed to the surface of the joint. The inferior surface of the legs is smooth, with the exception of a zone on the external edge of the propodus and the movable dactylus, onto which the above-mentioned stripes sometimes extend. The prehensile edges of the dactyli bear large white tubercles; the tips of the dactyli are strong, corneous and sometimes concave. The walking legs extend considerably beyond the chelipeds. The carpal joints are spinulose on their superior edges. The external side of all the joints – the meral joint excepted – have the same stripes as the chelipeds. The dactyli are stout; they are pubescent at their distal end, and bear strong, corneous claws. Owing to the above-mentioned stripes, this species can be easily recognized when compared with the other species of the genus. It has a brownish-red coloration.

169 Dimensions

Length of anterior part of carapace	19.0 mm
Width of anterior part of carapace	19.0 mm
Length of eyestalks	9.5 mm
Length of merus of left cheliped	17.0 mm
Length of carpus of left cheliped	16.0 mm
Length of chela of left cheliped	34.0 mm
Width of chela of left cheliped	20.0 mm
Length of left first walking leg	78.0 mm

The specimens may attain a large size. They are found at depths ranging from 37 to 600 m.

Distribution. Mediterranean and Adriatic Seas; Madeira; Senegambia; West Africa; Saint Helena Island; Red Sea; Australia; the Philippines; southern Japan; Sea of Japan, along the western shores of Japan northward to Niigata; from the continent reported at Fusan (Korea). Unfortunately, when mentioning this species from the northern part of the Sea of Japan, Yokoya (1933:78) omitted to indicate the exact location. The occurrence of P. arrosor in Brazil and the West Indies is doubtful.

Subfamily **PAGURINAE**, nom. nov.

Eupagurinae Ortmann, 1892: 270.

The bases of the third maxillipeds are very far apart. The right cheliped is longer than the left; in rare cases the two legs are subequal.

5. Genus PAGURUS Fabricius

Pagurus Fabricius, 1775: 410; Holmes, 1900: 132; Rathbun, 1904: 157; Schmitt, 1921: 130. Eupagurus Brandt, 1851: 105; Stimpson, 1858: 226; 1907: 215; Heller, 1863: 158; Henderson, 1888: 62; Ortmann, 1892: 297; Benedict, 1892: 1; Milne-Edwards and Bouvier, 1893: 139; Alcock, 1905: 122; Balss, 1913: 51; Terao, 1913: 364; Yokoya, 1933: 80; Bernhardus Dana, 1852:440.

Type species: Pagurus bernhardus (Linné).

The frontal edge bears a median outgrowth (rostrum). The eyestalks are mostly short and stout; the ocular scales are reduced and far apart. The scaphocerites are well developed. The antennae are long and almost naked. The bases of the third maxillipeds are very far apart; the coxopodites of these appendages are small and very short, not exceeding the length of the basal joints. In the space between the bases of the maxillipeds, a prominence of the second sternite is found; it frequently bears a denticle or a spiniform process. The chelipeds are unequal; the right leg is larger than the left; the tips of the dactyli are pointed; the dactyli move in a horizontal plane. The fourth pair of pereiopods have subchelae. The first and second abdominal segments do not bear paired appendages.

Pagurus is among the genera with the most numerous species. Its range covers chiefly the Boreal zone of both the Atlantic and Pacific oceans, although a few species also settled in the Arctic and Tropical zones. Most of the Soviet species of hermit crabs belong to this genus.

There is some duplicity concerning the synonymy of the genus Pagurus Fabricius. Most authors, including all the European authors, retained for this genus Brandt's name – Eupagurus; most of the American authors – and we agree with them – very correctly retained the old name for this genus – Pagurus. The genus Pagurus, which was created by Fabricius in 1775, with the type species bernhardus, actually contained two genera at first. In 1851, Brandt separated the subgenus Eupagurus with the same type species bernhardus; subsequently, this subgenus was elevated to the rank of an independent genus, and the generic name Pagurus, losing its type species, was applied to all species not included in the sphere of the genus Eupagurus, i. e., to what we might call the unnamed genus which Fabricius included in his comprehensive genus Pagurus. But this unnamed genus was separated from Pagurus Fabr. in 1875 by Paulson, as the genus Dardanus. Consequently, Eupagurus Brandt is synonymous with Pagurus Fabricius, while the Pagurus of most of the authors is merely Dardanus Paulson. The subgenera introduced by Benedict (Eupagurus, Trigonocheirus, Elassocheirus and Labidocheirus) have not been adopted in the present work.

Key to the Species

1 (6). Superior surface of propodus of right chela smooth and not hairy.

2 (3). Carpus of right cheliped as broad as chela. Superior surface of left chela convex, without upturned edges. . . . . †1. P. middendorffii Brandt.

3 (2). Carpus of right cheliped much broader than chela owing to a lateral aliform expansion. Superior surface of left chela flat, with upturned edges.

4 (5). Superior surface of carpus of right cheliped rounded and completely smooth. Scaphocerites do not reach tips of eyes . . . . . †2. P. gilli (Benedict).

5 (4). Superior surface of carpus of right cheliped with a distinct median carina, bearing on its proximal end a number of spiniform granules. Scaphocerites reach tips of eyes. . . . . 3. P. cavimanus (Miers).

171 6 (1). Superior surface of propodus of right chela covered with granules which are sometimes minute and scattered, chela thus sometimes appearing almost smooth; hairs, when present, are very short, often hardly visible to the naked eye. ★Or the superior surface of the propodus may be covered with spiniform granules, or more or less long conical spines; in such cases, hairs almost absent on propodus, or very reduced and form tufts at base of spines or granules. Or the superior surface of propodus of right chela may be covered with long, pointed spines and more or less long hairs, sometimes covering the entire armature of the propodus; in rare cases, spines of propodus short, but with long, soft hairs.★

7 (26). Superior surface of propodus of right chela covered with round granules which are sometimes very small and scattered, the chela thus appearing almost smooth; hairs – if present – are very small, generally hardly visible to naked eye.

8 (21). Superior surface of propodus of right chela without prominent crests or hollows; it is more or less evenly convex.

9 (16). Merus of right cheliped has neither prominent blunt spines nor large granules on inferior surface.

10 (11). Chela of right chelipeds much broader than carpus. Superior surface of propodus of left chela flat, with upturned edges . . . . . †4. P. tenuimanus (Dana).

11 (10). Chela of right cheliped either not broader than carpus, or slightly broader. Superior surface of propodus of left chela more or less convex, without upturned edges.

12 (13). Frontal edges of carapace without lateral denticles. Chelipeds hairy, with the exception of right chela. . †5. P. hirsutiusculus (Dana).

13 (12). Frontal edge of carapace with lateral denticles. Chelipeds almost naked.

14 (15). Propodus of right chela very swollen, covered with blunt granules, which impart a rough ("shagreened") appearance; dactyli stout. Scaphocerites triangular in cross section. Dactyli of walking legs stout . . . . . †6. P. bernhardus (Linnê).

15 (14). Propodus of right chela slightly swollen, covered with minute, scattered granules, imparting an almost smooth appearance. Scaphocerites not triangular in cross section. Dactyli of walking legs slender . . . . . †7. P. gracilipes (Stimpson).

16 (9). Merus of right cheliped with prominent blunt spines or large granules on inferior surface.

* [★ to ★ appears in the key to the species Pagurus Fabricius in section 7 (26) in the English summary of the book.]

17 (18). Inferior surface of merus of right cheliped with two large tuberculiform granules . . . . . 8. P. beringanus (Benedict).

18 (17). Inferior surface of merus of right cheliped with a single blunt, median spine.

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19 (20). Length of chela of right cheliped twice its width; exterior and interior edges almost parallel. Superior surface of propodus of left chela with long, soft hairs. . . . . †9. P. dubius (Ortmann).

20 (19). Length of chela of right cheliped less than twice its width, with rounded edges. Superior surface of propodus of left chela almost naked or with very short sparse hairs. . . . . †10. P. samuelis (Stimpson).

21 (8). Superior surface of propodus of right chela with a marked median crest.

22 (23). Crest on superior surface of right chela ending in a very prominent horn . . . . . 11. P. cornutus (Benedict).

23 (22). Crest on superior surface of right chela not ending in a horn, but descending rather abruptly toward the immovable dactylus.

24 (25). Crest on superior surface of propodus of right chela parallel to internal edge; depression with parallel edges between crest and internal edge. External surface of propodus of left chela convex . . . . . †12. P. undosus (Benedict).

25 (24). Crest on superior surface of propodus of right chela appears as a triangular prominence with its tip directed toward the base of the gap which is left open between the dactyli; depression between inner side of triangle and inner edge of propodus without parallel edges. External surface of propodus of left chela very concave. . . . . 13. P. tanneri (Benedict).

26 (7). Superior surface of propodus of right chela covered with spinform granules, or with more or less short conical spines; in the latter case, hairs almost lacking on propodus, or very short and disposed in tufts at base of spines or granules. In other cases, superior surface of propodus of right chela covered with long pointed spines and more or less long hairs, sometimes covering entire armature of propodus; in rare cases, spines of propodus short, but with long, soft hairs.

27 (42). Superior surface of propodus of right chela covered with spiniform granules, or with more or less short conical spines. Hairs on propodus almost lacking or very short, and disposed in tufts at base of spines and granules.

28 (31). Not just anterior part, but entire carapace hard.

29 (30). Median outgrowth of front narrow, long, and directed obliquely upward, with simple tip. Sharp prominent spine on lateral outgrowth of carapace, beyond cervical groove . . . . . †14. P. anomalus (Balss).

30 (29). Median outgrowth of front broad, shorter, directed horizontally forward, with three or four denticles at tip. Lateral outgrowth of carapace beyond cervical groove lacks sharp prominent spine. .

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. . . . . †15. P. splendescens Owen.

31 (28). Only anterior part of carapace hard.

32 (35). Width of anterior part of carapace exceeds length. Scaphocerites triangular in cross section, with highly iridescent internal surface. Chelipeds very robust compared with body; joints almost completely naked.

33 (34). Dactyli of walking legs lack longitudinal gutter on superior surface . . . . . †16. P. ochotensis Brandt.

34 (33). Dactyli of walking legs with longitudinal gutter on superior surface . . . . . 16a. P. ochotensis aleuticus (Benedict).

35 (32). Length of anterior part of carapace equal to its width or exceeding it. Scaphocerites not triangular in cross section, and not iridescent. Chelipeds of medium size compared with body; joints more or less hairy, the chela excepted.

36 (37). Carpus of right cheliped with a round tuft of hairs on the inner distal angle of its superior surface. Dactyli of left chela long, relatively slender, and strongly curved downward. . . . . †17. P. rathbuni (Benedict).

37 (36). Carpus of right cheliped lacks round tuft of hairs. Dactyli of left chela not very long, and either slightly curved or straight.

38 (39). Merus of right cheliped with two large tuberculiform granules on inferior surface. Left chela lacks distinct crest on superior surface . . . . . 18. P. granosimanus (Stimpson).

39 (38). Merus of right cheliped lacks such tuberculiform granules on inferior surface. Left chela with marked crest on superior surface.

40 (41). Meral joints of chelipeds with white stripe near distal ends. Spines on chelipeds fairly long and pointed. Right chela fairly narrow. . . . . 19. P. dalli (Benedict).

41 (40). Meral joints of chelipeds without white stripe near distal ends. Spines on chelipeds shorter and blunt. Right chela fairly broad . . . . . †20. P. pubescens Kröyer.

42 (27). Superior surface of propodus of right chela covered with long pointed spines and more or less long hairs, sometimes covering entire armature of propodus. In rare cases spines of propodus short, but long, soft hairs present.

43 (44). Merus of right cheliped with two very prominent blunt spines on inferior surface . . . . . †21. P. brachiomastus (Thallwitz).

44 (43). Merus of right cheliped without prominent blunt spines on inferior surface.

45 (46). Immovable dactylus of right chela twice as broad as movable one. Surface of propodus of right chela with short spines and long, soft hairs . . . . . †22. P. lanuginosus de Haan.

174 46 (45). Immovable dactylus of right chela as broad as movable one, or slightly broader. Surface of propodus of right chela with long spines and hairs.

47 (48). Scaphocerites triangular in cross section and with iridescent inner surface . . . . . 23. P. armatus (Dana).

48 (47). Scaphocerite not triangular in cross section and not iridescent.

49 (56). Spines on surface of propodus of right chela disposed in more or less regular longitudinal rows.

50 (53). Spines on surface of propodus of right chela form eight or nine longitudinal rows.

51 (52). Scaphocerites shorter than eyes. Median outgrowth of front pointed. Eyestalks slender, with broad bases. External edge of propodus of right chela bears a row of long, strong spines sharply dividing superior surface of chela from inferior one. . . . . †24. P. pectinatus (Stimpson).

52 (51). Scaphocerites longer than eyes. Median outgrowth of front blunt. Eyestalks fairly stout, widening at cornea. External edge of propodus of right chela lacks strong spines . . . . . 25. P. obtusifrons (Ortmann).

53 (50). Spines on surface of propodus of right chela form seven longitudinal rows.

54 (55). Scaphocerites longer than eyes. Hair on chelae much longer than spines . . . . . 26. P. setosus (Benedict).

55 (54). Scaphocerites shorter than eyes. Hair on chelae shorter than spines . . . . . 27. P. kennerlyi (Stimpson).

56 (49). Spines on surface of propodus of right chela scattered, not forming regular longitudinal rows.

57 (58). Lateral outgrowths of front rounded. Scaphocerites reach tips of eyes, or slightly less. Walking legs exceed right cheliped; dactyli twisted. . . . . †28. P. capillatus (Benedict).

58 (57). Lateral outgrowths of front pointed. Scaphocerites extend beyond eyes. Walking legs shorter than chelipeds; dactyli not twisted. . . . . 29. P. constans (Stimpson).

†1. Pagurus middendorffii Brandt (Plate 5, Figure 6).

Pagurus middendorffii Brandt, 1851: 108, Pl. 5, Figures 1 – 16; Holmes, 1900: 234; Rathbun, 1902: 35; 1904: 160. – Eupagurus middendorffii Stimpson, 1858: 250; 1907: 26; Ortmann, 1892: 301; Doflein, 1900: 340; 1902: 646; Lenz, 1901: 444; Alcock, 1905: 178; Balss, 1913: 58; Terao, 1913: 371.

The width of the anterior part of the carapace is almost equal to its length. The median outgrowth of the front has a broad triangular form, and is pointed; the lateral outgrowths are missing. The eyestalks are short and
175 moderately broad. The ocular scales are suboval, their superior surface is concave and bears strong submarginal spines. The scaphocerites reach the end of the eyes, and are sometimes even longer; their inner edge is slightly pubescent. The inner edge of the external outgrowth of the basal joint of the antennal stalk is denticulate. The chelipeds are very unequal; they are completely naked, with minute granules forming a rough surface. The right cheliped is very large in comparison with the body; the left one, however, is very small, reaching only the distal end of the carpus of the right cheliped; in small specimens it is even a little shorter. The merus of the right cheliped is triangular in cross section, with rounded carinae. The carpus is markedly longer than the merus and its protuberant superior surface passes smoothly onto the lateral surfaces. The chela is long, its external edge slightly curved; the inner edge of the movable dactylus forms an obtuse angle with the external edge. The surface of the chela bears such a minute granulation that to the naked eye it appears smooth. The dactyli are short, the granulation of their superior surface more apparent. The prehensile edges of the dactyli bear indistinct white tubercles and a few tufts of hairs. They do not have corneous tips. The merus and the carpus of the left cheliped are compressed and very slightly hairy on their inferior surface; the superodistal end of the carpus forms a small forward-directed process, and bears larger granules. The chela is narrow, with a protuberant superior surface; the inferior surface is slightly hairy, particularly

along the immovable dactylus. The dactyli have corneous ends and scattered tufts of hairs. The walking legs are weak and almost naked. The walking legs of the right side reach the middle of the propodus of the right chela; the walking legs of the left side exceed the left cheliped by the entire length of their dactyli. The elongated joints of both pairs are spinulose on the inferior side; the dactyli are slightly curved, not twisted, with small spines on the superior edge, stronger spines on the inferior one, and pointed, corneous claws. The coloration of living specimens is olive green, and of the specimens preserved in alcohol a uniform reddish orange. The distal half of the dactyli of the right chela is frequently white. The carpal joints and the proximal half of the propodal joints of the walking legs have a brownish-red longitudinal stripe, broad on the carpal joints and gradually tapering on the propodal joints.

Dimensions

Length of anterior part of carapace	8.5 mm
Width of anterior part of carapace	8.0 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	13.0 mm
Length of carpus of right cheliped	17.0 mm
Width of carpus of right cheliped	10.0 mm
Length of chela of right cheliped	19.5 mm
Width of chela of right cheliped	10.0 mm
Length of merus of left cheliped	9.0 mm
Length of carpus of left cheliped	8.5 mm
Width of carpus of left cheliped	3.5 mm
Length of chela of left cheliped	10.5 mm
Width of chela of left cheliped	5.0 mm
Length of right first walking leg	40.0 mm

176 Distribution. Sea of Japan, on the Soviet shores southward to Poset Bay; Northern Japan; Sea of Okhotsk; eastern shores of Kamchatka. Bering Sea to the parallel of Cape Olyutorsk (Lavrov Bay). The Aleutian Islands; along the American shores down to Vancouver.

This species does not attain large dimensions.

Ecology. Pagurus middendorffii is a common form of the littoral and the upper sublittoral; at low tide it can be frequently found on the shore between the boulders. On its abdomen parasitic Cirripedia (?Peltogastrella socialis Krüger) are frequently found.

†2. Pagurus gilli (Benedict) (Plate 3, Figure 1)

Eupagurus gilli Benedict, 1892: 20. – Pagurus gilli Rathbun, 1904: 161, Pl. 5, Figure 10; Stevens, 1925: 291, Figures 12, 13.

The anterior part of the carapce is slightly broader than long. The median outgrowth of the front is pointed and triangular; the lateral outgrowths are rounded, bearing blunt, submarginal spines. The eyestalks are cylindrical

and of medium length. The ocular scales are elongated and their edges are turned upward. The scaphocerites do not reach the end of the eyes and their internal edge is slightly hairy. The tip of the external outgrowth of the basal joint of the antennal stalk bears two spines. The chelipeds are completely naked. The merus of the right cheliped is short, and is triangular in cross section; the narrow end of the ischium almost reaches the anterior edge of the merus on the inferior side. The carpus has a broad triangular form, with a convex superior surface (Figure 68A). The lateral parts of the distal half continue with aliform widenings; the internal edge of the widening and the anterior edge of the carpus bear small, blunt spines. The inferior surface of the carpus with crescent-shaped cavity formed by the edges, which are turned downward; this is very marked on the external edge. The chela is narrower than the carpus and has parallel edges; in relation to the longitudinal axis of the carpus the chela is articulated obliquely inward. The external edge of the chela is slightly raised, and the middle of the immovable dactylus is slightly concave. The surface of the propodus is covered with small punctiform hollows, while that of the dactyli is porous. The left cheliped reaches the base of the movable dactylus of the right chela or only the middle of the propodus. The superointernal edge of the carpus bears a row of small spines. The superior surface of the chela is smooth and flat, with upturned edges. The proximal end of the propodus has a rounded
177 edge; the raised inner edge of the propodus forms a marked crest at the base of the movable dactylus, extending farther along it. The inferior surface of the chela is protuberant and smooth; the dactyli have corneous tips; on the right chela there are no such tips. The walking legs of the right side reach the middle of the propodus of the right chela; the walking legs of the left side exceed the left chela by almost the entire length of their dactyli. All the joints are flattened, and almost naked. The carpal joints bear from seven to nine spinules on their superior edge. The dactyli are slightly curved, not twisted, and equal in length to the corresponding propodi; their inferior edge bears 11 to 14 corneous spinules; the tips bear strong corneous claws. The coloration of the specimens preserved in alcohol is light orange-red. The tips of the dactyli of the right chela, the prehensile edges and the outer edges of the dactyli and of the propodi are white; the hollows, which produce the above-mentioned porosity in the dactyli, are also white.

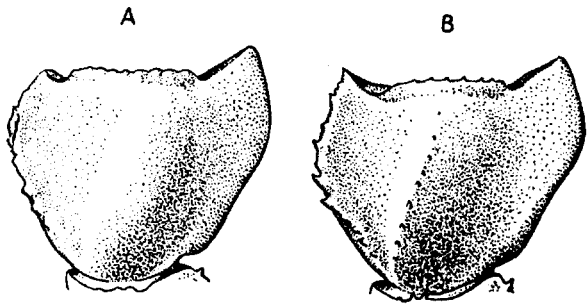

Figure 68. Carpal joints of right cheliped. A – Pagurus gilli (Benedict). B – Pagurus cavimanus (Miers).

With regard to the young specimens, B. A. Stevens (1925) remarks, "The young differ markedly from the adult specimens in that: the carpus of the large cheliped lacks almost entirely the thin wing-like expansions; the hand is slightly wider than the carpus; they may, however, be identified by the characteristically flat hand of the left cheliped."

This species differs from the closely related P. cavimanus by its more slender eyestalks, by the scaphocerites which do not reach the end of the eyes, by the more rounded and smooth carpus of the right cheliped, and by their stronger walking legs and broader dactyli.

Dimensions

Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	9.0 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	7.0 mm
Length of carpus of right cheliped	10.0 mm
Width of carpus of right cheliped	12.0 mm
Length of chela of right cheliped	15.0 mm
Width of chela of right cheliped	9.0 mm
Length of merus of left cheliped	5.0 mm
Length of carpus of left cheliped	6.5 mm
Width of carpus of left cheliped	3.5 mm
Length of chela of left cheliped	10.0 mm
Width of chela of left cheliped	4.5 mm
Length of right first walking leg	19.5 mm

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Distribution. Commander Islands, Aleutian Range, Alaska – south of Revillagigedo Island (southeastern Alaska), California, Kamchatka at Cape Lopatka, Sea of Japan at "Soviet Harbor" (Sovetskaya Gavan). Not long ago P. gilli was either considered as being a relatively limited local form of the Aleutian Range, or a subspecies of the widespread P. cavimanus (Miers). However, as a result of the study of the collection found in the Zoological Institute of the Academy of Sciences of the USSR, the range of P. gilli was recognized as being greater. The Kamchatkan specimens from the region of "Soviet Harbor" and from Japan, which were carefully compared with a specimen of P. cavimanus obtained from the U. S. National Museum (No 16, 656) must undoubtedly be considered as belonging to P. gilli. Thus, a different picture appears – P. gilli probably has a wider, arcuated range, which covers the Kuriles and the Aleutian Range, while P. cavimanus is merely a subspecies of P. gilli – if the determination of the specimens from Japan is considered erroneous. It is, therefore, hardly possible to draw a final conclusion until a large collection from Japan has been studied. Therefore, we maintain the existing synonymy and the current distributional pattern of the two species, enlarging, however, the range of P. gilli according to the above-mentioned new localities in which it was found.

Ecology. Like the preceding species, P. gilli is frequently found in the littoral zone, and it prefers sandy, rocky and pebbly bottoms; apparently found no deeper than 100 to 110 m.

3. Pagurus cavimanus (Miers).

Eupagurus cavimanus Miers, 1879: 21, 48, Pl. 3, Figure 1; Balss, 1913: 58; Figure 34; Terao, 1913: 365; Yokoya, 1933: 81. – Eupagurus munitus Benedict, 1892: 19. – Pagurus munitus Holmes, 1900: 150; Rathbun, 1904: 161, Pl. 5, Figure 2. – Eupagurus gotoi Terao, 1913: 366, Figure 2.

This species is closely related to P. gilli, from which it differs by the following characters: the eyestalks are thicker; the scaphocerites are long, reaching the tips of the eyes. The carpus of the right cheliped (Figure 68 B) bears a marked crest in the middle of the superior surface; this crest bears at its proximal end small spiniform granules (in P. gilli the surface of the carpus is rounded and entirely smooth). The superior surface of the propodus of the right chela is covered with uneven reticular lines composed of flat granules, and forming a peculiar pattern, which is clearly visible
179 only with a magnifying glass (in P. gilli the surface of the propodus is smooth, and only sparse punctiform hollows can be discerned with a magnifying glass). The walking legs are relatively weaker and their dactyli narrower. The coloration of the specimens preserved in alcohol (according to Benedict) is as follows: the meral and carpal joints of the cheliped are light purple; the chelae are yellow; the walking legs are dark reddish orange with small, round, pale spots.

Dimensions

Length of anterior part of carapace	10.5 mm
Width of anterior part of carapace	10.0 mm
Length of eyestalks	6.0 mm
Length of scaphocerites	4.5 mm
Length of merus of right cheliped	8.5 mm
Length of carpus of right cheliped	11.0 mm
Width of carpus of right cheliped	13.0 mm
Length of chela of right cheliped	18.0 mm
Width of chela of right cheliped	9.0 mm
Length of merus of left cheliped	6.0 mm
Length of carpus of left cheliped	6.5 mm
Length of chela of left cheliped	11.0 mm
Width of chela of left cheliped	5.0 mm
Length of right first walking leg	35.0 mm

Distribution. Northern Japan (Miers). Southern Japan (Yokoya). Bering Sea (56° 56'N), southward and eastward to Portlok Bank and Juneau (Alaska). At depths ranging from 36 to 250 m (Rathbun).

†4. Pagurus tenuimanus (Dana) (Plate I, Figure 2).

Bernhardus tenuimanus Dana, 1851: 269; 1852: 447, Pl. 27, Figure 7. – Eupagurus tenuimanus Stimpson, 1857: 447; 1858: 237; Smith, 1878-79: 211; Benedict, 1892: 1; Walker, 1898: 274. – Pagurus tenuimanus Holmes, 1900: 148; Rathbun, 1904: 160; Stevens, 1925: 293, Figure 14.

The anterior part of the carapace is slightly longer than it is wide, and is completely naked. The median outgrowth of the front is broadly triangular; the lateral outgrowths are broad and rounded, but appear pointed because of the fairly strong submarginal spines. The eyestalks are somewhat longer than half the length of the anterior part of the carapace and almost cylindrical. The ocular scales are long and narrow, with upturned edges and pointed subterminal spines. The lateral outgrowth of the basal joint of the antennal stalk has two apical spines. The chelipeds are very unequal, the right leg being much longer than the left. The merus of the right cheliped is short; it is triangular in cross section and completely smooth; the end of the anterior edge and the inferoexternal edge bear some spines. The carpus has a broad triangular form, with a swollen superior surface covered with white-tipped spiniform granules. The internal side of
180 the superior surface is clearly separated from the smooth inferior surface by a row of strong white spines directed forward. On its external side the superior surface passes smoothly to the inferior surface, and its granules gradually disappear. The smooth inferior surface has a cavity on its internal side, and a semicircular row of unequal spines extends from the middle of this surface toward the outer distal corner. The chelae are much broader than the carpus, and are fairly slender. Their superior and inferior surfaces are thickly covered with large granules, those on the inferior surface being smaller, and gradually disappearing toward the carpal articulation; the external edge of the propodus is evenly rounded toward the end of the immovable dactylus, and bears a border of minute granules; the inner edge of the propodus is covered with larger granules and forms an angular prominence at the base of the movable dactylus; the dactyli are broad and triangular, slightly concave on the superior surface, and without corneous tips. The chela widens to such an extent that it covers like an operculum the opening of the shell inhabited by the animal when it is hiding. The left cheliped reaches the middle of the propodus of the right chela. The merus is smooth and triangular in cross section. The sloping superoexternal surface of the carpus is covered with large white granules; the internal edge also bears large white denticles; the inferior surface is smooth and protuberant. The chela is as broad as the carpus, and has a relatively flat superior surface, covered with small scattered granules; the slightly raised edges of the propodus form a border of larger granules; the inferior surface is protuberant and smooth; the dactyli have corneous tips. The walking legs of the right side are slightly longer than the right cheliped. The carpal joints are covered with white denticles along their superior edge; the propodal joints are covered with red denticles on their superior edge; all the joints are compressed and naked; the dactyli are slightly curved; they are spinulose along their superior and inferior edges, and have a strong, corneous, terminal claw. The coloration of the live specimens (according to Stevens) is a light brownish pink or brown, with orange, chrome, and grayish-violet-blue spots. The chelipeds are brown, with bluish-chrome tints at their distal and proximal ends. The spines are white, the carpus brown with a slight chestnut tint. The tubercles are white, the chela brown. The meral joints of the walking legs have the same coloration as the chelipeds. The first three segments are light olive green at their distal ends. The antennal flagella are brown, with a chestnut stripe extending onto the external and the internal surfaces. The specimens preserved in alcohol are a pale

pinkish color. The carpal joints of the walking legs have three longitudinal red stripes on their external surface. The propodal joints have red spots on the external surface, partly fused to form stripes. There is a bright red stripe along the internal edge of the superior and inferior surfaces of the carpus of the left cheliped.

Dimensions

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Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	7.0 mm
Length of eyestalks	4.5 mm
Length of merus of right cheliped	7.0 mm
Length of carpus of right cheliped	10.0 mm
Width of carpus of right cheliped	10.0 mm
Length of chela of right cheliped	13.0 mm
Width of chela of right cheliped	13.0 mm
Thickness of chela of right cheliped	5.0 mm
Length of merus of left cheliped	6.0 mm
Length of carpus of left cheliped	6.5 mm
Width of carpus of left cheliped	4.0 mm
Length of chela of left cheliped	7.5 mm
Width of chela of left cheliped	4.0 mm
Length of left first walking leg	2.9 mm [sic]

Distribution. The Aleutians, westward, up to and including the Commander Islands. Along the American shores down to the Strait of Juan de Fuca and Puget Sound (state of Washington).

Ecology. This species is found at depths ranging from 1 to 225 m, but mostly at 20 to 70 m. Not encountered in the littoral proper.

†5. Pagurus hirsutiusculus (Dana) (Plate 3, Figure 4)

Eupagurus mertensii Brandt 1851: 112. – Bernhardus hirsutiusculus Dana, 1851: 270; 1852: 443, Pl. 27, Figure 3. – Eupagurus hirsutiusculus Stimpson, 1858: 250; 1907: 223; Alcock, 1905: 178; Balss, 1913: 62, Pl. 1, Figure 9; Terao, 1913: 369; Yokoya, 1933: 83. – Pagurus hirsutiusculus Holmes, 1900: 143; Rathbun, 1904: 159; Hilton, 1916: 69; Schmitt, 1921: 137 text-Fig. 89, Pl. 16, Figure 4; Stevens, 1925: 281, Figure 4.

The width of the anterior part of the carapace exceeds the length; the surface of this part is covered with short, delicate hairs, with the exception of a central section. The median outgrowth of the front is short and triangular; the lateral outgrowths are missing. The eyestalks are short and fairly broad, with a median constriction. The ocular scales are rounded, with curved tips and strong subterminal spines. The scaphocerites usually extend beyond the eyes, but may be shorter than the eyes. The chelipeds are hairy, except on the right chela. The left cheliped extends only to the middle of the propodus of the right chela. The superior crest of the merus of the right cheliped has transverse hairy wrinkles; the lateral edges

are relatively smooth; the convex surface of the carpus is granulated and covered with minute hairs; the inferior surface is smooth. The chelae have an almost regular oval form, evenly covered with granules, and bearing scattered hairs, which are barely visible even with a magnifying glass; the external edge is granulated, and sharply separates the superior from the inferior surface, which is covered with smaller and sparser granules; the
182 external edge of the movable dactylus bears two longitudinal rows of granules; the dactyli have very small corneous tips. The carpus of the left cheliped is narrow and hairy, with a granulated superior surface; the granules of the internal and external edges are larger; the inferior surface is less hairy. The left chela is similar to the right one, but is smaller; it is almost naked, and the external edge of the movable dactylus is smooth, with a few tufts of hairs. The walking legs are hairy; on the right side they slightly exceed the chelipeds; the dactyli are short and spinulose on the inferior edge, and they end in short corneous claws. The coloration of the live specimens varies (according to Stevens) from light aquamarine to olive green, which appears rather grayish on account of the numerous small hairs. The chelipeds are dark gray, with light greenish-blue granules; the dactyli are white on the superior side and sometimes blue on the inferior one. The propodi of the walking legs are white at their distal ends and blue at their proximal ends; the dactyli have a light greenish-blue coloration, with brown longitudinal stripes. The antennae are olivaceous-brown, with golden-yellow spots which alternate on each second or third joint of the flagellum, while each of the first ten joints has spots. Young specimens differ somewhat in color from adults. The chelipeds and the walking legs vary from Brazil red to dark blue, and in some cases to a light-olive color; the joints of the legs are either white or pale blue; on the distal end of the carpus of the left cheliped, a white triangular spot frequently appears; the antennae have the same coloration as in adults. The general coloration of the specimens preserved in alcohol is reddish yellow; the right chela is whitish, sometimes with a greenish tone; the distal ends of the propodi of the walking legs are white, with red longitudinal stripes.

Dimensions

Length of anterior part of carapace	7.0 mm
Width of anterior part of carapace	7.5 mm
Length of eyestalks	3.0 mm
Length of merus of right cheliped	9.0 mm
Length of carpus of right cheliped	8.5 mm
Width of carpus of right cheliped	7.0 mm
Length of chela of right cheliped	12.0 mm
Width of chela of right cheliped	8.0 mm
Length of merus of left cheliped	7.0 mm
Length of carpus of left cheliped	7.0 mm
Width of carpus of left cheliped	3.0 mm
Length of chela of left cheliped	8.0 mm
Width of chela of left cheliped	4.0 mm
Length of right first walking leg	31.0 mm

Distribution. Sea of Japan, on the Soviet shores only to Peter the Great Bay. Northern Japan (up to Tsugaru Strait); Sea of Okhotsk; eastern

shores of Kamchatka; Commander Islands; Aleutian Range; Pribilof Islands; on the American shores to San Diego (California).

183 Ecology. This species is one of the most common littoral forms, found chiefly on rocky shores; it is very often encountered under stones in the tidal zone. It is also found in the upper part of the sublittoral, down to approximately 30 m. The greatest depth at which it was ever found is 110 m (Tsugaru Strait, Yokoya, 1933).

†6. Pagurus bernhardus (Linné) (Plate 4, Figure 6)

Cancer bernhardus Linné, 1758: 631. – Pagurus bernhardus Fabricius, 1775: 411; Risso, 1828: 37; Milne-Edwards, 1836: 266; 1837: 215; 1849: Pl. 44, Figure 2; Bell, 1853: 171; Benedict, 1901: 452; Yarzhinskii, 1870: 317. – Pagurus streblonyx Leach, 1815. – Eupagurus bernhardus Brandt, 1851: 106; Heller, 1863: 160; Carus, 1884: 491; Ortmann, 1892: 303; Bouvier, 1896: 151; Birula, 1897: 436; Milne-Edwards and Bouvier, 1900: 239; Hansen, 1908: 25; Balss, 1912: 106; Dons, 1934: 40, 113. – Pagurus bernhardus var. granulata Brandt, 1851: 107. – Eupagurus acadianus Benedict, 1901: 454.

The length of the anterior part of the carapace is almost equal to its width, or slightly more. The median outgrowth of the front is pointed, triangular, somewhat exceeding the lateral outgrowths, which have strong submarginal spines. The eyestalks are short and broad, with a marked constriction in the middle. The ocular scales are oval, with strong subterminal spines. The scaphocerites extend slightly beyond the eyes; their inferior crests are marked but not sharp, while the superointernal crest is rounded and uneven, and bears tufts of short hairs. The lateral outgrowth of the basal joint of the antennal stalk bears a strong terminal spine, and there is another strong spine on its internal edge; the internal outgrowth also bears a strong spine. The merus of the right cheliped has almost smooth crests and a row of denticles along the superodistal edge. The superior surface of the carpus is covered with strong, blunt, conical granules, the tips of which are frequently bifurcated; even stronger granules are found on the internal edge; from the bases of the granules rise sparse hairs, almost invisible to the naked eye; the lateral surfaces bear sparse, flat granules. The chela is strong, with a rough, protuberant superior surface covered with minute blunt granules; larger granules form a V-shaped pattern on the middle of the propodus, the apex of the "V" directed toward the base of the dactylus. Spiniform granules border the external edge of the chela; larger granules are found also on the cylindrical thickening of the internal edge of the propodus; hairs are almost lacking; the inferior surface bears scattered flat granules; the dactyli are stout, with calcified tips. The left cheliped reaches the base of the movable dactylus of the right chela. The carpus bears a row of spines on its internal edge; its sloping external surface is covered with spiniform granules; between the internal edge and this surface is a smooth sector. The surface of the chela is covered with the same small granules as on the chela, and also often bears larger granules forming a V-shaped pattern;

the external edge bears stronger granules, while the raised internal edge
184 bears spiniform granules. The walking legs of the right side very slightly exceed the right cheliped. The carpal joints are spinulose on the superior side; the propodal joints are granulated on their superoexternal surfaces. The dactyli are strong, with strong corneous claws. They have a brownish-yellow coloration, sometimes with reddish spots, and the legs frequently bear reddish-brown longitudinal stripes.

Dimensions

Length of anterior part of carapace	13.0 mm
Width of anterior part of carapace	13.0 mm
Length of eyestalks	6.0 mm
Length of scaphocerites	5.5 mm
Length of merus of right cheliped	14.0 mm
Length of carpus of right cheliped	14.0 mm
Width of carpus of right cheliped	11.0 mm
Length of chela of right cheliped	23.0 mm
Width of chela of right cheliped	13.5 mm
Length of merus of left cheliped	12.0 mm
Length of carpus of left cheliped	12.0 mm
Width of carpus of left cheliped	6.0 mm
Length of chela of left cheliped	15.0 mm
Width of chela of left cheliped	8.5 mm
Length of right first walking leg	56.0 mm

Distribution. West Murman Coast (east of Kola Bay inclusively); shores of Norway, North Sea, Great Belt (rare); the Shetlands, shores of Scotland, England and Ireland; northern and western coasts of France (Bay of Biscay)*; Iceland; eastern shores of North America (from New Foundland Bank southward to Chesapeake Bay).

Ecology. On the Murman Coast P. bernhardus is less common than P. pubescens, and is chiefly found in the western part (Motka, Ara, Korabel'naya, Podpakhta). According to A. Birulya (1897), it does not advance farther east than the Rybachi Peninsula, a fact which is also confirmed by K. M. Deryugin (1915). More recent researchers** found this species also in Kola Bay (in the estuary of the Volkhov River and near Bol'shoi Olenii Island). According to verbal reports of scientific workers of the former Biological Station of Murmansk, a marked increase in the frequency of P. bernhardus was noted in Kola Bay in the last years of its operation. Thus, a tendency of this species to expand eastward may be assumed. P. bernhardus is generally found in shallow waters near the shore. From Iceland it is reported at depths to 108 m, and from the Faeroe

* The reports from the Portuguese coast and from the Mediterranean are doubtful; it is probable that these findings refer – as already suggested by Heller (1863) – to P. prideauxi Leach.

** N.P. Tanasiichuk. O novykh i redkikh dlya fauny Kol'skogo zaliva formakh zhivotnykh (On new and rare animals of Kola Bay). – Doklady Akademii Nauk SSSR. 1927.

Islands to depths of 180 m, and in Chesapeake Bay (eastern coast of North America) to 477 m.

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†7. Pagurus gracilipes (Stimpson) (Plate 4, Figure 4)

Eupagurus gracilipes Stimpson, 1858: 248; 1907: 217; Doflein, 1902: 647, Pl. 6, Figures 6-8; Alcock, 1905: 177; Balss, 1913: 56; Terao, 1913: 368. – Eupagurus nipponensis Yokoya, ibid.; 87, Figure 32 – Non Eupagurus gracilipes Yokoya, 1933: 89, Figure 33*.

The width of the anterior part of the carapace is the same as its length of slightly more. The median outgrowth of the front is triangular, extending beyond the lateral outgrowths, and bearing pointed, submarginal spinules directed forward and outward. The surface of the carapace is almost naked, with a few scattered tufts of hairs, chiefly on the peripheries. The ocular scales are oval, each with a rounded apex, a very concave surface, and rather short subterminal spines. The eyestalks are short and stout, broadening slightly at the level of the corneas. The external outgrowth of the basal joint is closely appressed to the next joint; it has a pointed tip and a denticulated internal edge. The scaphocerites are slightly curved, appreciably exceeding the tip of the eyes. The merus of the right cheliped is smooth and has a denticulated anterior edge. The surface of the carpus is spinulated, the spines generally disposed in four longitudinal rows with smooth intervals between them; the spines of the internal edge are large and pointed; the inferior surface is protuberant and bears a minute granulation. The propodus is slightly protuberant and is sparsely covered with small granules; larger granules border the very thin external edge of the propodus, extending onto the edge of the immovable dactylus; the internal edge of the propodus is thickened and cylindrical, and its granulation is denser than on the rest of the surface of the propodus; the inferior surface is protuberant and smooth; the dactyli are flat and smooth, almost without granulation except on the external edges; the tips are calcified. The left cheliped reaches the middle of the propodus of the right chela. The carpus bears two longitudinal rows of spines on its superior surface; the external surface is granulated. The structure of the chela is like that of the right side, the sole difference being that the granules on its surface are more spiniform; the tips of the dactyli are corneous. The walking legs of the right side exceed the right cheliped by more than the length of their dactyli. The carpal and propodal joints are spinulose on the superior side. The dactyli are long, slender, and twisted, and considerably exceed the length of their propodi; they have pointed corneous tips. All the appendages, as well as the carapace, bear very sparse hairs. When specimens preserved in alcohol dry

* Eupagurus [sic] yokoyai nomen. nov. Eupagurus gracilipes Yokoya, 1933: 89, text-fig. 33 (nomen. praeoccup.). Locality: St. 353, near Tanabe, Wakayama-ken [Prefecture], 192 m. 4 August 1928, 3 males, 3 females (1 ov.). "Near Eupagurus pectinatus Stimpson [Pagurus pectinatus (Stimpson) – Makarov], but it differs from this in the following points: ophthalmopods shorter. The peduncles of the first and the second antennae distinctly exceed the opthalmic cornea, and the hairy acicle of the second antenna reaches the distal end of the eye. Legs slender (Yokoya)." It is perhaps more closely related to Pag. brachiomastus (Thallw.).

up, the appendages show a faint mother-of-pearl shine. The carpal and pro-
186 podal joints of the walking legs have longitudinal red stripes on their external surfaces. The scaphocerites of the young specimens are much shorter than the eyes. On the superior surface of the carpus of the right cheliped only two longitudinal rows of spines are found, with a smooth space between them. The lateral outgrowths of the front are more prominent.

Dimensions

Length of anterior part of carapace	5.0 mm
Width of anterior part of carapace	5.0 mm
Length of eyestalks	2.5 mm
Length of scaphocerites	3.5 mm
Length of merus of right cheliped	7.0 mm
Length of carpus of right cheliped	6.0 mm
Width of carpus of right cheliped	4.0 mm
Length of chela of right cheliped	9.0 mm
Width of chela of right cheliped	5.0 mm
Length of merus of left cheliped	4.5 mm
Length of carpus of left cheliped	4.0 mm
Length of chela of left cheliped	6.0 mm
Width of chela of left cheliped	3.0 mm
Length of right first walking leg	26.0 mm

Distribution. Japan, chiefly the southern part; the northernmost locality in Japan is Hakodate. We give here the first report of this species from the continental shores of the Sea of Japan (Sidemi Bay, Troitsa Bay).

Ecology. This species is reported from depths ranging from 30 to 600 m, but is chiefly found between 50 and 150 m.

8. Pagurus beringanus (Benedict) (Plate 5, Figure 4)

Eupagurus beringanus Benedict, 1892: 17 – Eupagurus newcombei Benedict ibid.: 17. – Pagurus beringanus Rathbun, 1904: 159, Pl. 5, Figure 5; Schmitt, 1921: 135, Figure 87; Stevens, 1925: 283, Figure 6.

The length of the carapace exceeds its width; the surface of the carapace is naked, with a few lateral tufts of hairs. The median outgrowth of the front is very short, broad, and triangular. The lateral outgrowths have the form of obtuse angles, formed by the anterior edges of the carapace, and do not bear submarginal spines. The ocular scales are triangular, with a blunt tip and strong, blunt, subterminal spines. The eyestalks are long and almost cylindrical. The lateral outgrowth of the basal joint of the antennal stalk has a straight, pubescent external edge, a convex internal edge and a supplementary spine near the apical one. The scaphocerites are curved, shorter than the eyes, reaching the base of the corneas at most; the external edge of the scaphocerites is smooth, the internal one pubescent and denticulated. The merus of the right cheliped is triangular in cross section and has smooth lateral surfaces; the superior edge broadens

distally and forms a small area covered with short spines and a few hairs;
187 the anterior edge bears 15 or 16 spines; the inferior surface bears two large tuberculiform granules, the external one as a rule larger than the internal one; the semicircular distal edge is covered with spiniform granules and hairs. The superior surface of the carpus is protuberant and covered with blunt spiniform granules. Along the internal edge larger granules are found. Another row of larger granules extends obliquely upward from the inner proximal angle. The lateral and the interior surfaces are more or less smooth, almost naked. The width of the chela is the same as that of the carpus; the surface of the propodus is protuberant and covered with fairly dense, blunt granules; a number of larger, sometimes spiniform granules form a border on the protuberant edge. Larger granules also form on the middle of the propodus a V-shaped pattern, which is, however, not always clear; the tip of this pattern is directed forward and its inner branch extends onto the carpus to form the above-mentioned oblique row of granules; the inferior surface of the propodus is protuberant and smooth and bears sparse tufts of hairs; the dactyli are short, and have a granulated superior surface and small, corneous tips. The left cheliped reaches the middle of the propodus of the right chela, and in smaller specimens – the base of the movable dactylus. The merus is triangular in cross section and has a pubescent inferior surface. The sloping external surface of the carpus is granulated and its superior edge bears spines; the internal surface is flat and hairy, and bears scattered granules. The propodus does not bear a marked median crest; it has a protuberant external surface, covered with a dense granulation; larger granules are concentrated around the superior blunt crest; the external surface is smooth, covered with tufts of hairs, and bears a marked crest toward the inferior surface. When the dactyli are closed a small gap is left open. The walking legs do not reach the end of the right cheliped. The carpal and propodal joints bear spines and hairs on their superior edges. The dactyli are short and fairly broad, and bear pointed curved claws. The live specimens (according to Stimpson) have a brown coloration, with light spots. The chelipeds have bright red spines; the dactyli are pale grayish green, with a reddish tint; the distal end of the merus has a red stripe, ending in spines of the same color. The walking legs are lighter in color than the chelipeds; the propodi and dactyli are often greenish with irregular reddish brown spots. The specimens preserved in alcohol have a reddish-brown coloration.

Dimensions

Length of anterior part of carapace	10.0 mm
Width of anterior part of carapace	9.0 mm
Length of eyestalks	5.0 mm
Length of scaphocerites	4.0 mm
Length of merus of right cheliped	12.0 mm
Length of carpus of right cheliped	11.0 mm
Width of carpus of right cheliped	8.0 mm
188 Length of chela of right cheliped	14.0 mm
Width of chela of right cheliped	8.0 mm
Length of merus of left cheliped	9.0 mm
Length of carpus of left cheliped	8.0 mm

Length of chela of left cheliped	9.0 mm
Width of chela of left cheliped	5.0 mm
Length of right first walking leg	42.0 mm

Distribution. Bering Sea (parallel of Nunivak Island) southward along the Aleutians and along the shores of Alaska northward to Monterey Bay (California) (M. Rathbun).

Ecology. At depths between 0 and 82 m, chiefly on rocky bottoms.

†9. Pagurus dubius (Ortmann) (Plate 3, Figure 5)

Eupagurus dubius Ortmann, 1892: 307, Pl. 12, Figure 14; Doflein, 1902: 646; Balss, 1933: 55; Yokoya, 1933: 81.

The length of the anterior part of the carapace exceeds its width. The median outgrowth of the front is triangular, pointed, but sometimes more or less blunt; the lateral outgrowths are rounded. The eyestalks are fairly long and cylindrical; the ocular scales are rounded, with fairly strong subterminal spines. The scaphocerites do not reach the end of the eyes, but may be somewhat longer in smaller specimens. The chelipeds are very unequal. The merus of the right cheliped has a few hairs on its lateral surfaces; its anterior edge is denticulated; its inferior surface is more pubescent and bears a prominent spine in the middle. The superior surface of the carpus is covered with spiniform granules which gradually disappear on the lateral surfaces; the superior surface and the semicircular interior one have long slender hairs; the flat external surface is almost naked; on the external half of the inferior surface a naked prominence is found, while the internal half is hairy and covered with minute granules. The chela is very slightly broader than the carpus; its superior surface is completely naked and evenly covered with translucent granules; larger granules border the edge of the chela, the granules of the external edge being stronger than those of the internal edge; the external edge of the movable dactylus has two longitudinal rows of such granules; the tips of the dactyli are corneous. The left cheliped extends slightly beyond the distal end of the carpus of the right cheliped. The merus is flattened; it is hairy on its superior side, and naked laterally; the inferior surface is hairy and bears a prominent, blunt, central spine identical with the one on the merus of the right cheliped. The carpus is narrow and hairy and bears two rows of spines along the edge of the superior surface; the inferior surface is hairy on its internal half and naked on the external one. The chela is narrow, its superior surface pubescent and covered with spiniform granules; the inferior surface is smooth
189 and naked. When the dactyli are closed, a small basal gap is left open. The walking legs reach the end of the right cheliped, or extend slightly beyond it. The lateral surfaces of the joints are naked, the superior and inferior edges pubescent. The carpal joints bear spines along the superior edge. The dactyli are slightly curved, and have spinulose inferior edges. The coloration of the specimens preserved in alcohol is pale pinkish yellow. The carpal and propodal joints of the walking legs have red longitudinal stripes

on their external surfaces; the dactyli are red, with an elongate white spot in the middle; the superior surface of the propodus of the right chela usually has a peculiar red pattern of an irregular but more or less constant contour.

Dimensions

Length of anterior part of carapace. . . .	7.0 mm
Width of anterior part of carapace	6.0 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	9.0 mm
Length of carpus of right cheliped	8.5 mm
Width of carpus of right cheliped	6.0 mm
Length of chela of right cheliped	12.0 mm
Width of chela of right cheliped.	6.5 mm
Length of merus of left cheliped	6.0 mm
Length of carpus of left cheliped.	5.5 mm
Width of carpus of left cheliped	2.0 mm
Length of chela of left cheliped.	8.0 mm
Width of chela of left cheliped	3.5 mm
Length of right first walking leg.	31.0 mm

Distribution. Southern Japan; Sea of Japan, on the Soviet coast north of Olga Bay.

Ecology. This species does not reach a large size; it generally lives at depths ranging from 50 to 120 m; in rare cases it may be found at shallower depths.

†10. Pagurus samuelis (Stimpson) (Plate 3, Figure 6).

Eupagurus samuelis Stimpson, 1857: 482; 1858: 250; 1907: 224; Ortmann, 1892: 301; Doflein, 1902: 646; Alcock, 1905: 178; Balss, 1913: 61; Terao, 1913: 371. – Pagurus samuelis Holmes, 1900: 144; Rathbun, 1904: 160, Pl. 5, Figure 7; Hilton, 1916: 63; Schmitt, 1921: 139 text - Figure 90, Pl. 16, Figures 2, 3.

The length of the anterior part of the carapace exceeds its width. The median outgrowth of the front is broad, triangular and hidden by a tuft of long hairs; the lateral outgrowths are rounded. The eyestalks are long and cylindrical. The ocular scales are broad and triangular, with a blunt tip and a strong subterminal spine. The scaphocerites do not reach the end of the eyes and have hairs on their internal edges. The apex of the lateral outgrowth of the basal joint of the antennal stalk ends in two spines. The merus of the right cheliped has smooth edges, and bears hairs and spini-
190 form granules on the distal end of its superior surface; its inferior surface bears a strong, blunt median spine. The superior surface of the carpus is covered with hairs and spiniform granules; its lateral and inferior surfaces bear broad, low granules, and are less hairy. The protuberant superior surface of the chela is practically naked – a few minute hairs can be seen only with a magnifying glass; the entire surface is evenly covered with

pearl-like granules; the edges of the chela are bordered with larger granules; the inferior surface is covered with minute granules, chiefly on its inferior part. The dactyli have corneous tips. The merus of the left cheliped also bears a blunt spine on its inferior surface. The carpus is spinulose and hairy. The superior surface of the propodus is spinulose and almost naked; the inferior surface is smooth, with a few hairs. The movable dactylus is entirely naked. The carpal joints of the walking legs are spinulose on their superior edges. The dactyli are slightly curved and twisted; they are dark at their proximal and distal ends, and light in their median part. The specimens preserved in alcohol have a yellowish coloration. In live specimens the antennae are reddish brown; the superior surface of the distal joint of the stalk has narrow golden-yellow stripes. The distal third of the propodi of the walking legs is light blue or white; the proximal ends of these joints are blue, while on the rest of the surface are blue or greenish-brown stripes. The dactyli are blue, changing to white near the tips, while at the very claws they are reddish orange with three more or less clear bluish or greenish-red-brown stripes. The right chela is usually dark bluish green, and the tips of the dactyli are white; the spines of the left chela are often orange. On the basis of a survey of comprehensive material W. L. Schmitt (1921) notes that, with increasing age, the right cheliped of the male becomes elongated and has a relatively smoother granulation; the large granules on the external edge of the chela disappear. Large males differ from females to such an extent in these details that, if only these characters were taken into account and the others ignored, one could consider them as belonging to another species; on the basis of a complete series however, the whole gradual transition can be followed.

Dimensions

Length of anterior part of carapace. . . .	5.0 mm
Width of anterior part of carapace	4.5 mm
Length of eyestalks	3.0 mm
Length of merus of right cheliped	4.5 mm
Length of carpus of right cheliped	5.0 mm
Width of carpus of right cheliped.	4.0 mm
Length of chela of right cheliped	7.0 mm
Width of chela of right cheliped.	5.0 mm
Length of merus of left cheliped	4.0 mm
Length of carpus of left cheliped	4.5 mm
Width of carpus of left cheliped	2.0 mm
Length of chela of left cheliped	5.0 mm
Width of chela of left cheliped	3.0 mm
Length of right first walking leg	18.0 mm

191 This species is closely related to P. dubius (Ortm.), from which it differs by shorter scaphocerites, a blunter median frontal outgrowth, and a shorter propodus of the right chela. Other differences are the smaller granulation on the right chela, the lack of the red pattern on the propodus of this leg (so characteristic of P. dubius), the completely naked movable dactylus of the left chela, and the shorter dactyli of the walking legs.

Distribution. Japan; on the Soviet shores of the Sea of Japan it is at present known only from Nakhodka Bay and Olga Bay; the Kurile Islands

(Iturup Island); Avachinskaya Gulf, Kamchatka (according to Balss); on the American shores, from Sitka to San Diego, California.

†11. Pagurus cornutus (Benedict) (Plate 5, Figure 1)

Eupagurus cornutus Benedict, 1892: 12. – Pagurus cornutus Rathbun, 1904: 158, Pl. 5, Figure 3.

The width of the anterior part of the carapace somewhat exceeds its length; in large specimens, however, the width is equal to the length. The median outgrowth of the front is triangular and pointed; the lateral outgrowths are less prominent and bear small submarginal spines. The eyestalks are stout and of medium length; they broaden slightly at the corneas. The ocular scales are rounded, and bear strong subterminal spines. The scaphocerites extend beyond the eyes by almost half their length, and their internal edges are hairy. The lateral outgrowth of the basal joint of the antennal stalk bears an apical spine and three or four more spines on its internal edge. The chelipeds are strong. The merus of the right cheliped has a triangular cross section and bears spines on its superodistal edge; the blunt superior crest is covered with transverse wrinkles from which spring tufts of hairs; the inferior surface has spinulose edges. The superior surface of the carpus is sparsely covered with spines, in front of whose bases tufts of long hairs are found; the marginal spines, particularly those of the internal edge, are stronger. The chela has a straight internal edge and an arcuated external one. A strong diagonal crest extends anteriorly from the internal side of the base of the propodus and forms at the base of the movable dactylus a hornlike, pointed process directed forward; a second less marked crest rises from the external side of the base of the propodus and meets the first crest on the external surface of the horn. Thus, a prominence is formed at the base of the propodus by the two converging crests; this prominence is triangular and has a granulated surface. The remainder of the surface of the propodus is deeply concave and granulated. The external edge of the movable dactylus and that of the chela are covered with blunt spines, while the inferior side is densely covered with long soft hairs. The inferior surface of the chela is convex and smooth, and bears scattered tufts of hairs. The dactyli are flat and slender; their superior surfaces bear a minute granulation and their tips are corneous. The left cheliped reaches the middle of the movable dactylus of the right chela; in larger specimens, however, it extends only to its base. The merus is flattened and has wrinkles
192 similar to those on the right leg. The carpus bears two rows of spines which converge distally; it is slightly hairy and the distal, inferoexternal corner is very prominent. The chela bears a strong crest, extending from the base of the propodus to the immovable dactylus; it bears small spinules on its superior part and is covered with hairs; the internal side of the propodus is very narrow, not broader than the movable dactylus; the external side is broad, with a deeply concave, granulated surface, the inferior part of its external edge being covered with dense hairs; the inferior surface is smooth and bears tufts of hairs. The superior surface of the movable dactylus has a minute granulation; the movable dactylus is longer and has a smooth superior surface; the dactyli have corneous tips. The walking legs are strong,

and on the right side somewhat exceed the right cheliped. The meral joints are flattened; those of the first pair are granulated on their inferior side. The carpal joints of both pairs are spinulose on the superior side. The legs are slightly pubescent as a rule. The dactyli are curved and strongly twisted; they have slender, pointed, corneous claws. The specimens preserved in alcohol have a reddish-yellow coloration.

Dimensions (of large specimens)

Length of anterior part of carapace. . . .	17.0 mm
Width of anterior part of carapace	17.0 mm
Length of eyestalks	9.0 mm
Length of merus of right cheliped	24.0 mm
Length of carpus of right cheliped	24.0 mm
Width of carpus of right cheliped.	15.0 mm
Length of chela of right cheliped.	32.0 mm
Width of chela of right cheliped	15.0 mm
Length of merus of left cheliped	19.0 mm
Length of carpus of left cheliped	18.0 mm
Width of carpus of left cheliped.	6.0 mm
Length of chela of left cheliped.	25.0 mm
Width of chela of left cheliped	12.0 mm
Length of right first walking leg	94.0 mm

Distribution. The Aleutians, westward to the Commander Islands inclusively. Bering Sea, on the Soviet shores, from the Commander Islands northward to the parallel of Cape Navarin; on American shores from 55° 38′ N. latitude down to Queen Charlotte Sound (British Columbia).

Ecology. Deep-sea species, known at depths ranging from 160 to 830 m.

†12. Pagurus undosus (Benedict) (Plate 1, Figure 5).

Eupagurus undosus Benedict, 1892: 18. – Pagurus undosus Rathbun, 1904: 159, Pl. 4, Figure 6. – Eupagurus trigonochirus var. paulensis Balss, 1913: 64, Figures 38, 39.

The length of the anterior part of the carapace slightly exceeds its width. The triangular median outgrowth of the front is slightly more prominent than the lateral one; these outgrowths are rounded and bear submarginal spines. The eyestalks are cylindrical and of medium length. The
193 ocular scales are triangular, with raised edges and strong subterminal spines. The scaphocerites reach the end of the eyes and have hairy internal edges. The internal edge of the lateral outgrowth of the antennal stalk bears from two to four spines. The merus of the right cheliped has a triangular cross section and smooth lateral surfaces; the anterior edge bears spines; on the distal end of the superior crest are a few isolated granules and wrinkles which bear setae; the inferior surface is pubescent. The superior surface of the carpus bears small spinules, while on the internal

edge large spinules are found; the spines of the external edge are smaller but more dense than on the rest of the surface; the lateral surfaces are covered with spiniform granules; the inferior surface is protuberant, smooth, and hairy. The internal edge of the chela is almost straight, the external edge somewhat arcuated; extending from the middle of the base of the propodus to the gap left between the dactyli is a not very prominent crest, fairly abrupt on its distal end, and descending toward the internal edge of the immovable dactylus; the tip of the crest seen in profile forms a fairly straight line which is not raised at its end to form a tubercle, horn, etc. Owing to the fact that the internal edge of the propodus is cylindrically thickened, an elongated depression with parallel borders is formed between the edge and the crest; the proximal end of the depression easily reaches the base of the propodus, while the distal end is separated from the base of the movable dactylus by a raised sector. Outward from the median crest, the surface of the propodus is protuberant. The entire surface of the propodus is densely covered with round granules; larger granules are disposed in the middle of the crest and, in particular, at its distal end. The external edges of the propodus and of the movable dactylus bear conical spines. At the bases of the granules are crowns of very short hairs, visible only with a magnifying glass. The inferior surface of the chela is almost smooth and slightly hairy. The dactyli have slender corneous tips. The left cheliped reaches the base of the movable dactylus of the right chela. The carpus bears two rows of spines on its superior surface; the spines of the inner row are much larger than those of the outer row; the internal surface is hairy, the external one granulated, the inferior one hairy. The chela has a broad, triangular oblique external surface, convex in the middle and slightly concave on both sides; a sharp spinulose crest rises from the internal side of the base of the propodus and, in a somewhat diagonal direction extends to the immovable dactylus. The external edge of the propodus is sharp and bears blunt conical spines. The external oblique surface of the propodus bears a granulation like that of the right chela; the internal surface appears as a narrow granulated sector; the inferior surface bears a few granules and tufts of hairs. The walking legs of the right side reach the end of the right cheliped and in small specimens extend beyond it. The meral joints of the first pair are spinulated on their inferior side. The carpal
194 joints of both pairs are spinulose on their superior side. The dactyli are fairly stout, perfectly straight and not twisted, slightly hairy on their superior side, spinulose on the inferior one and bearing pointed, curved claws. The chelipeds of the specimens preserved in alcohol have a pinkish-yellow coloration, with a brownish-red stripe at the distal ends of the meri. The spines on the carpus of the chelipeds are red-tipped. The distal parts of the walking legs are brownish red, the median parts lighter; the tips of the dactyli are of a lighter color than the proximal parts; the claws are transparent and light brown.

Dimensions

Length of anterior part of carapace. . . .	8.5 mm
Width of anterior part of carapace	8.0 mm
Length of eyestalks	4.5 mm
Length of merus of right cheliped	10.0 mm
Length of carpus of right cheliped	11.0 mm

Width of carpus of right cheliped	8.0 mm
Length of chela of right cheliped	14.5 mm
Width of chela of right cheliped	8.0 mm
Length of merus of left cheliped	8.5 mm
Length of carpus of left cheliped	8.5 mm
Width of carpus of left cheliped	3.0 mm
Length of chela of left cheliped	11.0 mm
Width of chela of left cheliped	6.0 mm
Length of right first walking leg	36.0 mm

This species does not attain a large size.

Distribution. Sea of Japan, from the parallel of Furuhelm Island northward only along the Soviet shores (not found in Japan south of La Perouse Strait); Sea of Okhotsk; eastern shores of Kamchatka; Bering Sea (on the Soviet shores up to Cape Chaplin); the Aleutians down to the Pribilof Islands inclusive.

Ecology. This species is found at depths ranging from 15 to 100 m, chiefly on rocky bottoms. It sometimes inhabits sponges.

13. Pagurus tanneri (Benedict) (Plate 5, Figure 5).

Eupagurus tanneri Benedict, 1892: 10. – Pagurus tanneri Holmes, 1900: 140; Rathbun, 1904: 158, Pl. 4, Figure 7; Schmitt, 1921: 133, Figure 86.

The width of the anterior part of the carapace is almost the same as its length. The median outgrowth of the front has a broad triangular form; the lateral outgrowths are distinct, and bear pointed submarginal spines. The ocular scales are oval, with raised edges and very strong subterminal spines. The eyestalks are stout and relatively short, widening at the level of the cornea; the stalk and the cornea are slightly flattened dorsoventrally. The external outgrowth of the basal joint of the antennal stalk is pointed and has a denticulated internal edge. The scaphocerites are curved, and are the same length as the eyes or somewhat longer, and have pubescent internal edges. The merus of the right cheliped is smooth, and
195 its anterior edge is spinulose; the inferior surface is covered with groups of large granules along its internal and external edges. The protuberant surface of the carpus is spinulose, strong spines bordering the external and internal edges. The chelae are as broad as the carpus; in the middle of the propodus is a triangular prominence, the tip of which is directed toward the gap left open between the dactyli; a slight crest rises from the tip and extends along the surface of the immovable dactylus near its internal edge; the surface of the chela is concave on both sides of the prominence. The entire surface of the propodus and of the dactyli is covered with granules, while stronger granules are disposed along the crests of the triangular prominence; in addition, there is a row of five or six larger spinules on the surface of the triangle itself, near its external crest. The external edge of

the chela bears fairly strong spines; the inferior surface of the propodus is smooth and bears tufts of hairs. The dactyli have small corneous tips. The left cheliped extends slightly beyond the base of the movable dactylus of the right chela. The merus is flattened and spinulated on its anterior edge and on the edges of the inferior surface. The carpus bears two rows of spines on its superior edge; near the distal end, the outer row diagonally crosses the surface and meets the inner row at the inner distal angle. The propodus has a prominent crest which bears 13 or 14 spinules; the external surface of the propodus is deeply concave and densely covered with granules; the convex external edge bears spines which decrease in size at the transition toward the immovable dactylus; the internal side of the propodus has the form of a smooth deep trench; the dactyli meet closely. The left chela greatly resembles that of P. cornutus in form and sculpture. The walking legs of the right side exceed the right cheliped. The lateral surfaces of the two joints are smooth. The carpal joints of the first pair of walking legs bear pointed spines on their superior edges. The propodal joints of the first pair and the carpal joints of the second bear blunt spines or – more correctly – spiniform granules, on their superior edges. The dactyli are long, flattened, slightly curved, and not twisted; the spines on their inferior edges gradually increase in size toward the relatively short corneous claws.

Dimensions

Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	8.0 mm
Length of eyestalks	5.0 mm
Length of scaphocerites	5.0 mm
Length of merus of right cheliped	10.0 mm
Length of carpus of right cheliped	9.0 mm
Width of carpus of right cheliped	7.0 mm
Length of chela of right cheliped	13.5 mm
Width of chela of right cheliped	7.5 mm
Length of merus of left cheliped	8.9 mm
Length of carpus of left cheliped	7.5 mm
Length of chela of left cheliped	11.0 mm
Width of chela of left cheliped	5.5 mm
Length of right first walking leg	34.0 mm

196 Distribution. Bering Sea (in the vicinity of the Pribilof Islands) at depths of 87 to 140 m. From Unalaska southward to San Simeon Bay, California.

Ecology. This species is a deep-sea form, found at depths ranging from 90 to 1,000 m; on the Californian coast it is found exclusively from 380 m downward.

†14. Pagurus anomalus (Balss) (Plate 4, Figure 5).

Eupagurus anomalus Balss, 1913: 53, Figure 32; Yokoya, 1933: 80.

The width of the anterior part of the carapace is the same as the length. The whole surface of the carapace is hard, not just the anterior part as in most Paguridae. The carapace is covered with granules which bear crowns of minute hairs, directed forward. On the anterior part of the carapace, near the frontal edge, a number of fairly strong spines are found, curved in an anterior direction. The median outgrowth of the frons is long, triangular and directed obliquely upward at an angle of about 45° ; the lateral outgrowths also have the form of upward-directed spines; there are two such outgrowths on each side. On the internal side of the two medial lateral outgrowths, distinct submarginal spines are found. The eyestalks are stout and short, and have a slight median constriction. The ocular scales are small, pointed, and very hard. The scaphocerites extend slightly beyond the end of the eyes. The external outgrowth of the basal joint of the antennal stalk bears strong, pointed, apical spines. The chelipeds are relatively short, weak and subequal, the right one being slightly longer than the left. The merus of the right cheliped has a triangular cross section, the crests being rounded; the surface is covered with transverse wrinkles and crowns of hair on the superior side; the anterior edge bears a single long spine. The superior surface of the carpus is flat and smooth, with longitudinal rows of marginal spines; the lateral surfaces show wrinkles and hairs. The chela is elongated and the dactyli are fairly long; a row of minute spines extends along the internal edge of the propodus, and an irregular row of larger spines is disposed on the middle of the propodus; the dactyli are slightly shorter than the propodus; their prehensile edges bear two or three tubercles, and their tips are corneous. The left cheliped resembles the right one in structure, but is more slender; the chela is much narrower; the dactyli are longer than the propodus, and markedly curved downward. The walking legs are much longer than the chelipeds. The right first walking leg exceeds the cheliped by half the length of its propodus. All the joints are flattened, and covered-particularly on their external surfaces-with broad transverse wrinkles which bear hairs; these wrinkles impart to the legs a squamose appearance. The superior edges of the carpal joints terminate at their distal ends in a broad triangular denticle, which is almost straight and slightly twisted. The abdomen is short. A peculiarity of this species is that it chooses as a shelter only shells of a size sufficient
197 to cover its soft abdomen, while the other parts of the body remain unprotected. The specimens preserved in alcohol are yellow, with reddish stripes near the wrinkles. The appendages are slightly iridescent.

Dimensions

Length of anterior part of carapace	11.0 mm
Width of anterior part of carapace	11.0 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	12.0 mm
Length of carpus of right cheliped	8.0 mm
Width of carpus of right cheliped	3.0 mm
Length of chela of right cheliped	14.0 mm
Width of chela of right cheliped	5.5 mm
Length of dactyli of right chela	7.0 mm
Length of right first walking leg	53.0 mm

Distribution. Southern Japan, northward as far as Tsugaru Strait; Sea of Japan, on the Soviet coasts, from Furuhelm Island northward to De Kastri Gulf.

Ecology. This species is found at depths from 15 to 270 m, chiefly on rocky bottoms. On the coasts of the Maritime Territory it is generally encountered at depths between 20 and 60 m, in southern Japan–between 100 and 270 m.

†15. Pagurus splendescens Owen (Plate 4, Figure 2)

Pagurus splendescens Owen, 1839: 81, Pl. 25, Figures 1, 1a; Brandt, 1851: 111; Richters, 1883: 406; Holmes, 1900: 234; Rathbun, 1904: 161; 1919: 8; Stevens, 1925: 295, Figures 15, 16. – Eupagurus splendescens Murdoch, 1885: 138; Calman, 1898: 260; Alcock, 1905: 178; Balss, 1913: 62, text-Figure 36, 37, Pl. 2, Figure 2.

The width of the anterior part of the carapace exceeds its length. The whole carapace is hard as in the preceding species. The entire surface of the carapace is covered with tubercles bordered by short hairs. The median outgrowth of the frons is broad and triangular and directed horizontally forward, not upward as in P. anomalus; the tip of the outgrowth bears three or four blunt denticles. The lateral outgrowths of the front have the form of short spines. Beyond the lateral outgrowths, the edge of the carapace bears bifid tubercles, very marked in large specimens. Projecting from the cervical groove the eyestalks are short and stout, with a marked median constriction. The ocular scales are rounded, with a rounded tip and strong subterminal spines. The scaphocerites extend considerably beyond the end of the eyes; they have a triangular cross section and a smooth, shiny internal surface, and bear blunt spines on their external surface. The external outgrowth of the basal joint of the antennal stalk has a bifid tip. The chelipeds are fairly strong, the right leg being much longer than the left one. The lateral surfaces of the merus of the right cheliped are covered with transverse rows of tubercles which bear hairs; the superodistal edge bears two
198 or three spines, not a single spine as in P. anomalus. The superior surface of the carpus is flat, the lateral edges bearing rows of spines; there is an additional irregular median row of spines; the spines are transformed into compound tubercles in the larger specimens. The chela is elongated, and somewhat broader than the carpus; the edges are bordered by rows of spinules which clearly divide the superior from the inferior surface. The superior surface of the propodus is covered with multifid hairy tubercles; stronger tubercles form two median rows which converge toward the base of the immovable dactylus. The tips of the dactyli cross when the chela is closed; the prehensile edges bear three or four white tubercles with tufts of hairs above them; the tips are corneous. The left cheliped reaches the base of the movable dactylus of the right chela; it is similar to the right cheliped in structure, but the dactyli are longer, thinner, and curved upward. In the large specimens the inferior surfaces of all the joints of the chelipeds are covered with fairly dense hairs. The walking legs are long, the right first

leg exceeding the right cheliped by almost the entire length of its dactylus. The internal surface of all the joints is perfectly smooth, while the external one is covered with rows of tubercles like those of the merus of the chelipeds. The distal ends of the meral joints bear on their superior side a row of minute spinules, the median spinule being the longest; the inferior edge bears fairly thick simple spines. The inferior edges of the carpal joints are smooth, the superior ones spinulose. The dactyli are long, slightly curved, and twisted. The abdomen is short as in P. anomalus, and like this species, P. splendescens protects only its abdomen with the shell. The coloration varies (according to Stevens) from light brown to light mauve, and has a metallic iridescence of pink, green, pale violet and golden tints; the tubercles are dark. The inferior side of the chelipeds and the walking legs varies from pale pinkish yellow to pale mauve; the dactyli are dark olive green with white tips. The internal surface of the antennules has a bronze or golden sheen.

This species is closely related to P. anomalus (Balss) but differs in the form and orientation of the median outgrowth of the frons, the armature of the frontal edge of the carapace, the bifid external outgrowth of the basal joint of the antennal stalk, the different structure of the carapace, the absence of the spine on the prominence of the carapace beyond the cervical groove, longer chelipeds, etc.

Dimensions

Length of anterior part of carapace	15.0 mm
Width of anterior part of carapace	17.0 mm
Length of eyestalks	7.0 mm
Length of merus of right cheliped	21.0 mm
Length of carpus of right cheliped	16.0 mm
Width of carpus of right cheliped	10.0 mm
Length of chela of right cheliped	28.0 mm
199 Width of chela of right cheliped	13.0 mm
Length of dactyli of right cheliped	13.0 mm
Length of right first walking leg	84.0 mm

Distribution. Sea of Okhotsk; eastern shores of Kamchatka; Bering Sea, on the American coasts southward as far as Washington; Chuckchee Sea, northward to Point Barrow, westward to the mouth of the Kolyma River.

Ecology. Found at depths ranging between 1 and 411 m; on various bottoms, but apparently chiefly on soft, muddy and sandy-muddy bottoms.

†16. Pagurus ochotensis Brandt (Plate 2, Figure 2)

Pagurus bernhardus var. spinimana seu subsp. ochotensis Brandt, 1851: 108. – Pagurus bernhardus granulato-denticulata Brandt, ibid.: 107; Richters, 1883: 405. – Eupagurus alaskensis Benedict 1892: 2. – Pagurus alaskensis Holmes, 1900: 135; Benedict, 1901: 456, text-Figure; Rathbun, 1904: 157; Stevens, 1925: 277, Figure 1. – Eupagurus ochotensis Stimspon, 1907: 218; Balss, 1913: 60; Yokoya, 1933: 82. – Eupagurus ortmanni Balss, 1911: 7. – Eupagurus spinimanus Terao, 1913: 372.

The width of the anterior part of the carapace exceeds its length; its surface is almost naked, with the exception of two tufts of hairs behind the lateral outgrowths of the front. The median outgrowth of the front is short and triangular, bearing strong submarginal spines. The eyestalks are short and stout, and have a median constriction. The ocular scales are short and rounded, with a concave superior surface and strong subterminal spines—owing to which the scales appear pointed. The scaphocerites are strong, with a triangular cross section, and exceed the eyes by a third of their length; the superointernal angle bears 12 to 16 blunt spines, which are not always very visible; near the base of the scaphocerite these spines usually appear as smooth tubercles; in addition, this edge is hairy, while the flat sides are completely smooth; the internal side is very iridescent. The external outgrowth of the basal joint of the antennal stalk has a denticulated internal edge, the internal outgrowth being covered by a blunt spine. The chelipeds are strong and appear completely naked to the unaided eye. The merus of the right cheliped has a triangular cross section and smooth lateral surfaces; in its distal half the rounded dorsal crest bears groups of spines, which are disposed in short, transverse rows; along the anterior edge a naked concave space is found; the anterior edge bears spines which are directed forward; the inferior surface is granulated and spinulose along its external edge. The superior surface of the carpus is covered with spiniform granules or short conical spines, which have hairs in front of their bases; these hairs are visible only with a magnifying glass; the surface between these hairs is covered with minute spines; the largest spines are
200 found on the internal edge; the lateral surfaces are covered with spiniform granules, and their inferior surface bears a minute granulation. The chelae have an irregular triangular form; the superior surface is covered with granules or conical spines similar to those on the carpus; the spines of the external edge are the largest; the internal edge is cylindrically thickened; the lateral surfaces are granulated, the granulation gradually disappearing toward the inferior surface; thus, the proximal part of this is completely smooth; the prehensile edges of the chelae bear white tubercles and calcified tips. The left cheliped reaches the middle of the movable dactylus of the right chela. The merus and the carpus are similar in structure to the right leg. The chela has a slightly protuberant superior surface with an armature like that of the right chela; the edges are raised, particularly the internal one; the inferior surface bears scattered tufts of dark hairs; the dactyli have corneous tips, which leave an open slit when closed. The walking legs are strong, and exceed the chelipeds on the right side. The carpal joints of both pairs have spiniform granules on the superior edge, while the sides are completely smooth; the propodal joints of both pairs have spiniform granules on the superior edge as well as on the external surface. The dactyli are strong, considerably longer than the propodi, curved and twisted; they have a groove along the internal surface and are protuberant on the external one; the superior side is provided with three longitudinal rows of blunt spines or spiniform granules; the corneous tip is relatively short. In specimens preserved in alcohol the general coloration of the dorsal side is light purple with an iridescent sheen, while in very large specimens a violet shade clearly predominates; the ventral side is light in color with a slight reddish tint. Around the prehensile edge of the immovable dactylus of the right chela runs a red stripe, which subsequently

extends onto the internal edge of the propodus. The inferoexternal surface of the carpal joints of the walking legs has red distal parts.

Dimensions

Length of anterior part of carapace	17.0 mm
Width of anterior part of carapace	18.5 mm
Length of eyestalks	8.0 mm
Length of scaphocerites	10.0 mm
Length of merus of right cheliped	22.0 mm
Length of carpus of right cheliped	21.0 mm
Width of carpus of right cheliped	18.0 mm
Length of chela of right cheliped	31.0 mm
Width of chela of right cheliped	19.0 mm
Length of merus of left cheliped	15.0 mm
Length of carpus of left cheliped	16.0 mm
Width of carpus of left cheliped	10.0 mm
Length of chela of left cheliped	21.0 mm
Width of chela of left cheliped	13.0 mm
Length of right first walking leg	79.0 mm

The specimens of this species may attain large dimensions.

201 Distribution. Bering Sea; on the American shores down to Oregon; relatively rare on Soviet shores; Sea of Okhotsk; Sea of Japan southward to southern Japan inclusive.

Ecology. This species is found at depths ranging from 1 to 250 m, chiefly on sandy bottoms.

The problem of the synonymy between P. ochotensis and P. alaskensis is a very complex one. After studying the collection of the Zoological Institute of the Academy of Sciences, we reached the conclusion that Brandt did not study a specimen of P. ochotensis in the modern conception of this species. The type specimen P. bernhardus var. spinimana seu subsp. ochotensis (No 1075) should probably be included in P. alaskensis; in addition, we could not find any specimen which could be considered as P. ochotensis in the whole collection studied. Consequently, we think that two points must be stressed: 1) the character of the granulation on both chelipeds and walking legs of P. alaskensis is subject to great variations, ranging from very small blunt granules to spiniform granules (the latter term means large granules with pointed tips, or short conical spines); 2) it must be taken into account that, when describing P. ochotensis, Brandt compared his species with the European P. bernhardus, whose appendages are covered with very flat, blunt granules; when the appendages of P. alaskensis are compared with those of P. bernhardus, it undoubtedly appears that they are more spinulose, a fact which induced Brandt to separate not only his variety spinimana but also the variety granulato-denticulata, taking into account namely this variability. Both varieties, however, can be included in P. alaskensis. Bernhardus armatus described by Dana is indeed related to P. alaskensis, but differs markedly in that its chelipeds are covered with long, slender spines and hairs; this species was wrongly identified with P. ochotensis, probably owing to the fact that Brandt's

diagnosis was far too short and vague, as well as to the fact that its principal specific character (the spinulation of the chelae) corresponds also to Brandt's variety (spinimana). Thus, P. alaskensis (Benedict) whould be considered as P. ochotensis Brandt, while the species which Brandt himself considered as being P. ochotensis ought to be called P. armatus (Dana). We became even more convinced of our conclusion after studying specimens of P. ochotensis (No 52, 666) and P. alaskensis (No 16, 368) from the collections of the U. S. National Museum. Listed in the table below are the most striking differences which we found after comparing these specimens with each other and also with the specimens of the Zoological Institute of the Academy of Sciences of the USSR.

P. ochotensis Brandt	P. armatus (Dana)
1. Surface of carpus and propodus of chelipeds covered with granules or spiniform granules; tufts of hairs at bases of granules are lacking or hardly visible.	1. Surface of carpus and propodus of chelipeds densely covered with long, slender, pointed spines and tufts of hairs which rise from base of spines and reach their tips or even exceed them.
2. Right chela broad, external edge arcuated. Dactyli of chela do not cross when closed, distal end of chela thus appearing more blunt. Internal edge of propodus clearly cylindrical and thickened.	2. Right chela relatively narrow, evenly tapering toward distal end, which seems very pointed owing to the fact that tips cross when dactyli are closed. Internal edge of propodus without visible cylindrical thickening.
3. Internal edge of propodus of left chela has marked cylindrical thickening.	3. Internal edge of propodus of left chela has only incipient cylindrical thickening.
4. Superoexternal surface of propodal joints of both first walking legs covered with blunt or spiniform granules; short spines form a single row on superior edge; hairs, when present, are very short.	4. Superoexternal surface of propodal joints of both first walking legs covered with spines disposed in three longitudinal rows, the longest spines forming a row on superior edge of joint; tufts of hairs rise from base of spines; hairs as long as spines.
5. Superior edge of dactyli of walking legs bears a longitudinal row of blunt or spiniform granules.	5. Superior edge of dactyli of walking legs bears a longitudinal row of pointed spines which gradually become smaller distally.

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The lack of P. armatus Dana in our fairly extensive material is, in our opinion, because this species is a relatively limited local form of the western shores of North America. Therefore, all the reports of P. ochotensis from Kamchatka, the Sea of Okhotsk and the Sea of Japan should be considered as referring in fact to P. ochotensis, and not to P. armatus.

16a. Pagurus ochotensis aleuticus (Benedict) (Plate 2, Figure 3)

Eupagurus aleuticus Benedict, 1892: 3. – Pagurus aleuticus Holmes, 1900: 136; Benedict, 1901: 460, text-Figure, Rathbun, 1904: 157; Stevens 1925: 278, Figure 2.

All three outgrowths of the front are pointed and more prominent than in P. ochotensis. The eyestalks are more slender and slightly longer. The eyestalks are longer and blunter; the subterminal spines are not visible from above. The scaphocerites are broader at the bases than in the typical form. The chelipeds are strong. The carpal joints are provided with numerous short spines or spiniform granules. The dactyli of both chelae have a smooth oblique surface on the superior side, which is either flat or slightly concave; on the left chela this surface is neither hairy nor granulated, while on the right chela it is bordered by short, spiniform granules. The granules on both chelae are often bifid, the spiniform granules on the edges always stronger and simple. The dactyli of the right chela have corneous tips in adult as well as in young specimens (in typical forms such tips are found only in young specimens). The dactyli of the walking legs are
203 very broad and thin, their superior edge completely occupied by a longitudinal furrow, which is rather deep at the base of the dactylus and becomes shallower toward the tip (Figure 69). The coloration of the chelipeds and of the walking legs is light yellow ocher, and reddish on the superior side; the chelae and the dactyli are yellow.

Dimensions

Length of anterior part of carapace	10.0 mm
Width of anterior part of carapace	10.5 mm
Length of eyestalks	6.5 mm
Length of scaphocerites	6.0 mm
Length of merus of right cheliped	13.0 mm
Length of carpus of right cheliped	12.0 mm
Width of carpus of right cheliped	10.0 mm
Length of chela of right cheliped	19.0 mm
Width of chela of right cheliped	11.0 mm
Length of merus of left cheliped	11.0 mm
Length of carpus of left cheliped	10.0 mm
Width of carpus of left cheliped	6.5 mm
Length of chela of left cheliped	12.5 mm
Width of chela of left cheliped	7.0 mm
Length of right first walking leg	51.5 mm

Like P. armatus, this species is a local form belonging to the North American coast; as to its morphological features, P. aleuticus resembles P. ochotensis to a such degree that its subspecific status is certain.

Distribution. Bering Sea (in the vicinity of the Pribilof Islands), on the western shores of North America, southward to Oregon; from 14 to 435 m (Rathbun).

†17. Pagurus rathbuni (Benedict) (Plate 3, Figure 3)

Eupagurus rathbuni Benedict, 1892. – Pagurus rathbuni Holmes, 1900: 140; Rathbun, 1904: 158, Pl. 4, Figure 2. – Eupagurus (Trigonocheirus) polaris Sivertsen, 1932: 8, Pl. 2, Figure 3.

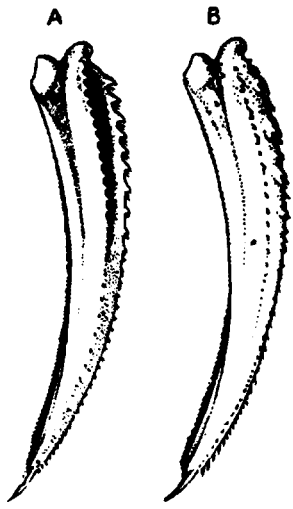

Figure 69. Dactyli of right first walking legs (posterodorsal view). A – Pagurus ochotensis subsp. aleuticus (Benedict); B – Pagurus ochotensis Brandt.

The length of the anterior part of the carapace is almost the same as its width. The median outgrowth of the front is pointed and triangular, considerably exceeding the lateral outgrowths, which are broad and triangular and bear fairly strong submarginal spines. The ocular scales are conical, each having a rounded apex and strong subterminal spines. The eyestalks are stout, slightly tapering in their proximal third, and widening at the corneas. The scaphocerites extend beyond the end of the eyes and have pubescent internal edges. The internal edge of the external outgrowth of the basal joint of the antennal stalk bears from three to five blunt spines, the apical spine included. The dorsal crest of the merus of the right cheliped is covered with sparse granules and transverse wrinkes; these bear hairs

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directed forward. The carpus has a quadrangular cross section, and is the same length as the merus; its protuberant superior surface is covered with granules, with short hairs growing out of their bases; at the inner distal angle of the superior surface is a hollow covered with a tuft of clearly visible, delicate hairs; in young specimens this tuft may be lacking, but the depression is always present; the internal and inferior surfaces are pubescent. The width of the chela is the same as that of the carpus, but its length is greater. Its superior surface is protuberant, and evenly covered with granules and short hairs, which are situated in front of the spines and are hardly visible to the naked eye. The external edge of the movable dactylus has a double row of granules. The prehensile edges of the dactyli bear white tubercles with tufts of hairs above them. The inferior surface of the propodus bears scattered, low, broad granules and tufts of hairs. The dactyli have corneous tips. The left cheliped extends slightly beyond the base of the movable dactylus of the right chela, but is shorter in large specimens. The merus is flattened, with hairy wrinkles on its superior crest. The carpus is somewhat shorter than the merus, and broadens distally; its superior surface is narrow and flat, and bears rows of marginal spines; the lateral and inferior surfaces are granulated and hairy. The chelae are one and one third times as long as the carpus; the external surface has a narrow triangular form and–like the surface of the right chela–is covered with granules and short hairs; the median crest is not very sharp; the

internal surface has a naked surface with a few granules, and on its external side two irregular rows of spines extend parallel with the internal edge; tufts of hairs grow out of the bases of the granules; the dactyli are flattened, almost twice as long as the propodus, and markedly curved downward at their distal ends; in large specimens a large gape is left open when the dactyli are closed; this gape is clearly visible, particularly from the inferior side. The walking legs of the right side extend slightly beyond the right cheliped. The meral joints of the first pair bear spinulose granules on their inferior edge, while the carpal joints have similar granules on their superior edges. The dactyli are curved and twisted, and are longer than the propodi; the internal surfaces of the superior and inferior edges are hairy, the external surfaces protuberant and naked, with a slightly marked longitudinal furrow; the internal surface is flatter and bears a row of hairs near the superior edge. Coloration of the specimens preserved in alcohol: the distal ends of the joints of all appendages are light red; the tips of the dactyli on the left chela are reddish or brown, frequently blackish brown, as though carbonized.

Dimensions

Length of anterior part of carapace	15.0 mm
Width of anterior part of carapace	16.0 mm
Length of merus of right cheliped	23.0 mm
Length of carpus of right cheliped	22.5 mm
205 Width of carpus of right cheliped	15.0 mm
Length of chela of right cheliped	30.0 mm
Width of chela of right cheliped	14.5 mm
Length of merus of left cheliped	17.0 mm
Length of carpus of left cheliped	15.0 mm
Length of chela of left cheliped	24.0 mm
Length of movable dactylus of left chela	15.5 mm
Length of right first walking leg	84.0 mm

Distribution. Sea of Japan (only on the Soviet shores; not found in Japan); Sea of Okhotsk; eastern shores of Kamchatka; Bering Sea; Chuckchee Sea, northward to the parallel of Wrangel Island, westward to the mouth of the Kolyma River (16 July 1912, 10 m, mud; one specimen).

Ecology. This species is found at depths ranging from 10 to 210 m, chiefly on muddy bottoms.

18. Pagurus granosimanus (Stimpson) (Plate 2, Figure 5)

Eupagurus granosimanus Stimpson, 1859: 90; Smith, 1878-79: 211. Pagurus granosimanus Holmes, 1900: 146; Rathbun, 1904: 10, Pl. 5, Figure 8; Schmitt, 1921: 141, Figure 91; Stevens, 1925: 282, Figure 5.

The length of the anterior part of the carapace considerably exceeds its width. The median outgrowth of the front is short, with a broad triangular

shape; the lateral outgrowths are rounded and without submarginal spines. The eyestalks are fairly strong and moderately long. The ocular scales bear very strong subterminal spines. The external outgrowth of the basal joint of the antennal stalk bears three apical spines, and has a spinulose internal edge; the internal outgrowth bears a strong spine. The scaphocerites are curved, much shorter than the eyes, and have hairy internal edges. The merus of the right cheliped is smooth, with a denticulated anterior edge; the inferior surface bears two tuberculiform granules. The surface of the carpus is covered with conical spines; their tips are directed forward. The chela has a fairly regular oval form and its length somewhat exceeds that of the carpus; the surface of the propodus and of the dactyli is covered with strong, blunt spiniform granules; the external edge bears pointed spiniform granules; the dactyli have pointed corneous tips. The left cheliped extends slightly beyond the base of the movable dactylus of the right chela. The superior surface of the carpus and of the chela is covered with granules similar to those found on the right cheliped. The chela does not bear an evident crest on its superior surface; the external surface does not form a marked crest with the inferior surface; the granules extend onto the inferior surface, but become sparser in the middle. The walking legs of the right side extend slightly beyond the right cheliped. The carpal and propodal joints of both pairs of legs are spinulose on the superior edge. The dactyli are almost straight, with long corneous claws. The walking legs
206 and the chelipeds are slightly pubescent. The coloration (according to Stevens) varies from olive yellow to olive green. The granules of the chelipeds are porcelain blue, and become light blue near the ends of the dactyli, particularly on the inferior side of the chela. The walking legs have small blue spots which bear small tufts of hairs. The antennae are apricot-orange and become olive green on the basal joints. The young specimens are lighter in color, with very few blue tones; the granules and spots are almost white; the walking legs have orange tips. The specimens preserved in alcohol have a dark-red coloration, with white tubercles on the chelae and darker red spines on the carpus and the merus of the chelipeds. The walking legs are red, with small white spots; the dactyli have a broad white median stripe. The tubercles on the inferior side of the merus of the right cheliped are white.

Dimensions

Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	7.0 mm
Length of eyestalks	4.0 mm
Length of scaphocerites	2.5 mm
Length of merus of right cheliped	6.5 mm
Length of carpus of right cheliped	7.0 mm
Width of carpus of right cheliped	4.0 mm
Length of chela of right cheliped	8.0 mm
Width of chela of right cheliped	4.5 mm
Length of merus of left cheliped	5.0 mm
Length of carpus of left cheliped	5.5 mm
Length of chela of left cheliped	7.0 mm
Width of chela of left cheliped	3.5 mm
Length of right first walking leg	23.0 mm

This species is related to P. beringanus, from which it differs by the following features: the granules on the chelipeds are more pointed; the external edge of the right chela is less arcuated; the external edge of the left chela does not form a sharp crest with the inferior surface, while in P. beringanus the transition between the two surfaces is fairly sharp; the subterminal spines of the ocular scales are longer and more slender; the walking legs are less hairy.

Distribution. From Unalaska to Ensenada (southern California). From the littoral to a depth of 27 m (Rathbun).

20. Pagurus dalli (Benedict) (Plate 1, Figure 4)

Eupagurus dalli Benedict, 1892: 9. – Pagurus dalli Holmes, 1900: 139; Rathbun, 1904: 158, Pl. 4. Figure 1; Stevens, 1925: 287, f. 8,9.

The length of the anterior part of the carapace very slightly exceeds its width. The median outgrowth of the front is pointed and triangular, and projects much more than the broad curved lateral outgrowths, which bear strong subterminal spines. The ocular scales are oval, each with a slightly
207 pointed tip and very strong subterminal spines. The eyestalks are cylindrical and fairly long. The external outgrowth of the basal joint of the antennal stalk has a pointed apical spine and two additional subterminal spines on its internal edge; the internal outgrowth bears a pointed spine. The curved scaphocerites bear tufts of short hairs on the internal edge and extend slightly beyond the eyes. The merus of the right cheliped bears strong spines on the anterior edge and two or three pointed spines on the superior crest near its distal end. The superior surface of the carpus has a fairly dense cover of pointed spines and short hairs which grow out of the bases of the spines. The chela is twice as long as it is wide; it has a narrow oval form, the contour of both edges being almost the same. Like the surface of the carpus the superior surface of the propodus is covered with pointed spines and fairly dense tufts of short hairs; the movable dactylus is long, and bears two longitudinal rows of spines on the external part of the superior surface; it has a smooth internal surface. The proximal halves of the prehensile edges of both dactyli bear irregular white tubercles; the distal half of the prehensile edge of the movable dactylus bears a comb of dense corneous spinules; the distal half of the prehensile edge of the immovable dactylus bears from three to five conical denticles, the spaces between them bearing corneous spinules. The tips of the dactyli are curved like hooks, and cross when closed; they are corneous. The left cheliped extends to the base of the movable dactylus of the right chela. The carpus is narrow, with two longitudinal rows of spines on its superior surface. The chela is relatively narrow, not widening at the base, with an oblique, triangular external surface; the median crest bears very pointed long spines, while the spines of the external surface are smaller. The walking legs of the right side exceed the right cheliped by almost one third of the length of their dactyli. The dactyli are slender, slightly curved at their distal ends, and not twisted. The coloration is similar to that of P. pubescens, but there

is a pronounced white stripe at the distal end of the meral joints of the chelipeds. In specimens preserved in formalin, the walking legs are yellowish red, with a light stripe on the middle of the joints, and a red one near the bases.

Dimensions

Length of anterior part of carapace	7.0 mm
Width of anterior part of carapace	6.5 mm
Length of eyestalks	5.0 mm
Length of scaphocerites	4.0 mm
Length of merus of right cheliped	7.5 mm
Length of carpus of right cheliped	8.0 mm
Width of carpus of right cheliped	5.5 mm
Length of chela of right cheliped	12.0 mm
Width of chela of right cheliped	5.5 mm
Length of merus of left cheliped	7.0 mm
Length of carpus of left cheliped	7.0 mm
Width of carpus of left cheliped	2.5 mm
Length of chela of left cheliped	8.5 mm
Width of chela of left cheliped	3.5 mm
Length of right first walking leg	32.0 mm

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Pagurus dalli is closely related to P. pubescens, but differs by its very prominent median frontal outgrowth, its more slender eyestalks, the more slender, pointed and longer spines of the chelipeds, a narrower right chela, which has a regular oval form; it also differs by the narrower base of the left chela and the more slender and not twisted dactyli at the distal end of the meral joints of the chelipeds [sic].

Distribution. Bering Sea (parallel of Nunivak Island) southward to Oregon. From the littoral to a depth of 172 m (Rathbun).

†20. Pagurus pubescens Kröyer (Plate 4, Figure 1).

Pagurus pubescens Kröyer, 1838: 314; 1838: 251; Brandt, 1851: 111; Goës, 1863: 166; Yarzhinskii, 1870: 317; Hoek, 1882: 6; Richters, 1833: 406. – Pagurus thompsoni Bell, 1853: 372. – Eupagurus trigonocheirus Stimspon, 1858: 249; 1907: 221, Pl. 26, Figure 2; Murdoch, 1885: 138, Pl. 1, Figures 1, 1a, 1b; Benedict, 1892; Balss, 1913: 63 (part.); Terao, 1913: 373; Yokoya, 1933: 83. – Eupagurus pubescens Miers, 1877: 32; Smith, 1880: 47; Sars, 1882: 42; 1886; 4; Stuxberg, 1886: 51; Pfeffer, 1890: 22; Ortmann, 1892: 305; A. Milne-Edwards and Bouvier, 1894: 74; Birulya, 1897: 437; 1899: 36, 431; Birula (Birulya), 1906: 10; Doflein, 1900: 341; Ohlin, 1901: 19; Stimpson, 1907: 222; Hansen, 1908: 27; Balss, 1912: 106; 1926: 32; Deryugin, 1915: 478; 1928: 289; Dons, 1934: 40, 113. – Eupagurus kröyeri Stimspon, 1859: 89; Smith, 1880: 48; Miers, 1881: 340. – Eupagurus pubescens var. kröyeri Henderson, 1888: 65. – Eupagurus brandti Benedict, 1892: 9. – Pagurus brandti Holmes, 1900: 139; Rathbun, 1904: 157, Pl. 4; Figure 4; 1919: 8; Stevens, 1925: 285, Figure 7. – Pagurus trigonocheirus Holmes, 1900: 138; Rathbun, 1904: 157; 1919: 7. – Pagurus kroyeri Rathbun, 1919: 14.

The length of the anterior part of the carapace exceeds its width. The three outgrowths of the front are equal in length; the median outgrowth is triangular and pointed, with a tuft of long hairs; the lateral outgrowths are blunter, with small submarginal spines. The eyestalks are fairly strong, with a very marked median constriction. The ocular scales have pointed tips, a flat superior surface, and strong subterminal spines. The scaphocerites have a thickly pubescent internal edge and extend beyond the eyes; in small specimens, however, they reach only the end of them or they may be even shorter. The chelipeds are strong, and their degree of pubescence is highly variable; the most hairy are the carpal joints, while the chelae are naked. The superior crest of the merus of the right cheliped has transverse wrinkles and hairs on its distal part. The protuberant surface of the carpus is covered with spines, with hairs growing out of their bases; the spines of the internal edge are the strongest; the inferior surface is protuberant and partly granulated and hairy. The superior surface of the chela is covered with conical spines, which bear tufts of hairs in front of their bases; the
209 hairs are shorter than the spines and are visible only with a magnifying glass; to the naked eye the chela appears almost naked. The spines of the external edge are the longest. The inferior surface bears scattered granules and tufts of hairs. The dactyli have small corneous tips, which may disappear in larger specimens. The dimensions of all the joints are subject to wide variations. In small specimens the left cheliped extends slightly beyond the base of the movable dactylus of the right cheliped, while in large specimens it only reaches it. The carpus bears two longitudinal rows of spines on the edges of its superior surface; its external surface bears spines and setae. The chela has an obliquely triangular external surface, which bears a fairly dense granulation. The oblique median crest is very sharp, and bears spines. The sharp external edge of the propodus widens at its base to varying degrees according to the sex; the degree to which it widens may even vary within the same sex, however. The movable dactylus is smooth, with tufts of dark hairs. The walking legs of the right side extend beyond the right chelipeds by half the length of their dactyli; in large specimens they are slightly shorter. The meral joints of the first pair are spinose on the inferior side, while the carpal joints of both pairs are spinose on the superior side. All the joints are hairy on their superior edges. The dactyli are curved and twisted, with strong corneous claws. The specimens preserved in alcohol are pale yellow. The distal ends of the meral joints of the chelipeds (in small specimens, also the carpal joints) are light red. The distal and proximal ends of all joints of the walking legs are red.

Dimensions

Length of anterior part of carapace	17.0 mm
Width of anterior part of carapace	16.0 mm
Length of eyestalks	8.5 mm
Length of merus of right cheliped	23.0 mm
Length of carpus of right cheliped	24.0 mm
Width of carpus of right cheliped	17.0 mm
Length of chela of right cheliped	30.0 mm
Width of chela of right cheliped	14.5 mm
Length of merus of left cheliped	17.0 mm
Length of carpus of left cheliped	18.0 mm

Width of carpus of left cheliped.	6.5 mm
Length of chela of left cheliped.	22.0 mm
Width of chela of left cheliped	10.5 mm
Length of right first walking leg	82.0 mm

The specimens of this species may reach fairly large proportions.

Distribution. White Sea, Barents Sea up to the parallel of Spitsbergen; North Sea, Skagerrak and Kattegat included; shores of Scotland and northern England (southward to Durham), on the southwestern end of the Irish coast; shores of Iceland; western shores of Greenland (relatively rare on the eastern shores). Along the eastern shores of North America from Baffin Bay (67° 57'N 55° 30'W) to 38° 08'N. Chuckchee Sea (east of Point Barrow,
210 the westernmost point reported is 70° 07'N 177° 17'E). Bering Sea; along the western shores of North America as far as Oregon; Aleutian Islands; eastern shores of Kamchatka; Sea of Okhotsk; Sea of Japan, along the Soviet shores reported southward to Furuhelm Island, along the Japanese shores down to Nagasaki. G. P. Gorbunov described to us how he captured several specimens of P. pubescens in the Kara Sea (until now this species was reported only from the eastern part of Yugorskii Shar and Matochkin Shar); it was also found on the western shore of the Yamal Peninsula, at two points — 71° 54'N, 67° 45'E and 69° 52'N, 65° 14'E. These findings, however, are but sporadic ones and we cannot, therefore, consider the Kara Sea as belonging to the range of this species; this is also confirmed by G. P. Gorbunov. Consequently, P. pubescens is a typically amphiboreal species.

Ecology. This species is found at depths down to 900 m. In the White Sea it is not encountered below 100 m, in Kola Bay it is found at a maximum depth of 330 m, and in the Barents Sea at 360 m. P. pubescens is one of the more common hermit crabs of the Soviet Far Eastern seas. It is usually encountered at depths ranging from 20 to 200 m, on various bottoms, but chiefly on muddy and sandy ones.

The specific status of P. trigonocheirus (Stmp.) is an old problem in the carcinological literature. Some authors (Brandt, Richters, Stimpson) reported P. pubescens from the Pacific basin. The first author to suggest—though purely theoretically—that P. trigonocheirus (Stmp.) may be a variety of the Atlantic species P. pubescens Kr. was Doflein in 1900. Hansen (1908) categorically expressed his opinion on the identification of both species. The minute differences which are, as a rule, cited as distinguishing the two species (the ratio between length and width of the left chela at its base, degree of pubescence, etc) completely fit both the individual variability of P. pubescens and its sexual dimorphism, a fact which was first noted by A. A. Birulya (1897: 439). The differences found by Balss (1913) between P. trigonocheirus (Stmp.) and P. pubescens Kr. are a result of the erroneous identification made by this author between P. trigonocheirus (Stmp.) and P. capillatus (Benedict); all these differences listed consequently refer to P. pubescens and P. capillatus, which are indeed easy to differentiate. As we had at our disposal abundant material from the European seas (White Sea and Bering Sea), as well as from the Far Eastern seas, we reached the conclusion—based on a detailed study—that P. pubescens and P. trigonocheirus are one species. The only specimen of P. pubescens from Greenland (No 1086) which we found in the collections is identical with the European

and Pacific specimens, and therefore Doflein's proposal to separate one particular variety (var. kröyeri) of the eastern shores of North America should be rejected. As to P. brandti (Benedict), after comparing a specimen of this species–which we received from the U. S. National Museum (No 19, 097)–we subscribed to the opinion of Hansen and Balss on the identity of this species with P. pubescens.

211 †21. Pagurus brachiomastus (Thallwitz) (Plate 2, Figure 6)

Eupagurus brachiomastus, 1891: 35; Ortmann, 1892: 312; Terao, 1913: 365.

The length of the anterior part of the carapace exceeds its width. The median frontal outgrowth is broad, triangular and blunt, and bears a tuft of long hairs. The lateral outgrowths are hardly visible. The eyestalks are slender, long, and cylindrical, and have small corneas. The ocular scales are suboval, with very strong subterminal spines. The scaphocerites do not reach the end of the eyes and have hairy internal edges. The chelipeds are pubescent. The merus of the right leg has a triangular cross section; it has spines on the anterior edge and smooth lateral surfaces; the inferior surface bears two strong blunt spines. The superior surface of the carpus is covered with spines and long hairs. The superior surface of the chela is covered with thick, long, soft hairs; these hide the fairly long spines which are evenly distributed over the entire surface of the propodus; stronger spines form a row along the external edge, and clearly separate the superior surface from the inferior one; the inferior surface is convex and almost smooth; on the internal edge the transition between the superior and the inferior surface is gradual, the spines becoming gradually smaller. The dactyli have corneous tips. The left cheliped reaches the middle of the propodus of the right chela. The merus is flattened, with smooth, naked lateral surfaces; there is a small blunt spine on the inferior surface toward the end of the ischium. The superior surface of the carpus bears two longitudinal rows of spines with a smooth interval between them; the lateral surfaces are hairy. The superior surface of the chela is covered with spines and long hairs; the inferior surface bears scattered tufts of hairs. The walking legs of the right side extend slightly beyond the right cheliped. All the joints are hairy on their superior edges. The dactyli are slightly curved, with strong corneous claws. The coloration is yellowish orange; the hairs are pale yellow, almost colorless; the dactyli of the chelipeds are often crimson-tipped.

Dimensions

Length of anterior part of carapace . . .	7.0 mm
Width of anterior part of carapace. . . .	6.5 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	9.0 mm
Length of carpus of right cheliped. . . .	9.0 mm
Width of carpus of right cheliped	6.5 mm
Length of chela of right cheliped	10.0 mm

Width of chela of right cheliped	6.5 mm
Length of merus of left cheliped	8.0 mm
Length of carpus of left cheliped	7.0 mm
Width of carpus of left cheliped	3.0 mm
Length of chela of left cheliped	8.0 mm
Width of chela of left cheliped	4.0 mm
Length of right first walking leg	28.0 mm

212 This species differs from P. lanuginosus de Haan by the presence of two blunt spines on the inferior surface of the merus of the right cheliped, by the narrow immovable dactylus of the right cheliped, by the corneous tips on the dactyli of the right chela, by the greater degree of pubescence and the absence of red spots on the joints of the appendages.

Distribution. Japan or China (Thallwitz), Sea of Japan, on the Soviet shores to the parallel of Furuhelm Island and northward to De Kastri Gulf; La Perouse Strait; Aniwa Bay.

Ecology. This species is found in the lttoral, and descends to depths of 55 to 160 m, chiefly on sandy and rocky bottoms; fairly frequent among fields of Corallina, Desmarestia, Zostera, etc.

†22. Pagurus lanuginosus de Haan (Plate 5, Figure 2)

Pagurus lanuginosus de Haan, 1850: 270, Pl. 49, Figure 5. – Eupagurus lanuginosus Ortmann, 1892: 312; Doflein, 1902: 647; Balss, 1913: 56, Figure 33; Terao, 1913: 370; Yokoya, 1933: 87.

The length of the anterior part of the carapace considerably exceeds its width. The median outgrowth of the front is pointed and triangular, and reaches half the length of the ocular scales. The lateral outgrowths barely show. The eyestalks are long and slender. The scaphocerites do not reach the end of the eyes; their internal edges are covered with long, dense hairs. The chelipeds are hairy. The merus of the right cheliped has smooth lateral sides; the inferior surface is almost naked. The superior surface of the carpus bears a row of strong spines on its internal edge and another row of smaller spines near the middle; the entire surface, with the exception of the space between these two rows, is covered with long, soft hairs; the internal surface is less hairy, the inferior and external surfaces almost naked. The chela is broader than the carpus; its internal edge is almost straight, while its external edge is broad and evenly rounded; the immovable dactylus is twice as long as the movable one; the whole surface is covered with dense tufts of long, soft hairs; the internal and external edges bear spines which clearly separate the almost flat superior surface of the chela from the very protuberant and completely naked inferior surface. The tips of the dactyli are corneous. The left cheliped reaches the base of the movable dactylus of the right chela. The merus is flattened and hairy on its inferior surface. The carpus bears two rows of spines on its superior surface, and there are also tufts of long hairs, particularly on its internal surface. The surface of the chela is protuberant and covered with spines and

setae like the right chela; the inferior surface is almost smooth, with scattered tufts of hairs; the tips of the dactyli are corneous. The walking legs of the right side extend beyond the right cheliped; all the joints of the walking legs are hairy, particularly on the superior edges. The carpal joints of the first pair are spinose on their superior side. The dactyli are short,
213 straight and not twisted, with strong claws curved downward. Specimens preserved in alochol have a yellowish-orange coloration, with red spots on the joints of all the appendages (particularly on the external surfaces of the walking legs); the hairs are pale yellow, almost white; the claws of the walking legs are dark brown.

Dimensions

Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	6.0 mm
Length of eyestalks	4.0 mm
Length of merus of right cheliped	5.4 mm
Length of carpus of right cheliped	5.0 mm
Width of carpus of right cheliped	4.0 mm
Length of chela of right cheliped	8.0 mm
Width of chela of right cheliped	6.0 mm
Length of merus of left cheliped	4.5 mm
Length of carpus of left cheliped	5.0 mm
Width of carpus of left cheliped	2.5 mm
Length of chela of left cheliped	5.0 mm
Width of chela of left cheliped	2.5 mm
Length of right first walking leg	20.0 mm

Distribution. Southern Japan – Nagasaki, Sagami Sea, Tokyo Bay; Tsugaru Strait. At depths ranging from 110 to 229 m. In the Soviet waters of the Sea of Japan this species is rare (in the collections of the Hydrobiological Institute there are 18 specimens from the region of Peter the Great Bay).

23. Pagurus armatus (Dana) (Plate 2, Figure 4)

Bernhardus armatus Dana, 1851: 270; 1852: 442, Pl. 27, Figure 2. – Eupagurus armatus Stimpson, 1857: 484; Bate, 1866: 287; Whiteaves, 1870: 471. – Eupagurus ochotensis Stimpson, 1858: 248. – Pagurus ochotensis Holmes, 1900: 137; Benedict, 1901: 463, text-Figure; Rathbun, 1904: 157; Schmitt, 1921: 130, Figure 84; Stevens, 1925: 279, Figure 3. – Non Pagurus (Eupagurus) bernhardus var. spinimana seu subsp. ochotensis Brandt, 1851: 108.

The width of the anterior part of the carapace exceeds its length. The three frontal outgrowths are almost equally prominent. The eyestalks are short and stout. The ocular scales bear strong subterminal spines, which are visible in dorsal view. The scaphocerites are not as strong as in P. ochotensis; they have a triangular cross section, and are smooth, strongly flattened and extend considerably beyond the eyes; their internal edges are hairy and very uneven, but not spinose as in P. ochotensis and P. ochotensis subsp. aleuticus; the internal surface is not highly

iridescent. The external outgrowth of the basal joint of the antennal stalk is very prominent; the internal outgrowth is spinose. The chelipeds are short, spinulose and hairy. The merus of the right cheliped extends only slightly beyond the eyes. The lateral sides of the carpus are flat and granulated; the superior surface of the carpus and of the chela is covered with long slender spines and hairs; the hairs may be shorter than the spines, equal, or sometimes even longer. The chela is elongated and evenly rounded
214 on the superior side; the movable dactylus bears a row of spines on its external edge and another row near the middle; when closed, the tips of the dactyli cross. The left cheliped extends slightly beyond the base of the movable dactylus of the right chela. The surfaces of the carpus and of the chela are covered with hairs and spines, as on the right leg. The meral, carpal and propodal joints of the walking legs are spinulose on their superior sides. The dactyli are spinulose; they are less broad and less curved than in P. ochotensis; they have a furrow on both the external and internal surfaces, and are almost the same length as the two preceding joints together. The coloration varies from olive yellow to apricot-orange, with brownish spots; the color is generally the same as in P. ochotensis, but the iridescent shine is replaced to a great extent by a violet shade.

Dimensions

Length of anterior part of carapace	6.0 mm
Width of anterior part of carapace	7.0 mm
Length of eyestalks	3.5 mm
Length of scaphocerites	4.0 mm
Length of merus of right cheliped	7.0 mm
Length of carpus of right cheliped	6.0 mm
Width of carpus of right cheliped	4.5 mm
Length of chela of right cheliped	10.0 mm
Width of chela of right cheliped	6.0 mm
Length of right first walking leg	30.0 mm

Distribution. This form is a species endemic to the western shores of North America, and has a relatively narrow range: from Unalaska to San Diego (California), at depths from 10 to 146 m. Not found in the Sea of Okhotsk or the Sea of Japan.

† 24. Pagurus pectinatus (Stimpson) (Plate 4, Figure 3)

Eupagurus pectinatus Stimpson 1858: 249; 1907: 220; Balss, 1913: 60, text-Figure 35, Pl. 1, Figure 8; Terao, 1913: 371; Yokoya, 1933: 83. – Eupagurus seriespinosus Thallwitz, 1891: 34, Terao, 1913: 372.

The length of the anterior part of the carapace exceeds its width. The median outgrowth of the front is short and pointed, and is hidden by a tuft of long hairs. The lateral outgrowths are rounded, and bear pointed submarginal spines directed obliquely outward. The eyestalks are long, slender and cylindrical, with broadened bases. The ocular scales are suboval and small, with strong subterminal spines. The scaphocerites are curved,

with hairy internal edges, and do not reach the end of the eyes. The tip of the external outgrowth of the basal joint of the antennal stalk bears several spines. The chelipeds are spinose and hairy. The merus of the right cheliped has rounded crests, smooth lateral sides and a hairy inferior surface; the superodistal edge bears from two to five spines. The superior surface of the carpus is smooth and covered with tufts of long hairs; the internal edge bears a row of strong spines directed forward; at the inner distal angle is a group of spines; the external surface is smooth and naked; the internal and inferior surfaces are slightly pubescent. The superior surface of the propodus is transversed by eight irregular longitudinal rows of long spines, including the marginal row; the spines of the external edge are the strongest; they are oriented obliquely outward and upward, and clearly separate the superior surface of the propodus from the protuberant, smooth and slightly hairy inferior surface. Long tufts of hairs arise from the base of the spines on the superior surface. The surface of the dactyli become concave in a fairly abrupt manner, owing to the relatively raised spines of the external edges. The prehensile edges bear strong white tubercles; the tips are corneous. The merus of the left cheliped is flattened and smooth, with one or two spines on the superodistal edge. The superior surface of the carpus bears two rows of spines on its edges, the space between these rows being smooth; the inferior surface is hairy. The superior surface of the chela bears a moderately high median crest which is formed by an irregular row of round spines; smaller spines, disposed in an irregular double row, border the external edge of the propodus. The external surface of the propodus is spinose, and bears tufts of long hairs; the internal surface is less spinose and hairy; the inferior surface is smooth, with scattered tufts of hairs. A fairly broad basal gape is left open when the dactyli are closed. The walking legs of the right side extend beyond the right cheliped. The meral joints are markedly flattened and slightly hairy on their edges. The carpal joints of the first pair are spinose on the superior edges; the propodal joints are hairy. The dactyli bear thick hairs on their superior edges; they are straight and have strong corneous claws. The specimens preserved in alcohol are yellowish orange; particularly striking is the protuberant bright-orange inferior surface of the right chela. The claws of the walking legs are dark brown.

Dimensions

Length of anterior part of carapace	14.5 mm
Width of anterior part of carapace	13.0 mm
Length of eyestalks	6.5 mm
Length of merus of right cheliped	13.0 mm
Length of carpus of right cheliped	13.0 mm
Width of carpus of right cheliped	9.0 mm
Length of chela of right cheliped	18.5 mm
Width of chela of right cheliped	10.5 mm
Length of merus of left cheliped	12.5 mm
Length of carpus of left cheliped	10.5 mm
Width of carpus of left cheliped	5.0 mm
Length of chela of left cheliped	14.0 mm
Width of chela of left cheliped	7.0 mm
Length of right first walking leg	50.0 mm

This species differs from P. capillatus by the following characters: shorter scaphocerites; the superior surface of the carpus of the right cheli-
216 ped, which bears no spines, with the exception of the row on the internal edge; the long hairs and spines on the propodus of the right chela, particularly on the external edge (here the spines are disposed in more or less regular longitudinal rows); the very protuberant and almost naked inferior surface of the right chela, which has an orange coloration; the greater width of the right chela and the marked concavity of its dactyli; the straight (not curved) dactyli of the walking legs.

Distribution. Sea of Japan; from Tsushima Island northward to De Kastri Gulf; Tsugaru Strait (Aomori, Hakodate), La Perouse Strait; Aniwa Bay.

Ecology. Pagurus pectinatus is found at depths ranging from 5 to 220 m, in Soviet waters, usually between 10 and 60 m, chiefly on hard bottoms; quite frequently found in sponges (Suberites domuncula).

25. Pagurus obtusifrons (Ortmann) (Figure 20)

Eupagurus obtusifrons Ortmann, 1892: 313, Pl. 21, Figure 18; Terao, 1913: 371; Yokoya, 1933: 85.

The median outgrowth of the frontal edge is blunt, and almost as long as the lateral outgrowths, which bear slender submarginal spines. The eyestalks are fairly stout with slightly swollen corneas; they are shorter than the antennal stalk, but almost as long as the scaphocerites. The carpus and the propodus of the right cheliped are covered with long hairs and spines. The spines on the propodus are disposed in eight or nine longitudinal rows, which become indistinct near the external edge. The external edge of the propodus is blunt, without strong spines. The superior

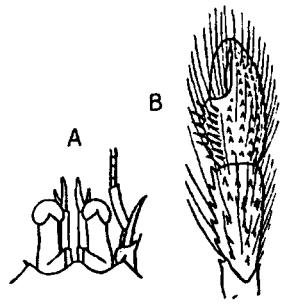

Figure 70. Pagurus obtusifrons (Ortmann)
A – frontal edge; B – right cheliped
(From Ortmann, 1892).

surface of the propodus is protuberant. The left chela is hairy and spinose. The first two pairs of walking legs are hairy and have fairly straight dactyli, which are longer than the penultimate joints (Ortmann).

Distribution. Southern Japan, northward not farther than Tsugaru Strait. At depths from 48 to 393 m.

26. Pagurus setosus (Benedict) (Figure 71)

Eupagurus setosus Benedict, 1892: 19. – Pagurus setosus Rathbun, 1904: 159, Pl. 5, Figure 1; Schmitt, 1921: 136, Figure 88; Stevens, 1925: 290, Figure 11. – Non Pagurus setosus Milne-Edwards, 1848: 64.

The length of the anterior part of the carapace slightly exceeds its width. The median outgrowth of the front is rounded and is slightly longer than the lateral outgrowths, which seem to be pointed owing to their submarginal
217 spines. The eyestalks are only slightly more than half the length of the anterior part of the carapace, and are much shorter and stouter than in P. kennerlyi. The ocular scales are very small and pointed, with strong subterminal spines. The scaphocerites exceed the eyes by one fourth

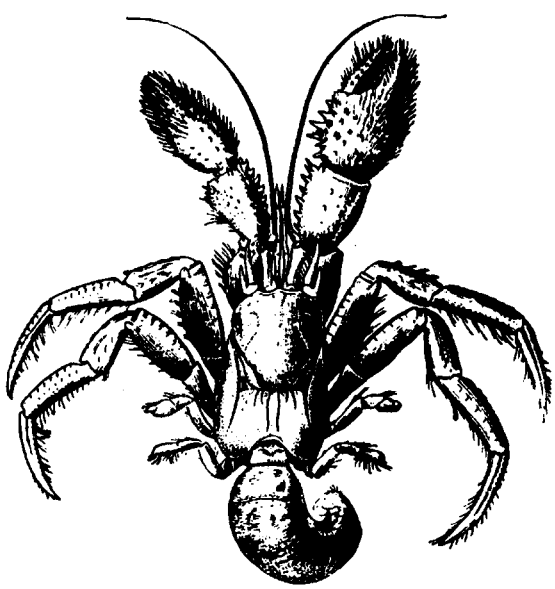

Figure 71. Pagurus setosus (Benedict) (From Schmitt, 1921)

of their length. Both chelae of the chelipeds are covered with dense, rigid setae. The right chela bears seven longitudinal rows of spines, including the marginal rows; the spines are shorter than in P. kennerlyi. The prehensile edges of the dactyli bear strong tubercles; the tips are corneous. The merus of the left cheliped is flattened. The carpus is stout and bears two carinae.

Usually the chelipeds greatly resemble those of P. kennerlyi in form, but their spines are shorter and the hairs longer. The walking legs are hairy, the superior edges without spines, with the exception of the carpal joints of the first pair. The dactyli are straight, exceeding by a third of their length the length of the anterior part of the carapace. The coloration is pinkish yellow, with irregular brown stripes, except on the chelae and the dactyli. The spines have apricot-orange tips. The hairs are brown at their bases and have yellow tips. The antennae are brown on the superior side and yellow on the inferior side. Young specimens are usually lighter in color. Specimens preserved in alcohol are pale yellow. The legs of specimens preserved in formalin have reddish-mauve stripes and mud-colored hairs.

Dimensions

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Length of anterior part of carapace	14.0 mm
Width of anterior part of carapace	13.0 mm
Length of right cheliped	48.0 mm
Length of chela of right cheliped	21.0 mm

As a rule, Pagurus capillatus greatly resembles P. setosus, apart from the slightly curved dactyli of the walking legs. The right chela is also proportionately shorter, and its more numerous spines are less strong and disposed in less distinct longitudinal rows. In specimens of equal dimensions, the spines of the right chela in P. capillatus are only half as long as those of P. setosus. The right chela of P. setosus is almost twice as long as broad and its dactyli are more concave than in P. capillatus. The right chela of P. capillatus is generally one and a half times as long as broad, and sometimes even one and three quarters. We found only a single specimen in which the chela was even longer–almost twice as long as broad; the peculiar armature of the right chela, however, left no room for doubt. In addition, the triangular external surface of the left chela of P. setosus is more rounded, and not as broad as in P. capillatus–its length more than four times its breadth. The triangular external surface of the left chela of P. capillatus is almost three times as long as broad (Schmitt).

Distribution. From Kodiak Island (Alaska) to the Santa Cruz Islands (California). At depths ranging from 9 to 480 m. Encountered much less frequently than P. kennerlyi.

27. Pagurus kennerlyi (Stimpson) (Figure 72)

Eupagurus kennerlyi Stimpson 1864: 153; Benedict, 1892: 19; Walker, 1892: 275. – Pagurus kennerlyi Holmes, 1900: 143; Rathbun, 1904: 159, Pl. 5, Figure 4; Stevens, 1925: 289, Figure 10.

The length of the anterior part of the carapace slightly exceeds its width. The median outgrowth of the front is short, triangular and sometimes hardly visible. The lateral outgrowths are small and rounded, with pointed submarginal spines. The eyestalks are of moderate length, straight and slender, not exceeding the antennal stalk; the corneas are somewhat broadened with an apical tuft of hairs. The scaphocerites are small, slender and hairy, and do not reach the end of the eyes. All the legs are highly pubescent. The chelipeds are very short and stout; both are much shorter than the walking legs and are densely covered with short spines. The merus of the right cheliped has an almost triangular cross section; the external surface is smooth, the inferior one spinose. The length of the carpus is almost equal to that of the propodus of the chela; the internal edge bears seven or eight slender, curved spines. The chela is slightly broader than the carpus and is traversed by seven fairly irregular longitudinal rows of pale slender spines (the marginal rows included); the hairs are not dense but are much longer
219 than the spines. The dactyli are shorter than the propodus; the movable dactylus bears two distinct rows of pointed tubercles. The prehensile edges bear strong tubercles; their tips are corneous. The left cheliped almost reaches the middle of the movable dactylus of the right chela. The merus is flattened and bears two rows of spines. The external, triangular surface of the chela is covered with strong spines. The walking legs are stout; the dactyli are straight. The coloration (according to Stevens) varies from pale pinkish yellow to a pinkish brown with brown spots. The spines of the chelae are white, the hairs brown. The walking legs are less brown than the chelipeds. At first sight, the antennae seem to be formed of brown and white rings, but when considered more carefully, it appears that approximately at the middle of the flagellum the rings are made up of four to six brown segments which alternate as follows: one white–two brown–another white; then the whole series is repeated, the rings becoming broader distally, as the number of the brown segments increases to eight to ten; the tip is made up of white segments. On the basal part there are less brown segments, many rings being incomplete. In younger specimens this alternation is less distinct.

Distribution. The Aleutians, southward to Washington, at depths from 3 to 177 m.

†28. Pagurus capillatus (Benedict) (Plate 3, Figure 2)

Eupagurus capillatus Benedict, 1892: 8. – Pagurus capillatus Holmes, 1900: 138; Rathbun, 1904: 157, Pl. 4, Figure 3; 1919: 7; Schmitt, 1921: 132, Figure 85. – Eupagurus trigonocheirus Balss, 1913: 63 (part).

The length of the anterior part of the carapace slightly exceeds its width. The median outgrowth of the front has a broad triangular form, with a tuft of soft, long hairs; the lateral outgrowths are rounded, with strong submarginal spines. The eyestalks are long and slender, with a slight median
220 constriction. The ocular scales are conical, with rounded tips, tufts of hairs on the superior surface, and strong subterminal spines. The

scaphocerites are curved and reach the end of the eyes or extend slightly beyond them. The external outgrowth of the basal joint of the antennal stalk has a terminal spine, with three additional spines on its internal edge; the internal outgrowth bears a strong spine. The chelipeds are long and hairy. The degree of pubescence is very variable, but the larger specimens are, as a rule, more hairy. The same is true of the spines, which vary both in dimensions and in density. The merus of the right cheliped has smooth, naked, or hairy edges; the superodistal edge bears spines; the inferior surface is spinose and hairy. The entire surface of the carpus is hairy; the superior surface is covered with spines, from the bases of which arise tufts of hairs which are longer than the spines. The chela is elongated; the protuberant superior surface is covered with scattered spines and hairs; the strongest spines are disposed on the middle of the propodus and on the external edge; the superior surface of the movable dactylus bears a longitudinal row of fairly strong spines, while its external edge is bordered by a double row of smaller spines. The inferior surface is protuberant, and bears sparse granules and hairs. The dactyli are moderately long, with corneous tips. The left cheliped reaches the base of the movable dactylus of the right chela, while in the large specimens it is slightly shorter. The merus is flattened and hairy, with a spinose inferior surface. The carpus bears two rows of spines on the edges of its superior surface, while the space between them is smooth and naked; the lateral and inferior surfaces are hairy. The chela has a narrow, oval, symmetrical form; the spinose median crest is not prominent and not very evident; the external surface, which is equally protuberant, is covered with spines and hairs; the internal surface bears only hairs. The dactyli are slightly curved downward. The walking legs are hairy, especially on their superior edges; on the right side they exceed the cheliped. The meral joints of the first pair are spinose on the inferior side, while the carpal joints are spinose on the superior side. The dactyli are long, curved and slightly twisted, having dense hairs on the superior and inferior edges and ending in strong, corneous claws. The coloration of the specimens preserved in alcohol is pale pinkish yellow. The hairs of the chelipeds are often muddy or sandy even after preservation.

Figure 72. Pagurus kennerlyi (Stimpson)
(From Stevens, 1925)

Dimensions

Length of anterior part of carapace	9.0 mm
Width of anterior part of carapace	8.0 mm
Length of eyestalks	5.5 mm
Length of merus of right cheliped	10.0 mm
Length of carpus of right cheliped	10.5 mm

	Width of carpus of right cheliped	8.0 mm
	Length of chela of right cheliped	15.0 mm
	Width of chela of right cheliped	9.0 mm
221	Length of merus of left cheliped	8.5 mm
	Length of carpus of left cheliped	8.5 mm
	Width of carpus of left cheliped	4.0 mm
	Length of chela of left cheliped	11.0 mm
	Width of chela of left cheliped	6.0 mm
	Length of right first walking leg	41.0 mm

We referred previously to Balss' synonymizing of this species with P. trigonocheirus (=P. pubescens). The two species can be easily distinguished by the peculiar structure of the superior surface of their left chelae; in P. pubescens this surface bears a distinctly pronounced median crest; the external surface of the chela is obliquely triangular, and the whole contour of the chela is asymmetrical; in P. capillatus the median crest of the superior surface is less pronounced, and the entire contour of the chela is symmetrical. In addition, the spines of P. capillatus are longer; the hairs are denser and have a pinnate structure (in P. pubescens they are simple). The length of the scaphocerites is equal to that of the eyes or even shorter, while in P. pubescens the scaphocerites are always longer than the eyes.

Distribution. Only on the western shores of the Sea of Japan, southward to Chogu-Chen-Dogu Bay (northern Korea); not reported from Japan; Sea of Okhotsk; eastern shores of Kamchatka; Bering Sea; on the American shores southward to California (36° 55'N); southern part of the Chuckchee Sea up to 66° 40'N.

Ecology. Found at depths ranging from 5 to 432 m; usually encountered between 10 and 100 m, chiefly on muddy bottoms.

29. Pagurus constans (Stimpson) (Figure 73)

Eupagurus constans Stimpson, 1858: 248; 1907: 218, Pl. 24, Figure 3; Henderson, 1888: 67, Pl. 6, Figure 8; Ortmann, 1892: 310; Doflein, 1892: 647; Alcock, 1905: 177; Balss, 1913: 55; Terao, 1913: 366; Yokoya, 1933: 81.

The anterior part of the carapace is protuberant and very hard, bearing two arcuated and diverging rows of tufts of setae, which may, however, be completely obliterated in old specimens. The median frontal outgrowth is moderately pointed and protrudes farther than the lateral outgrowths, which are also pointed. The eyestalks are fairly long, but do not reach the end of the antennal stalks; the corneas broaden slightly. The scaphocerites are long and hairy, extending beyond the eyes (according to Ortmann they are shorter, or at most, equal). On the edge of the second sternal segment are two pointed denticles or spines between the bases of the third maxillipeds. The right cheliped is very large, and extends considerably beyond the ends of the walking legs. The ischium bears a long pointed spine at its inner angle

(Ortmann could not find it in his specimens, but in Doflein s specimens this
222 spine was present). The merus bears a number of spines on the superoanterior edge. The length of the carpus slightly exceeds its width and is almost equal to that of the propodus, sometimes more. The superior surface of the chela is flat, its edges sharp. The dactyli are shorter than the propodus and they meet closely; they bear a row of dense tufts of hairs on their internal edges. The left cheliped extends beyond the base of the movable dactylus of the right chela. The armature of the two chelipeds is similar. The surface of the merus is almost smooth and is covered with short rows of hairs; these hairs are not dense and are disposed in faint transverse lines. The carpus and the chela bear spines on their superior surfaces and are thickly covered with hairs which arise from the bases of the spines and reach their tips. In the middle of the propodus of the right chela a row of stronger spines is found; the marginal spines of the propodus are also stronger. On the left chela this median row of spines extends onto the immovable dactylus; there is a row of spines on the external edge, and several scattered spines are found at the base of the internal side. Setigerous tubercles are found between these spines. The walking legs are slender, with a sparse hair covering; the carpal joints bear one or two spines on the superior edge; the dactyli are long, slender and straight, longer than the propodi; they bear short, rigid hairs; the corneous tips are very short. The coloration is pale orange, with small spots on the body. The legs have dark-red stripes on their superior sides.

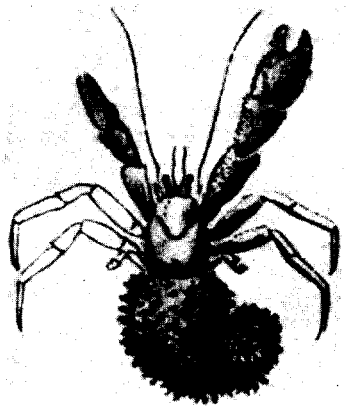

Figure 73. Pagurus constans (Stimpson)
(From Stimpson, 1907)

As shown by Stimpson and almost all the subsequent authors this species is always found in symbiosis with Hydractinia sodalis Stmp. ; this hydroid covers the small primary shell inhabited by the hermit crab, but subsequently grows to a such extent that the hermit crab is no longer able to change its primary shell–as most of the Paguridae do– but remains its whole life within this peculiar shelter formed by the hydroid; deep in the cavity inhabited by the hermit crab the primary shell can still be found. The species is sometimes found in sponges (Doflein, Balss) and it seems that in this case the sponge dissolves the primary shell of the hermit crab.

Distribution. Southern Japan, northward to Hakodate (Yezo). At depths ranging from 5 to 150 m.

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6. Genus PARAPAGURUS Smith

Parapagurus Smith, 1880: 50; 1882: 20; Henderson, 1888: 85; Milne-Edwards and Bouvier, 1893: 26; Stebbing, 1893: 166; Holmes, 1900: 155; Alcock, 1905: 98; Balss, 1912: 96; 1913: 49; Terao, 1913: 382;

Schmitt, 1921: 145. – Sympagurus Smith, 1883: 37; Henderson, 1888: 52; Milne-Edwards and Bouvier, 1893: 58; Stebbing, 1893: 166; Alcock, 1905: 103.

Type species: Parapagurus pilosimanus Smith.

The abdomen of the male bears paired appendages on its first and second abdominal segments. The female has only one oviduct, opening on the coxal joint of the left third thoracic limb. The bases of the third maxillipeds are far apart. The exopodite of the first pair of maxillipeds has no flagellum. The eyes are small. The antennules and the antennae are long. The sternal plates between the first and second walking legs are narrow. As in most of the Macrura, the gills are composed of numerous cylindrical papillae, and not of plates as in most of the Paguridae. The right cheliped is stronger than the left one; the dactyli move in a horizontal plane. The legs of the fourth pair have subchelae.

Key to the Species

1 (2). Eyestalks slender, tapering distally. Dactyli of left chela not longer than propodus. Inferior edge of dactyli of walking legs with very small, barely visible spinules . . . . . †1. P. pilosimanus Smith.

2 (1). Eyestalks stout, widening distally. Dactyli of left chela considerably longer than propodus. Inferior edge of dactyli of walking legs with distinct spines. . . . . 2. P. mertensii Holmes.

†1. Parapagurus pilosimanus Smith (Figure 74)

Parapagurus pilosimanus Smith, 1880: 51; 1883: 33, Pl. 5, Figures 3-5, Pl. 6, Figure 1a; 1882: 20, Pl. 2, Figure 4; Milne-Edwards and Bouvier, 1893: 28; 1894: 64, Pl. 9, Figures 1 to 17; 1900: 187, Pl. 6, Figure 2, Pl. 24, Figures 1 to 3; Alcock, 1905: 99, Pl. 10, Figure 1; Hansen, 1908: 29; Balss, 1912: 96, Pl. 11, Figures 1 to 6; 1913: 50; Terao, 1913: 385; Yokoya, 1933: 79.

The width of the anterior part of the carapace slightly exceeds its length; this part is almost naked. The median frontal outgrowth is broad and blunt; the lateral outgrowths are very small. The eyestalks are long, tapering distally and bearing long hairs on their superior surface; the corneas are very small. The ocular scales are small, slender, and pointed. The antennal stalks are very long and slender; the dorsal flagellum is densely covered with hairs on its inferior side. The scaphocerites reach the end of the eyes or extend slightly beyond them; they are very pubescent on
224their superior edge. The flagella of the antenna are almost entirely hairless. The right cheliped is large, almost equal to the length of the body. The merus bears small tubercles and is partly hairy on its external and inferior surfaces. The surface of the carpus is covered with small tubercles and delicate, soft, light-colored hairs. The chelae are equally protuberant on both superior and inferior sides, and have rounded lateral edges; the

entire surface–except for a small space at the base of the inferior side–and the surface of the basal part of the dactyli are tuberculated and covered with hairs, like the surface of the carpus. The immovable dactylus is fairly slender, and tapers considerably toward the corneous tip; the prehensile edge is thus obliquely directed to the right; the movable dactylus is almost the same length as the internal edge of the propodus. The prehensile edges of the dactyli are almost straight and bear a few short blunt tubercles. The left cheliped is very slender, and attains almost three fourths of the length of the right cheliped; the carpus and the chela are less tuberculated than those of the right leg, but they have a similar pubescence. The dactyli are almost the same length as the propodus; they are slender and slightly curved downward at their tips; the tips are corneous, the prehensile edges are sharp, and the surface of the dactyli is rounded and naked, with the exception of some scattered tufts of short hairs arising from small depressions on the surface. The walking legs extend beyond the end of the right cheliped; except the dactyli, they are almost smooth and naked. The second pair are somewhat longer and stouter than the first. In both pairs of legs the carpal joints are almost half the length of the meral joints, and reach the distal end of the carpus of the right cheliped; the propodal joints are slightly longer than the meral joints. The dactyli are considerably longer than the propodi; they are slender, strongly curved–especially toward their slender, pointed tips–and laterally compressed; their sides are naked, almost smooth, and bear a small longitudinal furrow which extends onto the strongly curved terminal part; this terminal part is even more compressed laterally, and very slightly curved; the inferior and the superior edges are rounded, with the exception of their terminal parts; the superior edge bears several scattered hairs, more numerous near the end of the edge, which becomes sharp in its terminal sector. The first pair of abdominal appendages of the male are close together, and are situated almost between the coxae of the posterior thoracic legs. Each appendage is composed of a single plate, which becomes slightly thicker near its base; its distal half broadens in a thin plate which forms a tube, slightly tapering for half its length; the cavity of this tube has a posteromedial direction. The second pair of appendages are articulated at the sides of the abdomen, some distance from the first pair; their bases are, therefore, very far apart. Each appendage is composed of a cylindrical basal joint, with which a longer and membranous terminal joint is articulated; the articulation is such as to form a tube when it is in line with the surface of the corresponding appendage of the first joint; its anterior side bears a small furrow terminating on the

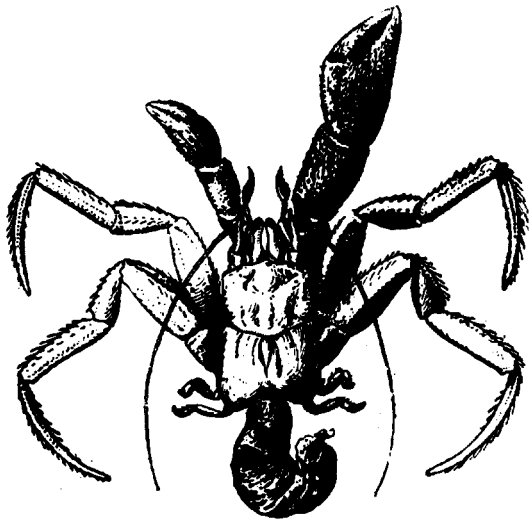

Figure 74. Parapagurus pilosimanus Smith

external side, not far from the tip; the tip of the appendage is slender, pointed, and hairy.

Dimensions

Length of anterior part of carapace	13.4 mm
Width of anterior part of carapace	12.0 mm
Length of eyestalks	6.3 mm
Length of carpus of right cheliped	18.0 mm
Length of propodus of right cheliped	26.0 mm
Width of propodus of right cheliped	13.7 mm
Width of left first walking leg	83.0 mm
Length of dactylus of right chela	14.0 mm

Distribution. Parapagurus pilosimanus is a typical deep-sea form (found from 210 to 4,000 m), and has a wide distribution, chiefly in the tropical and subtropical zones of the Atlantic Ocean: near Iceland; on the southwest shores of Ireland; the Bay of Biscay; the coast of Spain and Portugal; Morocco and Senegal; the Azores and the Canary Islands; Sierra Leone, Tristan Da Cunha; Patagonia (47°48'S); Nova Scotia; Sargasso Sea; the Bermudas. Indian Ocean; Arabian Sea and Bay of Bengal. Pacific Ocean: Banda Sea, near Paina; the Philippines; Japan at Yokohama
226 and Muroto Cape; Valparaiso; near the Galapagos Islands; Gulf of California. The northern distributional limit of P. pilosimanus is the 53° N. parallel; the southern limit is the 48°S. parallel. In Soviet seas this species was captured by the Bering Sea Expedition of the Hydrobiological Institute (1932), near the shores of Kamchatka (52° 42.5'N 159° 03.5'E) at a depth of 830 m.

2. Parapagurus mertensii Holmes (Figure 75)

Parapagurus mertensii Holmes, 1900: 155; Rathbun, 1904: 162, Pl.5, Figure 6; Schmitt, 1921: 146, Pl.16, Figure 5. – Non Pagurus mertensii Brandt, 1851: 112.

The median outgrowth of the front is prominent, somewhat elongated, with a rounded tip and subparallel edges; the lateral outgrowths are small. The width and length of the anterior part of the carapace are almost the same. The eyestalks are short, and are almost half as long as the anterior part of the carapace. The chelipeds are pubescent, spiniferous, and very unequal. The right cheliped is very large; the carpus is long, its internal and external edges are spinose, and the protuberant superior surface bears two rows of short spines. The chela is long, narrow, dorsoventrally flattened, and slightly curved downward toward the carpus; the rounded superior surface bears minute granules, disposed in irregular rows which become longer on the dactyli; the internal and the external edges are sharp and parallel, and bear dentiform granules. The left cheliped is long, slender, and weak. The carpus is subcylindrical and bears three rows of spines on its surface. The chela is narrow and much longer than the carpus; the propodus is very short, the dactyli are long, narrow and

Figure 75. Parapagurus mertensii Holmes
227 (From Schmitt, 1921)

curved ventrally. The dactyli of the walking legs are exceptionally long and slender, with numerous spines on their inferior sides.

This species furnishes one of the curious examples of commensalism between hydroid colonies and deep-sea hermit crabs. The hydroid colony, which covers the shell inhabited by the crab, forms a membranous crust which extends beyond the borders of the shell, and, according to Benedict, gradually dissolves it, so that the shelter of the hermit crab becomes membranous instead of calcareous. In the specimen that we studied, the shelter was formed partly by a broken fragment of a shell, but chiefly by a colony of hydroids. Such a shelter enables the crab to grow without the need of dangerous changes of the shell (Holmes).

Under the name Pagurus mertensii, Brandt in fact described a specimen of Pagurus hirsutiusculus (Dana). All the specimens found in the collection of the Zoological Institute of the Academy of Sciences which we studied–the original specimens of Brandt included–belong to the latter species. As actual locations of Parapagurus mertensii one should therefore include only those listed by Holmes (which were considered erroneous by M. Rathbun), namely: the Californian coast, between the Lobos Rocks (36° 25'40" N) and a point southwest of Nikolai Island (33° 00' 30" N), at depths of 139 to 479 m. All the other localities reported (Kodiak, Sitka, Vancouver, Kamchatka) refer to Pagurus hirsutiusculus, and not to Parapagurus mertensii.

7. Genus ORTHOPAGURUS Stevens

Orthopagurus Stevens, 1927: 247.

Type species: Orthopagurus minimus (Holmes).

The frontal edge of the carapace has a median outgrowth. The bases of the third maxillipeds are far apart. The exopodites of all three maxillipeds are flagelliform. The gills are of the phyllobranchiate type, 11 on each side. The chelipeds are unequal, the right leg stronger than the left. The fourth pair of pereiopods have subchelae. The abdomen is bent downward, not curved spirally and, in both sexes, bears unpaired pleopods on the left side. The uropods are symmetrical, or very slightly stronger on the left side.

The species of this genus do not reach large dimensions and dwell mostly in tubes of worms.

Key to the Species

1 (2). Right chela broadens distally; base narrow and convex; distal portion declivate with edges upturned. Lateral frontal outgrowths rounded . . . . . †1. O. minimus (Holmes).

2 (1). Right chela almost uniform in width; flattened or slightly convex. Lateral frontal outgrowths insignificant . . †2. O. schmitti (Stevens).

†1. Orthopagurus minimus (Holmes)

Pagurus minimus Holmes, 1900: 145; Rathbun, 1904: 160. – Pylopagurus minimus Schmitt, 1921: 144, Pl. 16, Figures 1a, 1b, 1c. – Orthopagurus minimus Stevens, 1927, 247, Figure 1.

The width of the anterior part of the carapace is almost the same as its length. The median frontal outgrowth is pointed and triangular, with a tuft of hairs; the lateral outgrowths are rounded, with marked submarginal spines. The eyestalks are long, broadening proximally; their length is almost two thirds that of the anterior part of the carapace. The ocular scales are triangular, with subterminal spines. The scaphocerites are
228 short and reach the middle of the eyestalks. The external outgrowth of the basal joint of the antennal stalk bears three apical spines. The chelipeds are less hairy than in O. schmitti. The merus of the right cheliped has a triangular cross section; it is smooth and slightly hairy on its inferior surface. The carpus broadens distally; its superior surface is slightly hairy, smooth near the external edge, but bearing spines at the inner distal angle; a row of fairly strong spines, curved forward, are found on its internal edge; the inferior surface is hairy. The chela is elongated, markedly broadening distally; the superior surface is evenly covered with short spines and barely visible hairs; the inferior surface is smooth, with scattered hairs. Both dactyli are the same width at their bases, and are equally rounded toward their tips, their edges being slightly raised and covered with fairly strong spines; the surface of the dactyli is distinctly lower compared with that of the propodus; the prehensile edges bear strong white tubercles. The tips are corneous. The left cheliped barely reaches the base of the movable dactylus of the right chela. The merus is flattened. The carpus bears two rows of spines on its superior side. The chela is rounded, its superior surface oblique; the dactyli are longer than the propodus; the general character of the chela resembles that of O. schmitti, but the dactyli are less twisted, and the gape left open when they are closed is narrower. The walking legs are slender and flattened; they reach the end of the right cheliped, and have hairy superior and inferior edges; the dactyli are slender, curved, and somewhat longer than the propodi. The general coloration is reddish, with dark-red spots. The large cheliped is of a darker red than the rest of the body, particularly at its distal end. The eyestalks have a pale median stripe.

Dimensions

Length of anterior part of carapace	3.0 mm
Width of anterior part of carapace	2.5 mm
Length of eyestalks.	2.0 mm
Length of merus of right cheliped	3.0 mm
Length of carpus of right cheliped	2.5 mm

Width of carpus of right cheliped	2.0 mm
Length of chela of right cheliped	4.0 mm
Width of chela of right cheliped.	3.0 mm
Length of merus of left cheliped	2.0 mm
Length of carpus of left cheliped	2.5 mm
Width of carpus of left cheliped.	1.0 mm
Length of chela of left cheliped	3.0 mm
Width of chela of left cheliped	1.5 mm
Length of right first walking leg	10.0 mm

This species is closely related to O. schmitti (Stevens), from which it differs by the more distinct lateral outgrowths of the front, its shorter scaphocerites, its right chela, which broadens distally and has raised edges, a slighter pubescence, and a narrower gape between the closed dactyli.

229 Distribution. Skidegate, Queen Charlotte Sound (British Columbia); San Francisco, Monterey Bay, Laguna beach and San Diego (California); from 27.4 to 64 m (Schmitt). We found only one specimen of this species in the collections of the Hydrobiological Institute; it was captured in Nel'ma Bay (Tatar Strait) at a depth of 20 m.

Ecology. Orthopagurus minimus usually inhabits worm tubes; it was also found in shells of Dentalium.

†2. Orthopagurus schmitti (Stevens) (Plate 2, Figure 1).

Pylopagurus schmitti Stevens, 1925: 298, Figures 17 to 22. – Orthopagurus schmitti Stevens, 1927: 249, Figures 1 to 4.

The length of the anterior part of the carapace very slightly exceeds its width. The median frontal outgrowth is pointed, with a tuft of long, slender hairs; the lateral outgrowths are barely visible. The eyestalks are long and slender, slightly broader at their bases. The ocular scales are short and triangular, with strong subterminal spines. The scaphocerites are short, and attain only two thirds of the length of the eyestalks. The external outgrowth of the basal joint of the antennal stalk has two apical spines and long hairs on its inferoexternal edge. The chelipeds are covered with relatively long, slender hairs, particularly on the carpal joints and on the chelae. The merus of the right cheliped has a triangular cross section, with slightly hairy edges and a more pubescent inferior surface. The superior, internal and inferior surfaces of the carpus bear long hairs, while the external surface is less hairy; the superior surface is covered with small red spines; larger spines, which are directed forward, form a row along the internal edge. The chela is somewhat broader than the carpus; it has almost parallel edges, and does not broaden distally; the protuberant superior surface of the propodus is covered with small red spines, which become larger on the internal edge; the spines on the dactyli are white, and form two longitudinal rows on the movable dactylus; the

inferior surface is smooth, slightly pubescent, and clearly separated from the superior surface by a row of marginal spines; the prehensile edge of the movable dactylus bears four white tubercles, while that of the immovable dactylus bears only two; the dactyli have corneous tips. As shown by B. A. Stevens, the superior surface of the chela varies greatly both in length and in the degree of protuberance; in young specimens it is shorter than it is broad, and is almost flat, while in old specimens it is longer and in most cases, protuberant. The left cheliped reaches the base of the movable dactylus of the right chela. The merus is flattened, and on its superior surface it is hairy. The carpus broadens slightly distally, and bears a row of spines on the superior side. The chela is elongated, with a narrow base; there is a slight crest, which starts from the base of the propodus and extends to the middle of the immovable dactylus; beyond this crest, the surface of the propodus is covered with small spines; the internal surface is smooth; the inferior and superior surfaces are both hairy. The dactyli are
230 long and twisted, and have corneous tips, which leave a large gape when closed. The walking legs are slender, flattened, and hairy—particularly on their superior and inferior edges—and do not exceed the chelipeds. The dactyli are slender, curved, and not twisted, with long, slender, corneous claws. The coloration is pale pinkish yellow or white, with irregular orange-brown spots and stripes; the dactyli have apricot-orange tips. The hairs are yellow, with a silver sheen.

Dimensions

Length of anterior part of carapace	5.0 mm
Width of anterior part of carapace	4.5 mm
Length of eyestalks	3.0 mm
Length of merus of right cheliped	5.0 mm
Length of carpus of right cheliped	6.0 mm
Width of carpus of right cheliped	4.0 mm
Length of chela of right cheliped	8.5 mm
Width of chela of right cheliped	4.5 mm
Length of merus of left cheliped	4.5 mm
Length of carpus of left cheliped	5.5 mm
Width of carpus of left cheliped	2.0 mm
Length of chela of left cheliped	6.5 mm
Width of chela of left cheliped	3.0 mm
Length of right first walking leg	21.0 mm

Distribution. Western coasts of North America, state of Washington, near the Puget Sound Biological Station (Reed Rock, near Brown Island, San Juan Islands, Turn Rock, near Lopez Island, etc); Sea of Japan, only on the Soviet shores, chiefly in the area of Vladimir and Olga bays. Not reported from Japan; not encountered in the intervening regions (Sea of Okhotsk, eastern shores of Kamchatka, Bering Sea).

Ecology. Like the preceding species, O. schmitti is found in worm tubes (Sabellaria cementarium, Serpula, etc). On rocky, shelly, and pebbly grounds, at depths from 6 to 220 m.

8. Genus SPIROPAGURUS Stimpson

Spiropagurus Stimpson, 1858: 236; 1907: 214; Henderson, 1888: 71; Milne-Edwards and Bouvier, 1893: 110; Stebbing, 1893: 165; Alcock, 1905: 117; Balss, 1913: 65; Terao, 1913: 385.

Type species: Spiropagurus spiriger (de Haan).

The anterior half of the carapace is fairly hard. The eyestalks are short, with broadened corneas. The antennae are long, the scaphocerites slender. The bases of the third maxillipeds are far apart; their coxal joints are small. The chelipeds are almost equal–one leg may be very slightly larger.
231 The dactyli move in a horizontal plane. The coxal joint of the fourth walking leg of the male bears an unpaired genital appendage, which has the form of a spirally curved membranous tube, the superior edge of this tube bearing a corneous stripe; this stripe gives the tube a certain elasticity; the telson if bifid distally, and the edges of the plates are denticulated.

The species of this genus are found in the tropical sublittoral zone (Panama, West Indies, western shores of Africa); in the Indo-Pacific region this genus is represented only by the species Spiropagurus spiriger (de Haan), which, in a northerly direction, extends to southern Japan. We included this species in our work on the basis of an indication, though doubtful, from the northern part of the Sea of Japan.

1. Spiropagurus spiriger (de Haan) (Plate 5, Figure 3)

Pagurus spiriger de Haan, 1850: 206, Pl. 49, Figure 2. – Spiropagurus spiriger Stimpson, 1858: 248; 1907: 214; Henderson, 1888: 72; 1893: 425; 1892: 297; Rathbun, 1902: 37; Alcock, 1905: 118, Pl. 13, Figure 1; Nobili, 1905: 3; Southwell, 1906: 216; Balss, 1913: 65; Terao, 1913: 386; Yokoya, 1933: 91.

The width of the anterior part of the carapace exceeds its length. The surface of both the anterior and posterior parts of the carapace is covered with flat prominences, which are somewhat scalelike and which bear on their anterior edges fairly long, soft, horizontal hairs. The median and lateral outgrowths of the front are rounded and equally prominent; the lateral outgrowths bear short, conical, submarginal spines. The ocular scales are broad, each with a rounded tip and concave surface, in the middle of which a high prominence is found; the edges are densely covered on the inferior side with hair. The eyestalks are short, dorsoventrally flattened, and widening at the corneas; the superior surfaces of the stalks bear rows of horizontal hairs; the cavity of the corneas is also bordered by a row of such hairs. The basal joint of the antennal stalk has a relatively blunt internal outgrowth and a pointed external one. The scaphocerites are hairy–particularly along their internal edges–and extend beyond the end of the eyes. The chelipeds are equal in length and similar in structure. The merus is narrow, with a triangular cross section; its inferior sides are rounded. The carpus is narrow, with rounded sides and a row of spines along the internal edge; the surface is covered with the same flat prominences as the carapace. The chela is long – elongated; its superior and

inferior surfaces are covered with arcuated rows of short horizontal hairs; the external and internal edges bear long hairs; the hairs on the surface of the dactyli are disposed in tufts. The prehensile edge of the immovable dactylus bears ten denticles, which become tuberculiform near the base; the prehensile edges of the movable dactylus bear three denticles on their proximal half; the spaces between these denticles on both dactyli, as well as the distal half of the prehensile edge of the movable dactylus, bear
232 short, seriated, corneous plates. The curved pointed tips of the dactyli cross when closed. The walking legs exceed the chelipeds by the length of their dactyli. All the joints are flattened, and both the external and internal sides are covered with rows of short hairs; the superior edges are hairy. The carpal joints bear spines at the superodistal ends. The dactyli are long, curved in their distal third, and very pubescent on their superior edge; the groove on the external surface is lined with hairs which are directed upward; on the internal surface are two rows of erect hairs: one of them is found on the inferior edge, the other in the middle. The corneous tip is short and relatively blunt. On the coxa of the left fourth walking leg of the male is a long spiral made up of two or three spires; this is the genital appendage. The coloration of the specimens preserved in alcohol is light reddish yellow, while that of living specimens is yellowish brown, sometimes slightly reddish; the hairs are light and shining.

Dimensions

Length of anterior part of carapace	8.0 mm
Width of anterior part of carapace	9.5 mm
Length of eyestalks	4.5 mm
Length of scaphocerites	4.5 mm
Length of merus of cheliped	9.0 mm
Length of carpus of cheliped	7.0 mm
Length of chela of cheliped	13.0 mm
Width of chela of cheliped	4.0 mm
Length of left first walking leg	46.0 mm

Distribution. East Indian Archipelago, Bay of Bengal, the Maldive Islands; Zanzibar; the Admiralty Islands; Torres Strait; China Sea; Japan (the northernmost locality is Tokyo Bay). As shown by Yokoya himself, the locality reported by this author (northern part of the Sea of Japan) is questionable, since the label was missing; Tsuruga Bay.

Ecology. This species swims freely, using its hairy walking legs and carrying its shell. Maximum reported depth: 20 m.

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8. Family **LITHODIDAE**

Lithodidae Dana, 1852: 1430; Ortmann, 1892: 271; 1901: 1147; Schmitt, 1921: 146.

The body is crablike. Most of the carapace is hard. The rostrum is well developed, triangular, acicular or spiniform, and provided with accessory spines. The linea anomurica is distinct. The eyestalks are without ocular scales at their bases. The scaphocerites are spiniform, frequently ramified. The third maxillipeds are pediform. The first pereiopods are chelate; the right leg is usually stronger than the left. The form and dimensions of the fourth pair of pereiopods are like those of the third pair. The fifth pereiopods are small, and bent under the carapace. Consequently, the members of this family appear as if they had only four pairs of legs. The gills are of the phyllobranchiate type, eleven on each side of the body, namely: one pleurobranchia on the left fourth pereiopod, two arthrobranchiae on the third maxilliped and on each of the four pereiopods. The abdomen is short and broad, not concealed in a shell, but bent under the carapace; the abdomen of the female is distinctly asymmetrical; the ventral surface is soft, the dorsal surface smooth or covered with several hard, calcified plates or nodules. The pleopods are completely lacking in the males. The females bear paired rudimentary pleopods on the first abdominal segment; segments two to five bear simple and uniramous pleopods (consisting of only one endopodite) on the left side. The uropods are lacking.

The family of the Lithodidae is divided into two subfamilies: Hapalogastrinae (= Hapalogastrica Brandt) and Lithodinae (= Ostracogastrica Brandt).

Key to the Subfamilies

1 (2). Rostrum short, broad and triangular. Abdominal segments three to five not completely calcified; abdomen usually in the form of soft, membranous, swollen sac . . . 1. Subfamily Hapalogastrinae.

2 (1). Rostrum prominent, blunt or spiniform. Abdominal segments three to five composed of well-calcified plates; abdomen usually flat. . . . . 2. Subfamily Lithodinae.

234 Subfamily **HAPALOGASTRINAE**

Hapalogastrinae Ortmann, 1901: 1147.

The carapace is slightly convex, covered with spines in a few cases; as a rule, its dorsal surface is neither tuberculated nor spinulated. The frontal edge is broad, the rostrum more or less flat, triangular, short, and generally is not longer than the eyes. The dorsal surface of the second abdominal segment has two marginal and two lateral plates, and one median plate, or a group of nodules instead of these plates. The dorsal surface of the three subsequent segments is soft and membranous, with a few calcified granules or small plates. The abdomen as a whole has the form of a soft, swollen sac, with the exception of the genus Placetron, in which it is more or less flattened. Up to the present time it was considered that the females of this subfamily have no pleopods on the first abdominal segment. Bouvier (1896) was the only author who assumed their existence in the females of Dermaturus. In all members of this subfamily which we studied, we found in the female rudimentary pleopods on the first abdominal segment. Consequently, Hapalogaster does not form a lateral branch in the phylogeny of the family Lithodidae, as believed by Bouvier, and thus the subfamily as a whole forms a natural link between the Lithodinae and the Paguridae.

The genera of this subfamily are primarily littoral and sublittoral forms (in the upper levels) and are found exclusively in the northern part of the Pacific Ocean.

Key to the Genera

1 (2). Lateral edges of carapace armed with spines beyond cervical groove. Chelipeds with pointed spines or denticles. Second abdominal segment with unpaired median plate (with the exception of H. cavicauda, in which it is replaced by a group of calcareous granules). Most species with a more or less strong hairy carapace and appendages . . . . . 1. Hapalogaster Brandt.

2 (1). Lateral edges of carapace smooth. Chelipeds with blunt or squamose prominences or transverse crests. Unpaired median plate absent on second abdominal segment. Slightly hairy forms.

3 (6). Chelipeds unequal, right leg usually larger than left; chelipeds very strong compared with walking legs. No tubercle on sternal surface between bases of chelipeds. No spines on inferodistal edge of meri of walking legs. Wide membranous interspace between lateral plates of second abdominal segment. Abdomen swollen, saclike.

235 4 (5). Surface of carapace and chelipeds covered with transverse crests. Scaphocerites straight and lanceolate. Last two joints of third maxillipeds not broadened . . . . . 2. Dermaturus Brandt.

5 (4). Surface of carapace covered with squamose prominences; chelipeds with round tubercles. Scaphocerites curved, halfmoon-shaped. Last two joints of third maxillipeds broadened. 3. Oedignathus Benedict.

6 (3). Chelipeds equal or subequal, not very well developed in comparison with the long walking legs. Tubercle on sternal surface between bases of chelipeds. Inferodistal edge of meri of walking legs with three slender, pointed spines. Lateral plates of second abdominal segment meet on median line, leaving a narrow suture, not a membranous interspace. Abdomen flat. . . . . 4. Placetron Schalfeew.

1. Genus HAPALOGASTER Brandt

Hapalogaster Brandt, 1850: 269; Schalfeew, 1892: 326 (part); Holmes, 1900: 113; Schmitt, 1921: 148.

Type species: Hapalogaster mertensii Brandt

The carapace, chelipeds and walking legs are fairly flattened and more or less pubescent. The chelae are triangular in cross section; they are obliquely articulated with the carpus and therefore move in a horizontal plane. The right cheliped is stronger than the left one and is usually longer than the walking legs. The carapace is poorly calcified and has a reticulum of noncalcified lines on the branchial areas; the lateral edges of the carapace bear several spines behind the cervical groove. The two distal joints of the last maxillipeds are broadened. The females have paired pleopods on the first abdominal segment; all the pleopods are one-jointed. The second segment of the abdomen is composed of a pair of narrow marginal plates, a pair of broad lateral plates, and an unpaired median plate; in other cases (in H. cavicauda) it bears only calcified nodules. The third to fifth abdominal segments in the female are calcified on the marginal part of the left side, and the segmentation into plates is therefore visible here; on the right side of each of segments three and four, only a small, round, unsegmented plate is found; the plate of the fifth segment is like that of the left side. In the male, the third to fifth segments each bear a pair of small round plates. The well-calcified plate of the sixth segment is situated above the equally
236 well-calcified plate of the telson. The flattened form of the carapace and of the appendages, the softness of the integument, and the horizontal plane in which the chelae move are adaptive features resulting from the fact that the species of this genus live concealed under stones.

Key to the Species

1 (4). Lateral edge of carapace with five spines beyond the cervical groove. Surface of joints of chelipeds covered with spines.

2 (3). Superoexternal surface of propodus of right chela with three longitudinal rows of spines. Middle of propodus of left chela without a spine. . . . . †1. H. grebnitzkii Schalfeew.

3 (2). Superoexternal surface of propodus of right chela with four longitudinal rows of spines. Middle of propodus of left chela with a spine. . . . . 2. H. mertensii Brandt.

4 (1). Lateral edge of carapace with seven spines beyond the cervical groove. Surface of joints of cheliped covered with tuberculiform prominences . . . . . †3. H. dentata (de Haan).

†1. Hapalogaster grebnitzkii Schalfeew (Figures 76, 77a).

Hapalogaster grebnitzkii Schalfeew, 1892: 329, Figures 3a, 3b; Holmes, 1900: 115; Rathbun, 1904: 163; Brashnikow, 1907: 64; Schmitt, 1921: 150, Figure 96, Pl. 29, Figure 2.

The carapace is evenly covered with short hairs. The rostrum is triangular, pointed, and extends beyond the spines at the orbital angles which are directed somewhat outward. It also extends beyond the strong denticles at the anterolateral angles, which in turn are directed forward and somewhat inward. Behind the cervical groove, the lateral edge of the carapace bears five spines which gradually decrease in size posteriorly. The scaphocerite has the form of a narrow pointed plate which slightly exceeds the strong spine on the external side of the first joints of the antennal stalks; the internal edge of the scaphocerite is hairy. All the pereiopods are pubescent. The ischium of the right cheliped bears three spines close together on its inner distal edge; the merus is short and swollen, bearing three strong spines on its internal edge; of these the median one is the longest; it also bears an additional smaller spine on the anterior edge; outward, beyond the small incision, the anterior edge bears a small spinule; the superoexternal surface bears a transverse row of three spines. The carpus bears two spines on its internal edge and three spines on its anterior edge, the inferoexternal spine being the largest. The superoexternal surface bears three low spines or tubercles, disposed in a row parallel to the internal edge, and another similar row more laterally. In the latter row, the distal spine is fairly strong; behind this spine, at the inferoanterior angle, a small spine is found. The chela is strong compared with the other joints. The internal surface of the propodus is slightly swollen and smooth;
237 the superior edge bears a longitudinal row of four small spines. Immediately beyond, there is a row of five spines, extending to the very base of the movable dactylus. Four of these spines are large, while the fifth – the proximal one – is small. The inferoexternal edge bears a row of five spines on its proximal two thirds; here, also, the proximal spine is smaller. Between these rows, the external surface appears flat and smooth. The inferior surface of the propodus and of the movable dactylus is flattened. The movable dactylus has a strong spine on its superior edge, near the base; its prehensile edge bears from 12 to 14 tubercles which extend also onto the partly spatulate tip. The prehensile edge of the immovable dactylus has a fairly strong flat tubercle in the middle; behind this tubercle, near the base, two small tubercles are found, and in front of it, the entire margin bears a fine denticulation. The tip has two larger tubercles – as shown by Shalfeev [Schalfeew] (1892). On the flat inferior surface of the propodus – in the larger specimens – an oval opening is always found near the base of the immovable dactylus; this opening is covered by a thick, noncalcified membrane. It is difficult to attribute to this formation a specific physiological function; it simply seems that the hard cover was rubbed away by the

constant friction between the massive chela and the hard substratum, and that the wound was cicatrized by this membrane. The same thing is found in H. mertensii. The merus of the left cheliped bears two large spines on its internal edge, as well as two very small spines at the proximal and distal ends of this edge; the anterior edge also bears a spine, which is, however, larger. The superoexternal surface bears three spines in a transverse row. The carpus has two spines on its internal edge, three on the anterior edge, and four on its superoexternal surface. The chela is more flattened and its axis is clearly bent at the level of the base of the dactyli. The superior edge of the propodus bears two rows of three spines each; at the proximal ends of both rows, small tubercles are found; the inferoexternal edge bears four large, strong spines; the dactyli

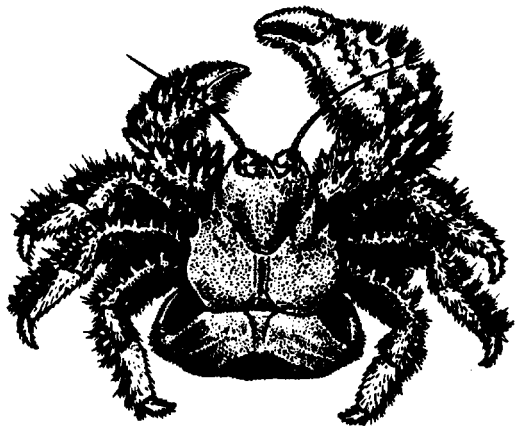

Figure 76. Hapalogaster grebnitzkii Schalfeew

238 are distinctly flattened, and their tips are bent downward; the superior edge of the movable dactylus does not bear any tubercles; it has a crest of small corneous plates, and there is a granule on its inferior edge beneath the actual tip; the prehensile edge of the movable dactylus bears small tubercles, while the spaces between these tubercles also bear corneous plates; a fairly large tubercle is found on the inferior edge, under the tip. The anterior edges of the meral, carpal and propodal joints of the three subsequent flattened legs each bear a pointed denticle. The posterior edge of the merus of the first walking legs is armed with pointed denticles. The posterior edge of the merus of the first walking legs bears a spine near its distal end, while the subsequent joints bear many spines. The dactyli are short, with corneous spinules on the inferior edge and slightly curved corneous tips. All the joints are hairy, and the hair cover must be removed in order to study the spines; the hairs are especially long on the inferoexternal edges of the chelae and on the anterior edges of the joints of the walking legs; the shorter hairs have thickened, clavate tips. The dorsal surface of the abdomen is covered with short hairs.

Specimens preserved in alcohol have a reddish-yellow coloration. The dactylus of the right chela has a rather bright red color, but the spines and lateral denticles are white.

Dimensions

Length of carapace.	19.0 mm
Width of carapace	18.0 mm
Length of merus of right cheliped	8.0 mm
Length of carpus of right cheliped.	10.5 mm
Length of chela of right cheliped	25.5 mm
Length of movable dactylus of right cheliped	12.0 mm

Distribution. Bering Sea, northward no farther than Bering Strait; on the western coast of North America southward to Humboldt Bay (California); the Aleutians; eastern shores of Kamchatka; Sea of Okhotsk; northern part of the Sea of Japan, on the Soviet shores to Sibiryakov Island. Not reported from Japan (southern Sakhalin excluded). Chiefly on rocky bottoms. Littoral, to a depth of 90 m.

2. Hapalogaster mertensii Brandt (Figure 77b)

Hapalogaster mertensii Brandt, 1850: 50; Schalfeew, 1892: 307, Figures 4, 5a; Holmes, 1900: 115; Rathbun, 1904: 162; Way, 1917: 382, Pl. 80, Figure 6.

This species greatly resembles H. grebnitzkii. The surface of the carapace bears tufts of longer hairs; the short hairs are clavate as in H. grebnitzkii. The differences between the two species consist chiefly in the different spinulation of the chelipeds. The carpus of the right cheliped is more spinose, as here all the spines are pointed and conical, while in H. grebnitzkii some of the spines are tuberculiform. On the external surface, in the space between the two rows of spines – which is smooth and flat in H. grebnitzkii – a third row of five spines is found in this species; consequently, there are four longitudinal rows of spines on the propodus in H. mertensii, while in H. grebnitzkii there are only three such rows. In addition, the inferior row in H. mertensii has six spines, and therefore extends closer to the base of the immovable dactylus. The superior edge of the movable dactylus bears two basal spines; this character, however, is not a constant one, as two of the specimens studied bore only a single basal spine; in most of the cases, however, there were two such spines. The left cheliped differs from that of H. grebnitzkii by the strong spine which occupies the middle of the propodus, approximately in front of the gape between the two dactyli. In other respects, this species completely resembles H. grebnitzkii.

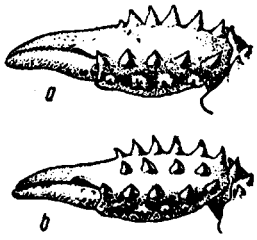

Figure 77. Chelae of right chelipeds (superoexternal view) of: a–Hapalogaster grebnitzkii; b–Hapalogaster mertensii.

The coloration (according to Way, 1917) is brownish red or grayish brown; the ventral sides of the legs are red.

Distribution. The Aleutians westward to Atka Island in the Andreanof Islands; southward along the western coast of North America to Puget Sound (Washington). Littoral, to a depth of 35 m.

†3. Hapalogaster dentata (de Haan) (Figure 78)

Lomis dentata de Haan, 1850: 219, Pl. 48, Figure 2. – Hapalogaster dentata (-tus) Miers, 1879: 47; Ortmann, 1892: 323; Stimpson, 1907: 198; Balss, 1913: 71; Yokoya, 1928: 758.

This species differs from the two preceding ones by its slighter pubescence. The gastric area is markedly swollen. The rostrum is narrow, triangular and pointed. The spines of the external orbital angles are small and are directly slightly downward. The spines on the anterolateral angles of the carapace have a broad triangular form. The lateral edge of the carapace bears seven spines behind the cervical groove; these spines decrease in size posteriorly. The eyestalks are markedly flattened on their superior side. The scaphocerites are flat and lanceolate, their tips

Figure 78. Hapalogaster dentata (de Haan)

curving slightly upward. The merus of the right cheliped bears two or three spines on its internal edge, a small spine on the anterior edge, and two or three additional small spines or tubercles on the superior surface. The internal edge of the carpus bears a strong spine on its proximal end and a broad denticle at the inferodistal angle; the superoexternal surface has large tuberculiform prominences, which in turn bear small round granules. The internal edge of the propodus bears five blunt tubercles; ten other tuberculiform prominences are disposed laterally in distinct longitudinal rows; these tubercles bear round, blunt granules, and are separated from each other by smooth spaces. Roughly in front of the gape between the two dactyli, the surface of the propodus bears a smooth, narrow, longitudinal furrow; beyond this furrow are six round prominences analogous to
240 those mentioned above; in front of each of these prominences, six pointed denticles are found on the inferoexternal edge; the anterior edge of the propodus bears a transverse, prominent, cylindrical thickening covered with

granules; the inferointernal surface of the propodus is smooth. The superior edge of the movable dactylus bears three tubercles or large granules, which decrease in size distally; on the inner side of these tubercles an irregular row of round granules is found; the prehensile edge bears four large tubercles and several additional smaller tubercles on its rounded tip; the prehensile edge of the immovable dactylus resembles that of H. grebnitzkii, with the only difference that the median tubercle is large. The merus of the left cheliped bears a large denticle at the inner distal angle; additional spines are sometimes found here; the carpus generally resembles that of the right leg. The propodus bears three spines on its internal edge; the proximal one may be very small. This is followed by a smooth, longitudinal furrow, five round prominences, and in front of them, on the external edge, five denticles. These prominences are sometimes not very pronounced, and therefore the longitudinal furrow seems broader. The movable dactylus and the immovable dactylus each bear a spine at the base of the internal edge; the prehensile edges are as in H. grebnitzkii. The three subsequent pairs of pereiopods have the same armature as in H. grebnitzkii; the spines of the anterior edges are, however, broader, almost dentiform; the dactyli have longer, more curved claws. The surface of the carapace and of the appendages is covered with short brown hairs; longer and lighter hairs border the inferoexternal edges of the chelae and the anterior edge of the walking legs.

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Dimensions

Length of carapace	15.0 mm
Width of carapace	16.0 mm
Length of merus of right cheliped	6.0 mm
Length of carpus of right cheliped	9.0 mm
Length of chela of right cheliped	21.0 mm
Length of movable dactylus of right cheliped	9.5 mm

Distribution. Southern Japan northward to Aomori and Hakodate. On the Soviet shores of the Sea of Japan, this species does not extend farther north than Peter the Great Bay, where it is encountered fairly seldom. Littoral, to a depth of 180 m.

We studied a female which, according to Shalfeev, was determined by Brandt as being H. dentata (No 844). All the features of this specimen indeed correspond to the characters of this species. The only indication of locality on the label was "Russo-American colony" without even the name of the collector. As this species has not been reported since then off the American coast, and Rathbun listed it (1904, p 162) only on the basis of this specimen, it seems almost certain that the indication on the label is erroneous and that this species is indeed not found on the western coast of North America.

2. Genus DERMATURUS Brandt

Dermaturus Brand [sic], 1850: 267; Holmes, 1900: 116. -Hapalogaster Schalfeew, 1892: 326 (part).

Type species: Dermaturus mandtii Brandt.

The carapace is hard and fairly swollen; the surface of the carapace bears large, transverse wrinkles; the lateral edges are smooth. The rostrum is triangular and simple. The scaphocerites are straight and lanceolate. The chelipeds are strong; the right leg is larger than the left. The articulation with the carpus is oblique, and the chela can therefore move diagonally (downward and outward). The last two joints of the third maxilliped are not broadened. The walking legs are not compressed, but are almost cylindrical. The female has a pair of rudimentary pleopods on the first abdominal segment. The second abdominal segment is composed of a pair of narrow marginal plates and a pair of narrow lateral plates. Instead of the unpaired median plate, a fairly large membranous sector is left. In other respects, the abdomen in both the female and the male is like that of Hapalogaster, the only difference being that in the female, segments three to five
242 are perhaps less calcified. The high degree of calcification of the carapace and the fact that the body is not flattened make us believe that this animal leads a freely creeping life.

†1. Dermaturus mandtii Brandt (Figure 79)

Dermaturus mandtii Brandt, 1850: 50; Stimpson, 1858: 232; Holmes; 1900: 116; Rathbun, 1904: 163; Brashnikov, 1907: 65. – Hapalogaster mandtii Schalfeew, 1892: 332, Figures 2, 5c.

The surface of the carapace is slightly swollen; the carapace broadens very slightly posteriorly. The rostrum is distinct and triangular, with a fairly pointed tip and a group of granules on its superior surface, near the tip. The frontal edge bears a large granule above the base of the antennules. The anterolateral angle of the carapace has the form of a fairly broad denticle, with apical granules in larger specimens. The surface of the carapace is covered with transverse wrinkles which bear short, erect hairs. The lateral edges of the carapace are smooth. The eyestalks bear a transverse row of short hairs. The scaphocerite has the form of a narrow, slightly concave plate, with a fairly rounded tip and hairy edges. The spine on the external edge of the second joint of the antennal stalk has a broad triangular form, and extends somewhat beyond the middle of the scaphocerite; it has a smooth internal edge and a denticulated external one. The merus of the right cheliped has a small denticulated lobe on its internal edge. The internal edge of the carpus bears three denticles, the proximal one being the largest. The superior surfaces of the merus, the carpus and the propodus are covered with slightly diagonal transverse crests bearing round granules. These granules are particularly large on the surface of the propodus, and resemble beads. The furrows between the crests are covered with short erect hairs, arising from the anterior edges of the base of the crests. The crests become shorter at the base of the immovable dactylus, and resemble a group of large granules. On the internal edge of the propodus, each of these crests bears a larger granule (sometimes two); the crests extend onto the inferior surface of the propodus, almost up to the middle. At the base of the movable dactylus is an irregularly formed crest and a group of granules. The tips of both dactyli are smooth and bear a tuft of fairly long hairs; the inferior surface of the propodus and of the dactyli also bears

tufts of hairs; the prehensile edges bear large tubercles; the tips of the dactyli are slightly concave and appear bifid owing to their tubercles. The left cheliped has the same form as the right one; the dactyli, however, are flatter, smooth and close together, and are covered by tufts of long, soft hairs. The three subsequent pairs of legs are fairly flat, smooth and, like the carapace, are covered with transverse hairy wrinkles; the inferior edges of the propodi and of the dactyli bear tufts of fairly long hairs; the dactylus is short, with corneous spinules on the inferior edge and a strongly curved corneous claw.

243 Dimensions

Length of carapace	23.0 mm
Width of carapace	23.0 mm
Length of merus of right cheliped	13.5 mm
Length of carpus of right cheliped	17.5 mm
Length of chela of right cheliped	33.0 mm
Length of movable dactylus of right cheliped	18.0 mm
Length of first walking leg	41.0 mm

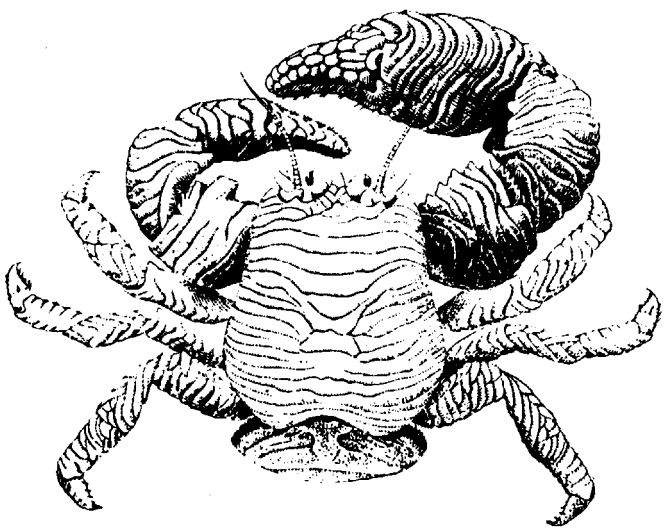

Figure 79. Dermaturus mandtii Brandt

Distribution. In the eastern half of Bering Sea, northward to the Pribilof Islands; along the Asiatic coasts northward to Cape Olyutorsk. Along the western coast of North America, southward to Sitka; eastern shores of Kamchatka; Sea of Okhotsk; northern part of the Sea of Japan. Up to the present time, this species has not been reported farther south than the southern end of Sakhalin. In the collections of the Zoological Institute of the Academy of Sciences we found four specimens collected by M. Pavlenko, 3 to 4 miles from the mouth of the Tuman-Ula River. In addition, we found five specimens collected by Roshkovskii in Japan (30 July 1917, Misaki, dredging at a depth of 15 to 20 m). It is difficult to decide

whether the information on these labels is correct. The latter record seems particularly doubtful, since no other record is available concerning the presence of D. mandtii in Japan, and Misaki is one of the best studied areas of Japan.

Littoral and to a depth of 72 m, chiefly on rocky bottoms.

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3. Genus OEDIGNATHUS Benedict

Oedignathus Benedict, 1894: 487; Holmes, 1900: 117. – Hapalogaster Schalfeew, 1892: 326 (part).– Dermaturus Balss, 1913: 71 (part).

Type species: Oedignathus inermis (Stimpson).

This genus resembles Dermaturus. The carapace is hard and swollen, and is covered with semicircular squamous prominences. The lateral edges of the carapace are smooth. The rostrum is triangular and simple. The scaphocerite is flat, strongly curved, and crescent-shaped. The last two joints of the third maxillipeds are markedly broadened. The chelipeds are strong and unequal, the right legs longer than the left. The walking legs are almost cylindrical; the female has a pair of pleopods on the first abdominal segment. The abdomen has the same structure as in Dermaturus.

†1. Oedignathus inermis (Stimpson) (Figure 80)

Hapalogaster inermis Stimpson, 1860: 243. – Hapalogaster brandti Schalfeew, 1892: 330. Figures 1, 5b. – Oedignathus gilli Benedict, 1894: 487. – Oedignathus brandti Holmes, 1900: 118, Pl.1, Figures 17-20. – Oedignathus inermis Holmes, 1900: 119; Rathbun, 1904: 163; Schmitt, 1921: 151, Figure 97, Pl. 19, Figure 1; Yokoya, 1928: 759. – Dermaturus inermis Balss, 1913: 71.

The length of the carapace somewhat exceeds its width. It is slightly heart-shaped, truncate at its anterior edge and broadened in its posterior part. Its superior surface is covered with smooth, low, more or less rounded squamous prominences, which bear short, erect hairs on their anterior edges. The cervical groove is shallow; the areas are generally indistinct, yet discernible. The lateral edges of the carapace are smooth. The rostrum has a narrow triangular form; it is slightly bent downward and almost reaches the middle of the eyestalks. Instead of a spine, a small, round granule is found at the outer orbital angles. The anterolateral angles of the carapace have the form of short, blunt outgrowths, each with two apical granules. The scaphocerites have the form of broad crescent-shaped plates, with concave internal edges, and convex external ones; the external edge bears four round granules, one of which is apical. The right cheliped is very strong; its ischium is smooth; the internal edge of the merus bears a denticulated lobe and has a deep transverse furrow; the internal edge of the carpus has a prominence near its proximal end and a transverse furrow on the external half of the superior surface, near the distal end; the propodus has a narrow base, but is very broadened distally. Short tuberculiform prominences cover the superior surfaces of the merus,

the carpus, and the propodus, as well as most of the surface of the dactyli. These prominences bear minute granules, and thus resemble strawberries; between the large prominences, small round granules are found; each pro-
245 minence is encircled by a crown of short, erect hairs, and from the superior surface of the large prominences, sparse, short, darker hairs arise between the granules; the tubercles gradually disappear on the dactyli. The inferior surfaces of all the joints is naked, and covered with small, low granules. The prehensile edges of the dactyli have low, slightly prominent tubercles, the most pronounced being the one near the middle of the prehensile edge of the immovable dactylus. The broad internal edges are concave, particularly near the ends; these consequently appear somewhat spoonlike. A fairly broad gape is left open when the dactyli are closed. The left cheliped is much smaller, but its structure is identical to that of the

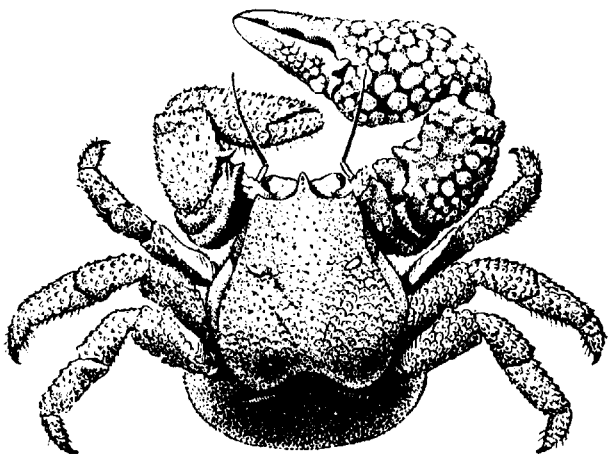

Figure 80. Oedignathus inermis (Stimpson)

right cheliped, except that the dactyli close tightly, and their prehensile edges have a different armature. The prominences on the superior surface of the joints do not resemble strawberries, since they usually bear but a single granule in the center. The three subsequent pairs of legs are only slightly flattened, almost cylindrical, and smooth (apart from a small prominence on the superior edges of the meri, near the distal end, which has the form of a small, blunt denticle). The legs are covered by the same prominences as the carapace and the left cheliped; the dactyli are stout, bearing tufts of fairly long hairs; they have strong corneous spines on the inferior edge and a large, curved, corneous claw. In a smaller but adult specimen which we studied, the spines at the anterolateral angles of the carapace were more rounded and the scaphocerites narrower, with a rounded tip, and without granules on the convex external edge.

246 Dimensions

Length of carapace	17.0 mm
Width of carapace	16.0 mm
Length of merus of right cheliped . . .	9.0 mm

Length of carpus of right cheliped	11.0 mm
Length of chela of right cheliped.	24.0 mm
Length of movable dactylus of cheliped . .	14.5 mm
Length of first walking leg	31.0 mm

Distribution. The western coast of North America, from Unalaska to the Pacific Grove, California; Japan: from the Tsushima Strait to Aomori (Tsugaru Strait); Patrocles Bay, Peter the Great Bay.

4. Genus PLACETRON Schalfeew

Placetron Schalfeew, 1892: 333. – Lepeopus Benedict, 1894: 487.

Type species: Placetron wosnessenskii Schalfeew.

The carapace is flat and slightly calcified, and – like all the appendages – is covered with peculiar scalelike prominences; the lateral edges of the carapace are smooth. The scaphocerites are short and flat. The last two joints of the outer maxillipeds are not broadened. The chelipeds are not very strong in comparison with the long walking legs, which are almost the same length. The axis of the articulation between the chela and the carpus is in the horizontal plane. The dactyli are long, and spoonlike (concave) on their internal edges. The walking legs are long and partly flattened; the propodi bear three spines at the distal ends of the inferior side. The sternal surface of the cephalothorax bears a tubercle between the bases of the chelipeds. The marginal plates of the second abdominal segment are fused with the broad lateral plates, which approximate along the median line; the median plate is lacking. On the left side of segments three to five in the female, fairly broad well-calcified plates are found; on the right side, the dorsal surface of the abdomen is membranous. In the male, the entire abdomen is membranous, with the exception of the second and sixth segments and the telson. The general form of the abdomen is flat and therefore different from all the other genera of the Hapalogastrinae. Unfortunately, since most of the available specimens of this genus are very old and most of the soft parts of the body were not preserved, we could not ascertain whether the females have paired pleopods on the first abdominal segment or not; it seems, however, that there are such pleopods.

1. Placetron wosnessenskii Schalfeew (Figure 81)

Placetron wosnessenskii Schalfeew, 1892: 333, Figure 6; Rathbun, 1904: 163, Plate 6, Figure 1. – Lepeopus forcipatus Benedict, 1894: 488.

The integument of the entire body is poorly calcified. The carapace is flattened, its width exceeding its length, and broadening markedly
248 in a posterior direction; in smaller specimens, however, the smooth

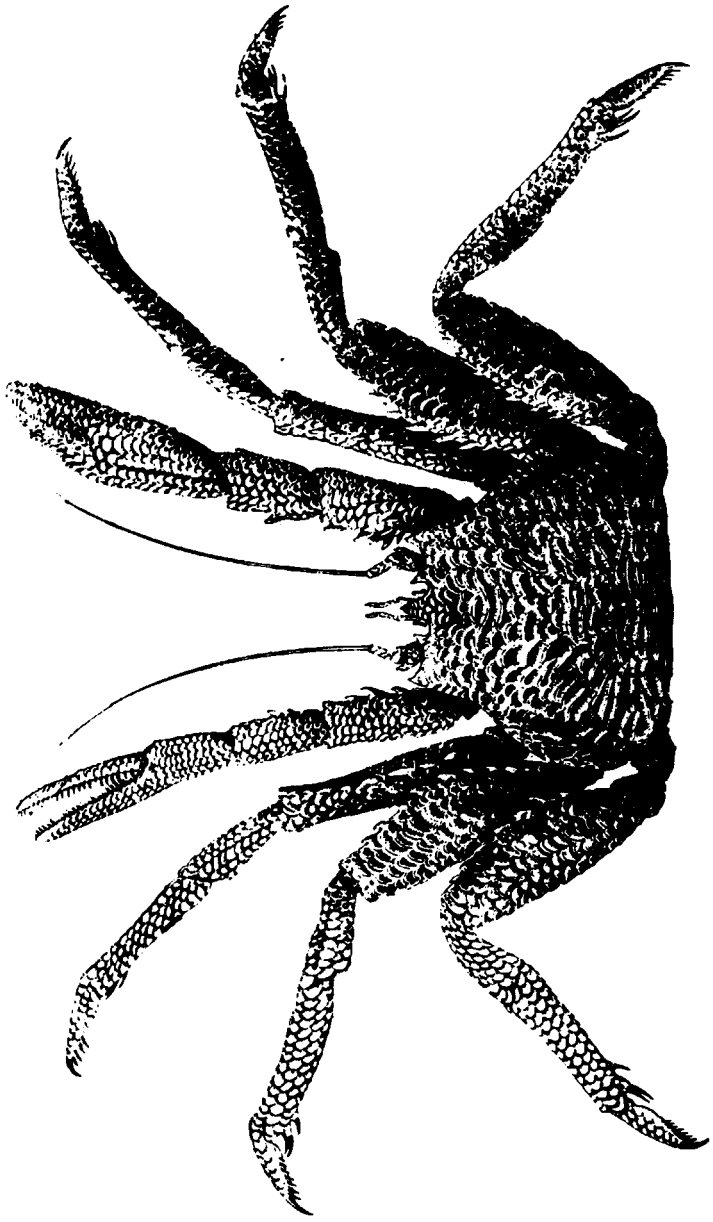

Figure 81. Placetron wosnessenskii Schalfeew

lateral edges are almost parallel. The surface of the carapace is covered with round, raised, squamous prominences, which are fused on the gastric area and the posterior part of the carapace to form longer, transverse crests. Short, erect hairs arise from the anterior edges of these crests. The rostrum is triangular, extending slightly beyond the eyes, it has a rounded tip and a deep longitudinal furrow on its superior surface; seen in profile its tip is clearly bent downward. The anterolateral angles of the carapace have the form of large, pointed spines. The frontal edge – above the base of the antennae – bears a distinct spine, which, however, is sometimes missing. The scaphocerite has the form of a short, fairly thick, apically rounded plate. The chelipeds are subequal, the right leg being somewhat thicker than the left. This difference becomes more pronounced with increasing size. The chelipeds are somewhat shorter than the walking legs, and are by no means as strong as in the other genera of the Hapalogastrinae; the surfaces of their joints are covered with scales similar to those on the carapace, but here the scales are smaller. The merus bears three spines on its internal edge and four on its superior surface. The structure of these spines is a peculiar one: each spine slightly resembles a large, semicircular scale under which a pin has been introduced and then raised to an angle of almost 45°, resting on its point; the result is a plate resembling a hut, the sloping side of which is directed forward. The carpus bears a spine on its anterior edge. The propodus is long and narrow, hardly broadening distally. The dactyli are long and equal; they are almost equal in length to the propodus, and have a deeply concave internal edge and broadly rounded tips. The prehensile edges bear small tubercles; above the edges there is a row of small tufts of hairs. Both dactyli have pointed corneous claws. The dactyli of the left chela are markedly longer than the propodus. The three subsequent pairs of legs are distinctly flattened, and the surface of their joints is covered with larger scales than those on the chelipeds; the anterior edge of the meri bears from five to eight spines; the carpi are smooth; the posterior edge of the propodi bears needlelike spines at the distal end; when bent, the dactylus is sheltered between these two spines; behind them is a similar, third, unpaired spine. The dactyli are flat, with ten to twelve corneous spinules on the posterior edge, which increase in size toward the strong terminal claw. Consequently, the whole animal has a peculiar squamate appearance. The abdomen is flat. The second segment is composed of a pair of marginal plates which are fused with a pair of large lateral plates, touching along the median line. The dorsal surface of the plates is covered with pubescent crests like those on the posterior part of the carapace. There is a depression in the center of each of the lateral plates.
249 The rest of the abdomen in the male is membranous, with the exception of the sixth segment and the telson; in the female, the left side of the abdomen bears three fairly well calcified plates; the dorsal surface of these plates shows arcuated hairy stripes.

Dimensions

Length of carapace	61.5 mm
Width of carapace	73.3 mm
Length of right cheliped	131.8 mm
Length of merus of right cheliped	31.0 mm
Length of chela of right cheliped	57.7 mm

Length of movable dactylus of cheliped. .	31.0 mm
Length of left cheliped	128.0 mm
Length of first walking leg	152.8 mm

Distribution. The Aleutians, and southward to British Columbia (Graham Island).

Subfamily **LITHODINAE**

Lithodinae Ortmann, 1901: 1147.

The carapace is swollen, oval or triangular, well calcified, covered on the dorsal surface with tubercles, other larger prominences and spines. In rare cases the dorsal surface is smooth. The rostrum is usually longer than the eyes; it is pointed and spiniform, bearing accessory spines. Sometimes it sppears like a blunt prominence; in rare cases it is flat and bifid. The dorsal side of the second abdominal segment is always completely covered by two marginal plates, two lateral plates, and one median plate, which may be clearly separated by sutures, or in some cases completely fused. The dorsal surface of the subsequent three segments is covered with hard, well-calcified plates and also with smaller calcified granules or nodules; the surface of the plates is frequently covered with tubercles, and in the middle of the plates there is sometimes a membranous sector. The females have paired pleopods on the first abdominal segment. The abdomen, on the whole, has a flattened form.

The genera of this subfamily are represented in almost all the seas, but are specific chiefly to the northern part of the Pacific Ocean. Their bathymetrical distribution is very broad.

Key to the Genera

1 (14). Lateral plates of third to fifth abdominal segments without membranous areas in the center.

2 (7). Superior surface of carapace covered with pointed or blunt spines. Rostrum spinelike, armed with a varying number of spines.

250 3 (6). Abdomen well calcified. Median plates of third to fifth abdominal segments replaced by membranous interspace bearing a varying number of calcareous nodules, sometimes fusing into minute plates. Carapace usually armed with sharp spines; gastric region bearing not less than four spines.

4 (5). Second abdominal segment covered by five distinct plates: an unpaired median plate and paired lateral and marginal plates. Scaphocerites well developed . . . . . 6. Paralithodes Brandt.

5 (4). Plates of second abdominal segment completely, or partly fused i.e., median plate fuses with the lateral ones, or the lateral plates fuse with the marginal ones. Scaphocerites rudimentary. . . . . 7. Lithodes Latreille.

6 (3). Abdomen more or less slightly calcified. Median plates of third to fifth abdominal segments distinct. Carapace usually armed with numerous short and blunt spines; gastric region bearing one strongly prominent spine. . . . . 8. Paralomis White.

7 (2). Superior surface of carapace smooth, or covered with large prominences of different shape and minute tubercles. Rostrum in the shape of a more or less large, blunt process, or flat and truncated.

8 (13). Carapace not forming large lateral enlargement covering the ambulatory legs; its surface not smooth, but bearing prominences of different shapes, and depressions. Rostrum neither flat nor truncated.

9 (12). Second abdominal segment entire. Marginal plates of third to fifth segments present. Carapace cardiform [sic] or of pentagonal-hexagonal shape, its posterior lateral angles without blunt prominences. Upper surface of carapace without deep hemispherical cavity.

10 (11). Carapace cardiform, its surface with large prominences of different shape. Rostrum with broad, rounded apex, and of a macelike shape. Ambulatory legs longer than the widest part of carapace. . . . . 10. Sculptolithodes Makarov.

11 (10). Carapace of pentagonal-hexagonal shape, its surface with minute tubercles. Rostrum short. Ambulatory legs shorter than the widest part of carapace. . . . . 11. Lopholithodes Brandt.

12 (9). Second abdominal segment consists of five distinct plates; marginal plates of third to fifth abdominal segments wanting. Carapace of triangular shape with highly prominent posterior lateral angles. Upper surface of carapace with deep hemispherical cavity. . . . . 9. Rhinolithodes Brandt.

13 (8). Carapace forms wide lateral enlargements almost completely covering ambulatory legs; its surface almost smooth.

251 Rostrum broad, flat, with truncated or more or less rounded apex. . . . . 12. Cryptolithodes Brandt.

14 (1). Lateral plates of third to fifth abdominal segments with concave membranous areas in the center. . 5. Phyllolithodes Brandt.

5. Genus PHYLLOLITHODES Brandt

Phyllolithodes Brandt, 1849: 175; Holmes, 1900: 121; Schmitt, 1921: 153. – Petalocerus White, 1856: 134.

Type species: Phyllolithodes papillosus Brandt.

The carapace is triangular, its surface covered with large granules; in the middle of the dorsal surface of the carapace is a depression, which is actually composed of two small hollows; the lateral edges of the carapace bear spines. The rostrum is long, with two swollen apical prominences. The scaphocerite is well developed, and is made up of three foliaceous lobes. The chelipeds and the walking legs are covered with long, cylindrical, blunt spines, and shorter, erect spines on the surfaces of the joints. The second abdominal segment is made up of a median plate and

two lateral plates, which are fused with the marginal plates. The lateral plates of the three subsequent segments have a hollow, membranous median sector, which is covered with calcified nodules; the membranous spaces between the lateral plates are also covered with nodules, which are, however, more or less fused with each other to form small, narrow, median plates.

1. Phyllolithodes papillosus Brandt (Figure 82)

Phyllolithodes papillosus Brandt, 1849: 175; Holmes, 1900: 122 (from the literature); Rathbun, 1904: 104; Way, 1917: 354, Figure 7; Schmitt, 1921: 153, Figure 99, Pl. 22, Figure 2.

The carapace has a triangular form; the gastric region is elevated; it bears cylindrical thickenings, directed backward; the thickenings form a heart-shaped pattern on the surface of the carapace, parallel to the edges of the carapace; the center of this pattern is occupied by two deep hollows, connected in their anterior part by means of a deep furrow. The rostrum is fairly long, digitiform, oriented obliquely upward, and bearing two swollen apical prominences; the superior edge bears two tubercles near the base; the anterior tubercle is larger and laterally compressed, while the posterior one is rounded; near the base the inferior edge bears a spiniform outgrowth, directed forward and bent upward; above the base of this outgrowth a pair of small spines is found. The anterolateral angle of the carapace bears a long, blunt spine, and the frontal edge bears a similar smaller spine above the base of the antennae; this spine is directed slightly downward. The swollen lateral edge of the carapace, behind the cervical groove, bears three long, blunt spines which are directed obliquely upward and outward; the anterior one of the three spines is shorter than
252 the other two. The posterolateral angles of the carapace are thickened, and bear three blunt prominences; the strongest of these – the anterior one – is oriented upward, outward, and forward; the posterior spine is small, short, and rounded. The posterior edge of the carapace is straight, with no median cavity, cylindrically thickened, and slightly swollen on both sides of the median line. The surface of the lower parts of the carapace is covered with flat granules with a flowerlike contour; the surface of the raised part of the carapace, of the rostrum, and of the spines is covered with smaller granules, which have the form of strawberries. The eyestalks are covered with flat spines, particularly on the superior side, near the cornea. The scaphocerite is made up of three foliaceous lobes; the innermost lobe is directed forward, the other two forward and outward; the edges of the lobes are very slightly denticulated. The chelipeds have a similar form, the right leg being somewhat larger than the left; the merus and the carpus bear two types of spines: long spines, which extend vertically and have the same form as those of the lateral edges of the carapace, and sparse short spines, which extend vertically upward and then curve in a right angle parallel to the surface of the carapace; in addition, the tips of these latter spines are always parallel to the longitudinal axis of the joint. The internal edge of the propodus bears long spines, while the superior surface and a part of the inferior surface near the internal edge are covered with erect spines of the second type; these spines frequently bear apical tufts of hairs.

The dactyli are smooth, and bear tufts of red hairs; the external edge of the movable dactylus has a blunt basal spine; the prehensile edges of the dactyli of the right chela bear large white tubercles; on the immovable dactylus these tubercles are disposed in two rows; the tips are blunt, rounded, and corneous; the tubercles of the prehensile edges are smaller on the left chela, and they are not disposed in two rows on the immovable dactylus. The walking legs also bear spines of the two above-mentioned types; the long spines are particularly well developed on the meral and carpal joints. The dactyli are covered at their bases with spines, which are parallel to the axis of the dactylus; the inferior edge bears short corneous spinules; the tip bears a strongly curved, corneous claw. The second abdominal segment is made up of a median plate and two lateral plates, which are fused quite closely with the marginal plates: the suture between them is barely visible; the central parts of the lateral plates are depressed on both sides of the median plate; their bottom is formed of a membrane covered by several calcified nodules. The three subsequent segments have large lateral plates, and are also depressed in the middle; there are small marginal plates which, in the female, are fused on the left side with the lateral plates. Between the lateral plates of these three segments, narrow median plates are found; each of these plates is bipartite, and is separated from the adjacent plates by a membranous space; all the membranous spaces are
253 covered with calcareous nodules. The telson of the male bears two terminal spines. The cylindrical thickenings of the dorsal surface of the carapace are less distinct in the younger specimens, the papillae still have the same form, and the spines bear numerous additional spinules; the smaller spines of the appendages are still vertical; the rostrum is short and has the form of an outgrowth bearing three round, apical swellings; only the two anterior lobes of the scaphocerite are still developed and have denticulated edges.

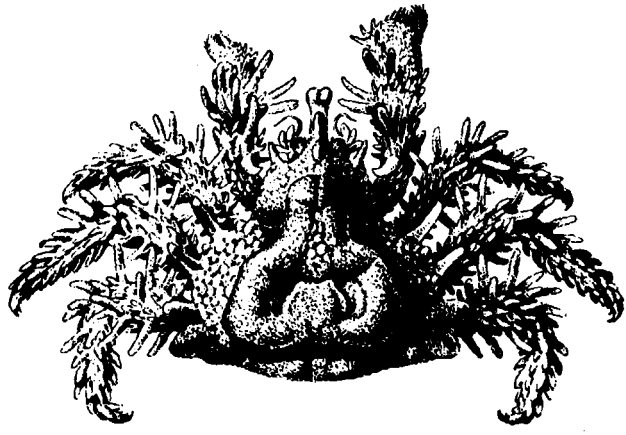

Figure 82. Phyllolithodes papillosus Brandt

Dimensions

Length of carapace	31.0 mm
Width of carapace	31.0 mm

Length of merus of right cheliped.	8.5 mm
Length of carpus of right cheliped	6.0 mm
Length of chela of right cheliped	13.0 mm
Length of first walking leg.	32.0 mm

Distribution. Western coast of North America, from Unalaska southward to Monterey, California. On rocky bottoms, from the tidal zone, to a depth of 30 m.

6. Genus PARALITHODES Brandt

Paralithodes Brandt 1849: 173.

Type species: Paralithodes brevipes (A. Milne-Edwards and Lucas).

The rostrum is, as a rule, fairly long and spiniform, with a pointed tip (in a few cases, a blunt tip), bearing several additional spines. The scaphocerites are well developed and spiniform; they are either simple or
254 bifid. The dorsal surface of the carapace is spinulose. The dorsal surface of the second abdominal segment is made up of five plates separated by distinct sutures, namely, two marginal and two lateral plates, and a median plate. The three subsequent abdominal segments are made up of three pairs of lateral plates and a variable number of marginal plates; the anterior and posterior edges of the lateral plates of these segments are adjacent. The middle of the dorsal surface of the abdomen, between these three pairs of lateral plates, is membranous, and bears some calcified nodules, which are disposed in more or less regular transverse rows.

Paralithodes, established by Brandt as a subgenus of Lithodes, was subsequently raised to the rank of an independent genus. The species of this genus are exclusively limited to the northern Pacific*.

Key to the Species

1 (2). Scaphocerite simple, sharp, spinelike in shape. Dorsal surface of rostrum bearing strong unpaired spine, the apex of which is usually bifurcate; tip of strong lower process sharp. Carapace rather uniformly covered with spines; gastric region bears six larger spines, set in two longitudinal rows with three spines in each. . . . . †1. P. camtschatica (Tilesius).

2 (1). Scaphocerite of different shapes, bifurcate or with four branches. Rostrum shorter and without strong unpaired spine on dorsal surface. Spines on surface of carapace more sparse.

3 (4). Scaphocerite of the shape of a long spine with two branches; tip of lower process of rostrum short; small spine between it and the pair of dorsal spines wanting. Cardiac region of carapace with six spines. Ambulatory legs spiny, the fingers comparatively long. . . . . †2. P. platypus Brandt.

* On the economic importance of the species of Paralithodes, see Introduction.

4 (3). Scaphocerite of the shape of a spine with four branches. Tip of lower process of rostrum blunt, often macelike and swollen; between it and the pair of dorsal spines, small spine usually found. Cardiac region of carapace with four spines. Ambulatory legs highly spinous, the fingers comparatively short . . . . . †3. P. brevipes (M. Edwards and Lucas).

†1. Paralithodes camtschatica (Tilesius) (Figures 83, 84, 85)

Maja camtschatica Tilesius, 1815: 336, Pl. 5, 6 – Lithodes spinosissimus Brandt, 1849: 172. – Lithodes camtschatica (-us) de Haan, 1850: 217, Pl. 47; Brandt, 1851: 94; Benedict, 1894: 483; Rathbun, 1904: 165. – Paralithodes camtschatica Brashnikow, 1907: 54, Figure 1, Pl. 2, Figure 3.

The width of the carapace in adult specimens slightly exceeds its length;
256 the superior surface of the carapace is evenly, but not densely, covered with fairly short, pointed, conical spines; the spines of the lateral edges of the carapace are very slightly larger than those of the surface; the surface spines are of two types: larger spines, with smaller spines scattered among them. The gastric area bears six larger spines disposed in two parallel longitudinal rows of three spines each. The cardiac area has six such spines distributed in the same way. The rostrum is provided with four spines: a strong inferior outgrowth with a pointed tip, directed forward and extending considerably beyond the eyes; a strong unpaired spine – directed obliquely upward and forward, and usually having a bifid tip – rises from the dorsal side of the rostrum, almost at the level of the eyestalks; there are, however, specimens in which the tip of this spine is simple and pointed; finally, the lateral edges of the broadened basal part of the rostrum each bear a small spine behind the unpaired dorsal spine. The scaphocerite has the form of a simple pointed spine. The chelipeds and the walking legs are covered with spines similar to those of the carapace; the inferior edges of the dactyli of the walking legs are frequently smooth in the adult specimens, as the spines found in the young specimens gradually disappear. Another difference between young specimens and adults is that the carapace has a slightly different form: in the young, the length exceeds the width and it is, therefore, more triangular; the most striking difference is the great length of the spines on the carapace – this induced Brandt to separate the species spinosissimus; the disposition of the spines is, however, similar to that of adult specimens; the relative length of the rostrum is also greater in young specimens than in adults.

Dimensions

Length of carapace (including rostrum). .	105.0 mm
Width of carapace	92.0 mm
Length of merus of right cheliped	35.0 mm
Length of carpus of right cheliped. . . .	30.0 mm
Length of chela of right cheliped	56.0 mm
Length of merus of first walking leg. . .	64.0 mm
275 Length of carpus of first walking leg. . .	39.0 mm
Length of propodus of first walking leg. .	45.0 mm
Length of dactylus of first walking leg . .	34.0 mm

Figure 83. Paralithodes kamtschatica (Tilesius)

Figure 84. Paralithodes camtschatica (Tilesius) rostrum, lateral view

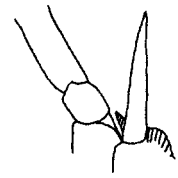

Figure 85. Paralithodes camtschatica (Tilesius), right scaphocerite

Distribution. Japan, coasts of Hokkaido; in the Soviet waters of the Sea of Japan this species extends to Cape Gamova; Sea of Okhotsk; eastern shores of Kamchatka; southern part of Bering Sea; along the Asiatic coast it probably extends no farther than Cape Olyutorsk; the Aleutians; along the western shores of North America from Norton Sound to Queen Charlotte Islands, British Columbia. The report made by M. Rathbun(1919) from the region of Point Barrow is based only on the finding of a propodus of the left cheliped, but this probably belongs to P. platypus. At depths ranging from 14 to 250 m.

†2. Paralithodes platypus Brandt (Figures 86 to 91)

Lithodes platypus Brandt, 1850: 236; 1851: 94. – Lithodes camtschaticus Richters, 1883: 404, Figures 9, 10. – Lithodes brevipes Benedict, 1894: 484 (part). – Paralithodes platypus Brashnikow, 1907: 58, Figure 2, Pl. 1, Figure 2.

The carapace is heart-shaped; the superior surface is covered with a few short, fairly blunt spines. The gastric area – as in P. camtschatica – bears six spines disposed in two longitudinal rows of three spines each. In the larger specimens an additional fairly strong spine is found behind the posterior pair. The cardiac area bears four spines; each branchial area bears six spines. Between the spines, the surface of the carapace is covered with small flat granules, which impart to it a rough [shagreened] appearance. The lateral and posterior edges of the carapace bear spines which appear as a border, owing to the fact that the spines on the actual surface are sparse. The spines of the posterior edge and of the rounded posterolateral corners are smaller than those on the edge of the anterior part of the branchial areas. There is a certain variability in the number and disposition of the spines on the carapace. Thus, for instance, in a large female specimen each branchial area bears seven spines, the cardiac area bears three spines in the left row, two spines in the right row, and two other small, but visible spines behind these rows. The rostrum is relatively short, directed slightly downward, and bears only three large pointed spikes: the unpaired inferior outgrowth is short and has a pointed tip; above it, on the dorsal side, a pair of pointed conical spines is found. Behind these spines the rostrum becomes broader and thicker and bears four minute spines which are visible only in large specimens. One of these spinules is situated in the middle, behind the pair of large spines, two are situated on the lateral edge somewhat beyond the median spine, while the fourth, a

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Figure 86. Paralithodes platypus Brandt

very small one, and not always visible, is also situated in the middle, behind the lateral spinules. One of the specimens has an abnormally shaped rostrum. Instead of a pair of strong spines on the dorsal side, it bears a
(259)

Figure 87. Paralithodes platypus Brandt, lateral view of rostrum

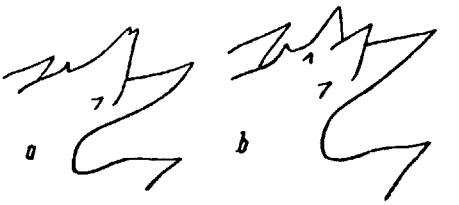

Figure 88. Paralithodes platypus Brandt, superolateral view of rostrum: a–abnormal form; b–normal form

Figure 89. Paralithodes platypus Brandt, right scaphocerite

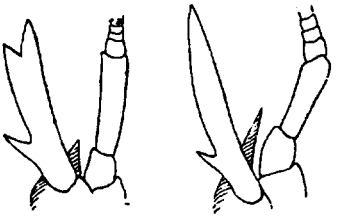

Figure 90. Paralithodes platypus Brandt, abnormal form of left scaphocerite

260 stout conical spine with a bifid tip. The scaphocerite has the form of a bifid spine, the inner branch being somewhat larger than the outer one. The external edge of the scaphocerite sometimes bears one or two additional

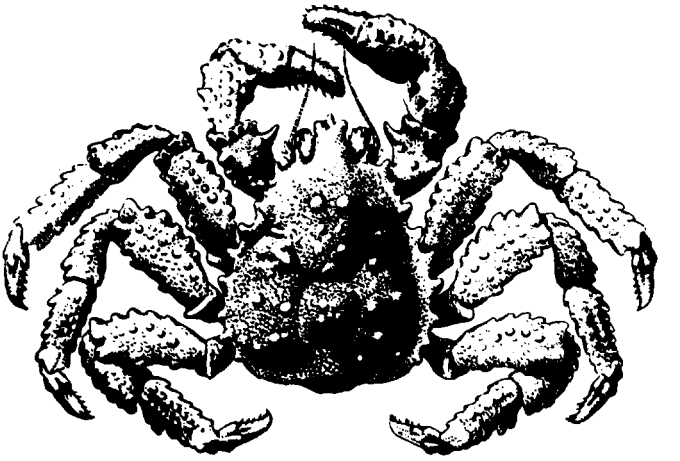

Figure 91. Paralithodes platypus Brandt, young specimen

minute spinules. In a large female both scaphocerites have an abnormal form: the right scaphocerite is stout, ramified only at its very tip, the left one is also stout but not ramified at all. In another female the right scaphocerite is normal, the left one has a normal inner branch, but instead of an outer branch it bears only two short adjacent spinules. The chelipeds and the walking legs are sparsely spinulated, the spines being situated chiefly on the superior edges of the joints. The joints of the walking legs of the smaller specimens are appreciably compressed. A young specimen of P. platypus is characterized by the lack of spines on the surface of the carapace and on the legs. Instead of spines there are round tubercles, their number and disposition corresponding exactly to the number and disposition of the spines in adults. Thus, in P. platypus, the process of formation of the spines is inverse compared to the process which takes place in the other two species of Paralithodes. In these species, the young specimens are those bearing longer and more pointed spines; these spines become shorter with increasing age, finally becoming tubercles in the largest specimens. In P. platypus, however, the largest specimens are those that bear the most pointed spines. In young specimens, the surface of the carapace is thickly covered with small round granules. The rostrum of young specimens is distinguished by the fact that the two large dorsal spines still have the form of rounded tubercles.

Dimensions

Length of carapace (including rostrum). .	90.0 mm
Width of carapace	82.0 mm
Length of merus of right cheliped	33.0 mm
Length of carpus of right cheliped. . . .	28.0 mm
Length of chela of right cheliped	55.0 mm
Length of merus of first walking leg. . .	45.0 mm
Length of carpus of first walking leg. . .	30.0 mm
Length of propodus of first walking leg. .	36.0 mm
Length of dactylus of first walking leg . .	33.0 mm

Distribution. Northern part of the Sea of Japan, along the Soviet shores southward to Cape Gamova; not reported from Japan; Sea of Okhotsk; eastern shores of Kamchatka; Bering Sea northward not farther than Bering Strait. The problem of the distribution of P. platypus on the American shores of Bering Sea is somewhat unclear. This species is not mentioned at all in the American works; it is only on the basis of Richter's data (1883) that we can indicate the presence of P. platypus in the region of the Pribilof Islands. It is found at depths ranging from 12 to 500 m. The report by J. Zachs (1936) of this species at depths of 800 to 1,000 m is erroneous. The Bering Sea Expedition of the Hydrobiological Institute found this species at a maximum depth of 93 m.

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†3. Paralithodes brevipes (M. Edwards and Lucas)

Lithodes brevipes A. Milne-Edwards and Lucas, 1841: 465; Pl. 24, 25, 26, 27; Brandt, 1851: 99; Benedict, 1894: 484 (part); Rathbun, 1904: 165.

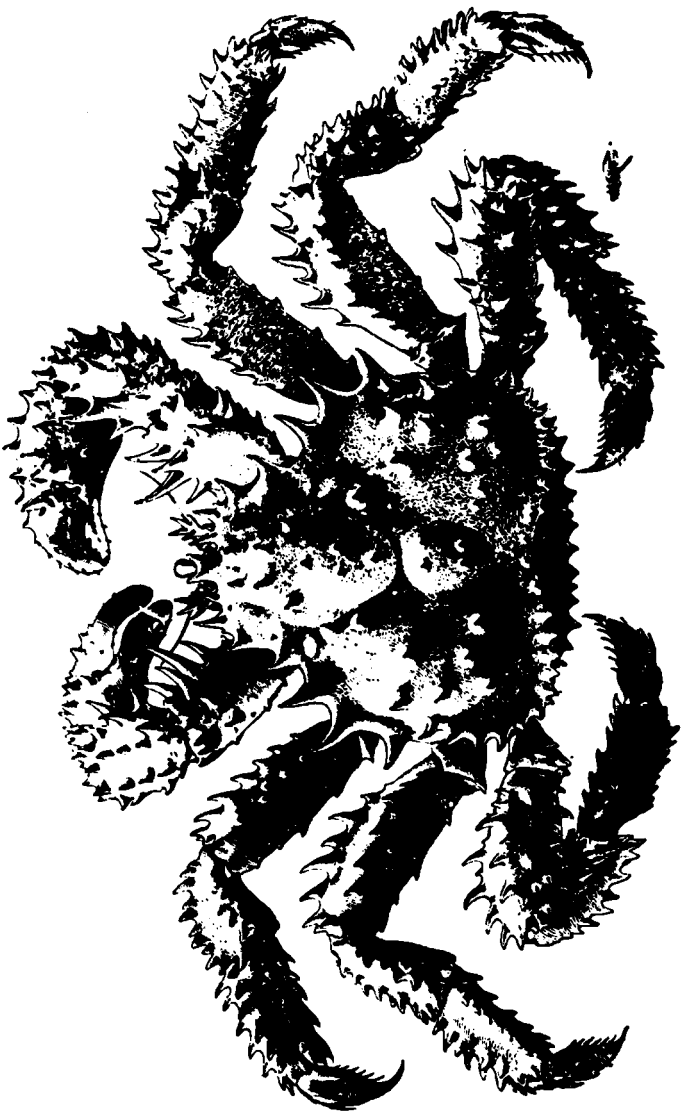

Figure 92. Paralithodes brevipes (M. Edwards and Lucas)

The width of the carapace somewhat exceeds its length. Between a few large spines, the surface of the carapace is completely smooth. The gastric area bears ten spines, disposed differently than in P. camtschatica and P. platypus: the anterior part bears two pairs of spines; beyond them

Figure 93. Paralithodes brevipes (M.-Edw. and Lucas), lateral view of rostrum

Figure 94. Paralithodes brevipes (M.-Edw. and Lucas), right scaphocerite

another pair of more widely spaced spines is found; these are followed by an unpaired median spine, then by a pair of spines very close together, and finally by a posterior unpaired median spine. The branchial area usually bears seven spines; sometimes, a number of spines on the posterior part of the branchial area are bifid. The lateral edges of the carapace bear large spines, which form an even more distinct border than in P. platypus. The anterior edge of the narrower anterior part of the carapace bears three spines on each side of the rostrum. Two of these spines are directed forward, while the third is already found on the lateral edge. Between these spines, small additional spines are sometimes found. Each lateral edge also bears four large spines, the anterior one of which is still found on the narrow anterior part of the carapace in front of the cervical groove, while the subsequent three spines are found on the edge of the rounded, broadened part. Finally, the rounded posterolateral corners and the posterior edge of the carapace bear 12 or 13 smaller and denser spines on both sides. The rostrum is fairly short, composed of an inferior, unpaired outgrowth, which is curved, directed downward, and has a clavate, broadened terminal end. The dorsal surface of the rostrum bears a pair of spines, directed upward; in front of them, on the sloping dorsal part of the rostrum, is a small spine which, however, is sometimes lacking. The tip of the rostrum is more pointed in young specimens. In a specimen captured by M. Yu. Bekman and K. A. Vinogradov in Akhomten Bay (eastern shores of Kamchatka), the tip of the rostrum is pointed as in P. platypus, though all its other features refer the specimen to P. brevipes. The scaphocerite has the form of an outgrowth with four spines: three large spines directed forward and outward, and a fourth, smaller spine located on the internal edge. The chelipeds and the walking legs bear numerous large spines. Exceptionally long spines are found on the internal edge of the merus and the carpus of the chelipeds.
263 The walking legs are also very spinose, the spines on the propodal joints disposed in four longitudinal rows; the dactyli of the walking legs are short and broad, bearing dark, pointed spines along their inferior edge. The spines on the median plate of the abdominal segment are disposed differently than in P. camtschatica and P. brevipes; in these latter species the four large spines form a square, and the two inferior spines are situated on the posterior edge of the plate; in P. brevipes the four spines form a rhombus, which is located in the center of the plate.

Dimensions

Length of carapace (including rostrum).	83.0 mm
Width of carapace	86.0 mm
Length of merus of right cheliped . . .	35.0 mm
Length of carpus of right cheliped . . .	35.0 mm
Length of chela of right cheliped. . . .	62.0 mm
Length of merus of first walking leg . .	48.0 mm
Length of carpus of first walking leg. .	34.0 mm
Length of propodus of first walking leg.	32.0 mm
Length of dactylus of first walking leg .	27.0 mm

Distribution. Northern part of Sea of Japan, not passing south of Cape Povorotnyi; Sea of Okhotsk; eastern shores of Kamchatka; southern part of Bering Sea (in the region of the Aleutian Range). We cannot admit the existence of P. brevipes in all parts of the Bering Sea. As pointed out by J. Zachs (1936), this species probably does not extend farther than the Commander Islands and Unalaska. Consequently, it does not extend farther north than the Aleutian Range. In the littoral zone, and to a depth of 50 m.

7. Genus LITHODES Latreille

Lithodes Latreille, 1806: 39; Milne-Edwards, 1837: 184; Bell, 1853: 163.

Type species: Lithodes maja (Linné).

The rostrum is long and spinulated. The carapace is broad, and covered with spines. The scaphocerites are rudimentary or lacking (only in two cases are there well-developed scaphocerites, namely, in L. antarctica and L. panamensis, but here there are also deviations in the structure of the second abdominal segment; both cases are considered by Bouvier as being atavisms). The median plate of the second abdominal segment is fused with the lateral plates, which in turn are also very frequently fused with the marginal plates. In such cases the whole segment looks as though formed of a single plate. As in Paralithodes, the three subsequent abdominal segments bear marginal plates, and the central part is covered with calcified nodules. The species of this genus are found in the oceans of both hemispheres.

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Key to the Species

1 (2). Carapace evenly covered with spines of almost equal size; spines on lateral margins of same size as surface spines or only slightly longer. Rostrum armed with nine spines. Scaphocerite has the form of a fairly long bifid spine. . †1. L. aequispina Benedict.

2 (1). Surface of carapace covered with relatively large and small spines; spines on lateral margins distinctly longer than spines on surface of carapace. Rostrum armed with eight spines. Scaphocerite rudimentary.

3 (4). Anterolateral margin of carapace armed with long spines; no large spines on margins of branchial region. Terminal part of rostrum relatively stout, with bifid tip. Chelipeds and walking legs covered with relatively long spines. Dactylus of first walking leg considerably more than half the length of the propodus. Surface of second abdominal segment spinose. . . . †2. L. maja (Linné).

4 (3). Anterolateral margin of carapace armed with moderately long spines; only on rounded margins of branchial region two very long spines project on each side. Terminal part of rostrum slender, with bifid tip. Chelipeds and walking legs covered with short spines. Dactylus of first walking leg barely half the length of the propodus. Surface of second abdominal segment covered with tubercles . . . . . 3. L. couesi Benedict.

†1. Lithodes aequispina Benedict (Figures 95 to 97).

Lithodes aequispinus (-na) Benedict, 1894: 481; Rathbun, 1904: 166; Yokoya, 1933: 94. - Paralithodes longirostris Navosov-Lavroff, 1929: 174, Figures 3 to 5.

The carapace is evenly and fairly densely covered with conical, pointed spines which are only slightly longer on the lateral edges of the carapace than on the surface. The areas of the carapace are fairly distinct. The external orbital angles bear long spines, directed forward and usually reaching the tips of the eyestalks. The rostrum has a fairly broad base and bears nine strong spines. Two spines are found on each of its lateral edges. There are two more on the dorsal surface of the rostrum, directed obliquely upward and forward; the first of these spines is situated in front of the anterior pair of lateral spines, while the second is situated in the space between the first and second pair of lateral spines. On the tip of the terminal part
266 of the rostrum are two spines directed horizontally forward and outward, the distal end of the rostrum thus appearing bifid. Finally, under the base of the rostrum is a strong curved spine directed somewhat downward. The scaphocerite has the form of a bifid spine whose inner branch is longer than the outer one. The chelipeds are relatively weak, the right leg only slightly larger than the left one; all the joints are spinose, the longest spines being those at the inner distal angle of the merus and on the internal edge of the carpus. The walking legs are densely covered with relatively long pointed spines. The median plate of the second abdominal segment is fused with the lateral plates; the sutures between the lateral and the marginal plates are still distinct. The three subsequent segments are made up of lateral and marginal plates; the space between the lateral plates is covered with small plates bearing conical spines. The surface of the second segment bears spines; the spines on the lateral plates are marginal. The spines of the surface are relatively longer and more slender in the young specimens, which somewhat resemble, therefore, young specimens of Paralithodes camtschatica.

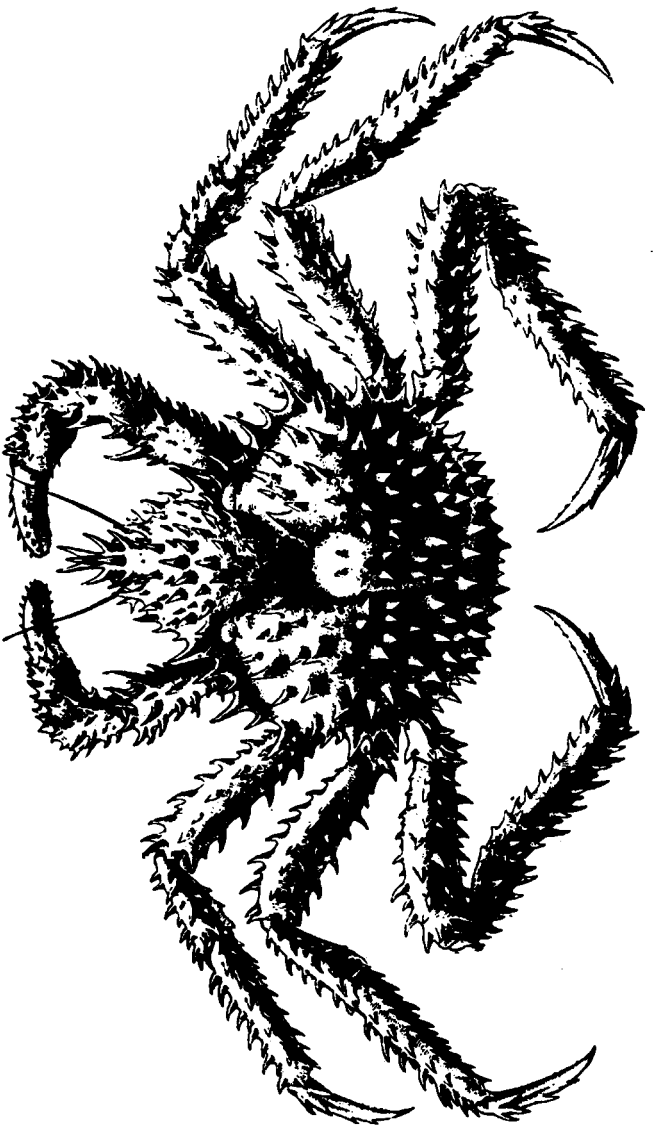


Figure 95. Lithodes aequispina Benedict

Dimensions

Length of carapace	101.0 mm
Width of carapace	80.0 mm
Length of rostrum	20.0 mm
Length of merus of right cheliped	30.0 mm
Length of carpus of right cheliped	24.0 mm
Length of chela of right cheliped	46.0 mm
Length of first walking leg	161.0 mm

Distribution. Bering Sea, in the region of the Pribilof Islands; Sea of Okhotsk; Japan: east of Siwoya Cape. At depths ranging from 315 to 730 m.

Figure 96. Lithodes aequispina Benedict, lateral view of rostrum

Figure 97. Lithodes aequispina Benedict, right scaphocerite

267 †2. Lithodes maja (Linné) (Figures 98 to 100)

Lithodes maja Leach, 1815, Pl. 24; Bell, 1858: 165; Ortmann, 1892: 320; Hansen, 1908: 22. – Lithodes arctica Milne-Edwards, 1837: 186; Boas, 1880: 117; Bouvier, 1894: 181, Pl. 10, Figure 7, Pl. 12, Figures 5a, 5b.

The carapace has a fairly regular pear-shaped or heart-shaped form, with clearly defined areas. The surface is covered with small granules and relatively short conical spines; on each branchial area, five or six of the longest spines are found; there are four spines on the swollen cardiac area, while on the gastric area, six spines are disposed in two longitudinal rows of three spines each. The rostrum bears eight spines; it is either horizontal or directed slightly upward. Two pairs of spines are found on the lateral edges of the rostrum, the posterior pair small in comparison with the strong anterior pair; the spines of this pair are fused by their broad bases. Between these lateral pairs of spines on the dorsal surface, but nearer to the posterior pair, a small unpaired spine is found. In front of the anterior pair of lateral spines the rostrum has the form of a smooth tip, which is slightly flattened dorsoventrally and appears bifid owing to its two apical spines. Finally, below the base, there is a strong unpaired spine, directed downward and forward. The length of the smooth elongated part of the rostrum, between the distal bifurcation and the anterior pair of lateral spines is equal to the length from this point to the base of the rostrum. The anterolateral edge of the carapace bears six long, pointed spines

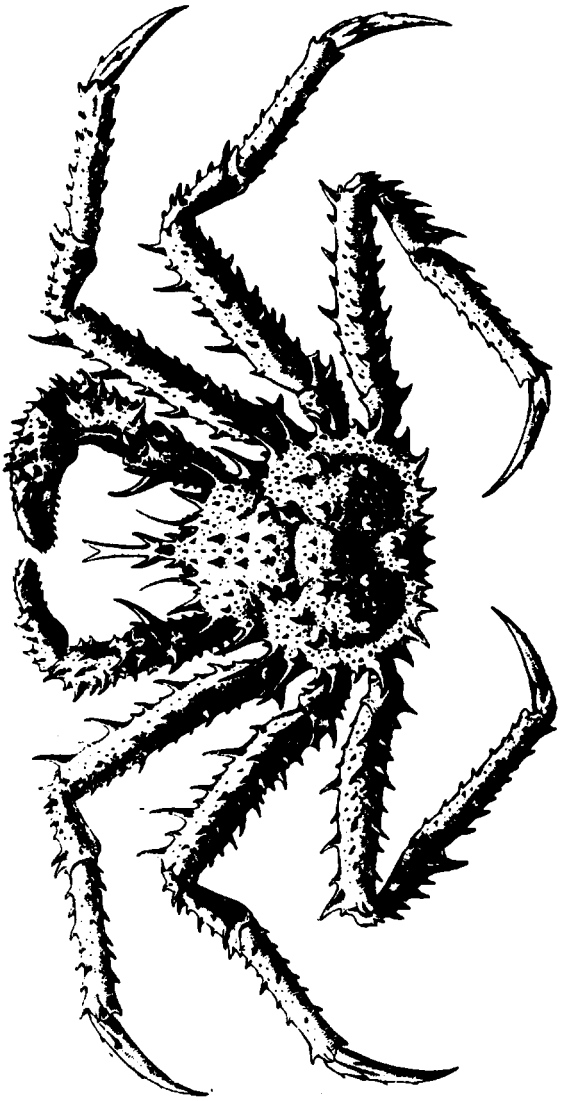


Figure 98. Lithodes maja (Linné)

which are directed upward and outward; the longest of these spines are the two posterior ones, while the anterior spine, located at the external angle of the orbit, is the smallest; the posterolateral and posterior edges bear small, but strong spines with some weaker spines among them; the median pair of spines on the concave posterior edge of the carapace is more erect than the other lateral spines. In the middle, between the spines of this pair and slightly in front of them, is another small unpaired spine, which is also erect. Thus, the posterolateral edges each bear some 15 spines, all of them considerably longer than those on the surface of the carapace. The eyestalks are small. Each scaphocerite has the form of a short, flattened spine with two small spinules on the internal edge. The right cheliped is larger than the left one; the merus bears numerous pointed spines, the longest of which is situated on the internal edge, near the distal end; the carpus bears two strong spines on its internal edge; the chela is evenly swollen; the dactyli are stout and bear strong tubercles on their proximal edges. The walking legs are fairly slender, long, flattened, and spinulose, particularly along the edges of the joints; the dactyli are long and curved, very slightly armed, and are considerably more than half the length of the propodi. There are four spines on the distal end and two or three small spines on the superior edge; the claw is long and pointed. The first abdominal segment has a pair of median spines on the posterior edge. The second segment is not divided, though sometimes the marginal plates are quite clearly defined. The two round lateral depressions on the surface of this segment are connected by a transverse furrow; two strong
269 median spines are found on the posterior edge; in addition, the posterior edge bears four strong spines; the two median spines are situated one above the other; the rounded anterior edge bears several stronger spines near the lateral corner, while the surface of the segment is covered with smaller spines. The three subsequent segments have large lateral plates and

Figure 99. Lithodes maja (Linnĕ) lateral view of rostrum

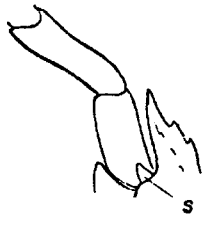


Figure 100. Lithodes maja (Linnĕ), right scaphocerite(s)

several marginal ones; the surface of all these plates is covered with short spinules; the membranous median sector is covered with large and small calcareous nodules, which are sometimes fused to form small irregular plates.

Dimensions

Length of carapace (including rostrum). .	108.0 mm
Width of carapace	79.0 mm
Length of rostrum	30.0 mm
Length of merus of right cheliped	35.0 mm
Length of carpus of right cheliped	28.0 mm
Length of chela of right cheliped	58.0 mm
Length of merus of first walking leg . . .	67.0 mm
Length of carpus of first walking leg. . .	35.0 mm
Length of propodus of first walking leg. .	51.0 mm
Length of dactylus of first walking leg . .	42.0 mm

A large male specimen belonging to this species is found in the Collections of the Zoological Institute of the Academy of Sciences (No 4,020, collected by Greving), and is labeled "variety", probably because of the form of its rostrum; it seems, however, that this form is the result of a regeneration of the rostrum, and therefore does not justify the creation of a
270 variety. A short spine is directed forward from the broad base of the rostrum, which – as in normal cases – bears three spines on the dorsal surface. Neither the unpaired ventral spine nor the two dorsal spines are present, and the rostrum does not have a bifid tip. All the other features of this specimen correspond to the typical L. maja. The exact locality where this specimen was captured is not mentioned; it is possible that this isolated find is due to a chance appearance, since this species is unknown in the White Sea and no author has reported it from there.

Distribution. The Shetlands and the Faroes; the shores of England; rarely on the Belgian shores; North Sea; Skagerrak and Kattegat; shores of Norway; west Murman coast (as far as Teriberka). The northernmost locality: 74°25'N 17°36'E and on the western coast of Spitsbergen (this report is somewhat doubtful); Iceland; eastern and western Greenland. Eastern coast of North America from Newfoundland to 40°N. latitude. Usually at depths between 40 and 80 m, but may reach a depth of 500 m.

3. Lithodes couesi Benedict (Figure 101)

Lithodes couesi Benedict, 1894: 481; Rathbun, 1904: 166; Schmitt, 1921: 162, Pl. 28, Pl. 29, Figures 3 to 5.

[Original description of Benedict, 1894]

"This species reminds one of L. maia. The largest spines of the carapace are arranged about the margin; they are slender and sharp. The longest are situated at the outer orbital angles, the antennal angles, the hepatic regions, and three on the margin of the branchial regions. The spines on the intervening spaces of the margin are more numerous and much smaller. The surface of the carapace is set with short, sharp, conical spines. The gastric region is swollen and well defined. The cardiac region

is barely indicated between the confluent branchial regions. The depression between the gastric and cardiac regions is very deep. The rostrum is 20 mm long, and made up as in L. maia, but the terminal portion beyond the distal lateral branches is slender and bifid rather than bifurcate as in L. maia; the basal branches are a little further forward. The scale is rudimentary; the spine at the outer angle is branched at the base, the branch consisting of a single short, sharp spine on the outer surface. The abdomen is without spines; the spines of L. maia are replaced by tubercles; those of the first segment are very much closer together than the corresponding spines in L. maia. The tubercles on the lower margin of the second segment are low and somewhat oblong at base; those in the center of the segment are larger.

"The chelipeds are slender and weak. The armature of the fingers of the right hand is slight; the fingers gape. The fingers of the left hand are long and slender and gape at base. The spines of the chelipeds and ambulatory legs are numerous and arranged about as in L. maia, but are shorter" (Benedict).

[From Schmitt, 1921]

"From the Shumagin Banks, Alaska ('Albatross' station 3338), Benedict records three young specimens which he refers to this species 'without hesitation.' Regarding them he says: 'The rostrum differs in being bifurcate as in L. maia. It is possible that additional specimens of the adult might show the rostrum to be bifurcate rather than bifid.' This does not prove to be the case, however, for two adult males from off San Diego ('Albatross' stations 4400 and 4333) have the characteristic rostrum of the type. Two other young specimens were also taken off San Diego in 500 to 530 fathoms ('Albatross' station 4335)." (Schmitt).

The length of the carapace (type ♂), the rostrum included, is 105 mm, and its width 81 mm.

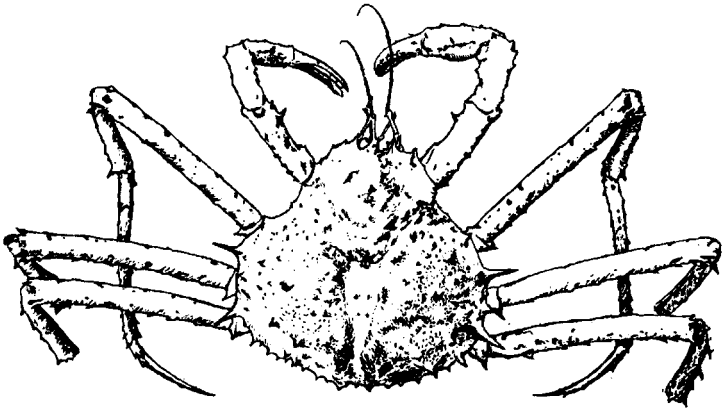


Figure 101. Lithodes couesi Benedict (From Schmitt, 1921)

Distribution. Bering Sea, north of Unalaska near the Shumagin Islands, Alaska; near San Diego, California. At depths of 542 to 1,125 m.

8. Genus PARALOMIS White

Paralomis White, 1856: 134; Stimpson, 1858: 69; Henderson, 1888: 44; Schmitt, 1921: 158. Leptolithodes Benedict, 1894: 484. - Pristopus Benedict, 1894: 486.

Type species: Paralomis aculeata (Henderson).

The carapace has a rough granulation, or bears numerous, short and often blunt spines. The gastric area usually bears a strong spine which may be clearly distinguished, since its size greatly exceeds the other surface spines. The carapace does not form lateral expansions. The rostrum usually bears three spines; two of them are symmetrical, the median one, being asymmetrical. The scaphocerite is more or less triangular; its external edge is usually spinose. The walking legs are either flattened and spinose on the anterior and posterior edges, or they are angular
272 and have a triangular cross section, with spines on the crests. The second abdominal segment is undivided. The marginal plates of the third abdominal segment are fused with the respective lateral plates. The marginal plates of the subsequent segments are often fused. The median plates of the third to fifth segments are distinct, often separated from each other by membranous spaces; the nodules which cover these spaces are often fused, forming something like small plates.

The species of this genus are chiefly abyssal forms.

Key to the Species

1 (2). Carapace spinose, particularly on the margins, and on the gastric and rostral areas. Walking legs angular, not all flattened, with spines disposed in rows on the angles or on the crests. . . . . †1. P. multispina (Benedict).

2 (1). Carapace tuberculated, margins spinose; a single pointed spine is found on the gastric area. Walking legs markedly flattened; anterior and posterior edges bear pointed spines. . 2. P. verrilli (Benedict).

†1. Paralomis multispina (Benedict) (Figure 102)

Leptolithodes multispinus (-na) Benedict, 1894: 484; Rathbun, 1904: 165. - Paralomis multispina Schmitt, 1921: 159, Pl. 23, Pl. 30, Figures 7, 8.

[Original description of Benedict, 1894]

"The carapace is about as broad as long; the areolations are well defined. On the median line at the summit of the gastric region there is a sharp spine about four mm in length. The lateral margins are armed with from twelve to sixteen spines about three mm in length. In the young and in some of the adults there are small spines on the branchial region. A semicircular line of six or seven spines marks the limits of the branchial

and intestinal regions. The carapace is thickly studded with blunt spines, each terminating in a flattened face or surface cut obliquely to the surface of the carapace; this face is encircled by a fringe of short stiff bristles. The rostrum consists of a simple median spine with two basal spines. Under the rostrum proper there is a very short conical spine homologous with the subrostral spine of Lithodes; behind the spine are one or more spinules. The abdomen in the male is composed, after the second segment, of several rows of leathery plates; the second segment is better calcified and harder. The abdomen of the female is twisted to the right as in Lithodes.

"The chelipeds are moderately slender and extend almost to the distal end of the carpal joints. The spines on the inner margin of the carpal segments are the most prominent. The ambulatory legs are long and slender and thickly set with spines. The spines of the merus are not so distinctly
273 arranged in rows as on the carpal and propodal segments; there is, however, a distinct row on the upper margin. The spines of the carpus are arranged in eight more or less distinct rows; on the propodal segment the spines are arranged in six full rows and two half rows. There are four short rows of spines on the proximal end of the dactylus. The dactyli are compressed, slightly bent and a little twisted. An average-sized specimen measures 80 mm in length, 78 mm in breadth, and the distance from tip to tip of the ambulatory legs is 360 mm " (Benedict).

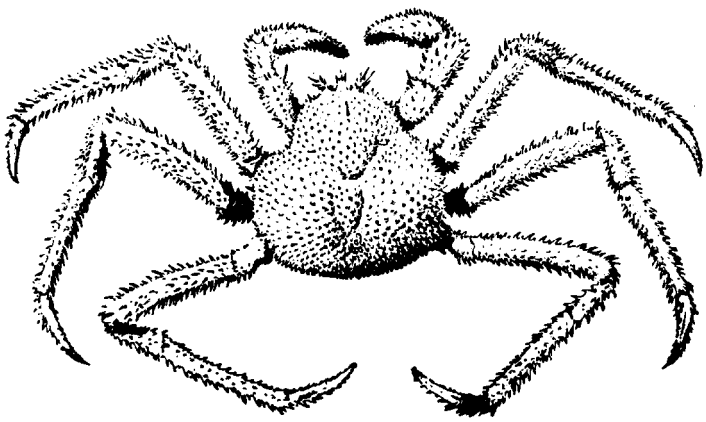


Figure 102. Paralomis multispina (Benedict) (From Schmitt, 1921)

Distribution. Western coast of North America, from the Shumagin Islands to San Diego, California; at depths ranging from 1,125 to 1,577 [meters]. A specimen of this species (juvenile male) was captured by the Bering Sea Expedition of the Hydrobiological Institute, on the eastern shores of Kamchatka, 52°42.5'N, 159°03.5'E, at a depth of 830 m.

2. Paralomis verrilli (Benedict) (Figure 103)

Pristopus verrilli Benedict, 1894: 486; Rathbun, 1904: 165. – Paralomis verrilli Schmitt, 1921: 159, Pl. 24, Pl. 30, Figures 5, 6.

[Original description of Benedict, 1894]

"The carapace is verrucose, the areolations prominent. The gastric region is much elevated and is surmounted by a small spine. On each side, on the border of the branchial region, there is a deep pit. A groove runs from the pits to the depression between the gastric and cardiac regions. There are about twelve spines, two to three mm in length on the lateral border of the carapace. The posterior boundary of the intestinal region is marked by a semicircular row of tubercles. The cardiac region is triangular; the apex of the triangle cuts well into the intestinal region where the depression that marks it runs into a deep slit or oblong median depression.
274 The frontal margin is broad and straight. The spines of the anterior angles and the orbital spines point forward; the orbital spines are a little the longer. Between the spine on the angle and the orbit there is a row of smaller spines and one or two granules. The trispinose rostrum is composed of a bifurcate rostrum proper and the subrostral spine which extends much beyond the two upper rostral spines. The antennal scale tapers to a sharp point and has three sharp spines or branches on each side. The lateral plates on the left of the abdomen in the female are fringed with short, slender, blunt spines.

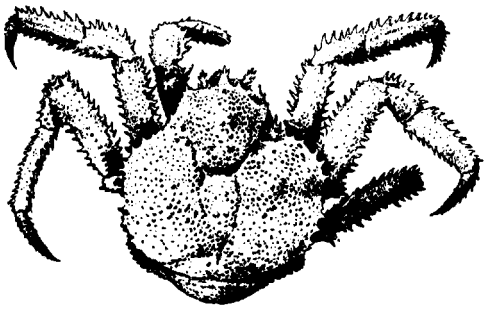


Figure 103. Paralomis verrilli (Benedict) (From Schmitt, 1921)

"The chelipeds extend a little beyond the middle of the propodal segment of the first pair of ambulatory feet. The right cheliped is stouter than the left. The prehensile edges of its fingers are strongly tubercular. The upper margin of the palm is spiny; there are also some small spines on the middle and on the lower margin. There are three long spines on the inner margin of the carpus. The left cheliped is similar but smaller, and the prehensile edges of the fingers are sharp. The ambulatory feet are wide and much compressed. The anterior and posterior margins are armed with sharp spines, alternating in general large and small. On the upper surface of the proximal end of the merus of the fourth pair of feet there is a row of fine spines; the corresponding spines on the third pair of feet are smaller, and on the second pair still smaller" (Benedict).

Length of carapace, including rostrum, 90 mm; length of rostrum 9 mm; width of carapace 82 mm.

Distribution. Bering Sea, from the region of the Pribilof Islands southward to Cortez Bank, California. At depths from 1,238 to 1,480 m.

9. Genus RHINOLITHODES Brandt

Rhinolithodes Brandt, 1847: 174; Schmitt, 1921: 157.

Type species: Rhinolithodes wosnessenskii Brandt.

The carapace has a clumsy triangular form with very produced posterolateral angles; the central part of the dorsal surface is occupied by a deep semicircular depression which separates the fairly smooth, spherical cardiac area from the other regions of the carapace, which are covered with flat, slightly prominent granules. The rostrum is short and blunt. The second abdominal segment is made up of five distinct plates. Each of the three subsequent segments is made up of a median plate and a pair of lateral plates; the marginal plates are missing, as they are completely fused with the lateral plates.

Figure 104. Rhinolithodes wosnessenskii Brandt

1. Rhinolithodes wosnessenskii Brandt (Figure 104).

Rhinolithodes wosnessenskii Brandt, 1849: 174; Rathbun, 1904: 164; Way, 1917: 354, Figure 11; Schmitt, 1921: 158, Figure 103, Pl.22, Figure 1.

The general appearance of the animal is very clumsy. The carapace has a triangular form, with a very inflated gastric area. Behind this area is a deep semicircular depression, the convex part of which is directed anteriorly, the posterior ends reaching the posterior edge of the carapace; the center of this depression is occupied by the spherical, inflated cardiac area. This area is covered with low, flat papillae, though to the naked eye it appears absolutely smooth. The rostrum has the form of a fairly short cylindrical prominence bearing a strong dentiform apical spine, which is
276 oriented anteriorly. Both sides of this spine are covered with small spinules, and, in dorsal view, its tip exceeds the swollen part of the rostrum.

The frontal edge of the carapace bears irregular spines disposed in a rather irregular manner. The most distinct are those of the anterolateral angles of the carapace and those above the base of the antennal stalk. The lateral edge of the carapace bears seven rather short conical spines behind the cervical groove. The posterolateral angles of the carapace are elongated to form conical, blunt, extremely prominent outgrowths. The surface of the carapace is covered with flat, round granules having the form of strawberries; the median semicircular depression has a completely smooth surface. The eyestalks bear numerous spines on their superior surface. The second joint of the antennal stalk bears an external outgrowth composed of three spines: the anterior one, the strongest, is directed forward; the second, the smallest, and the third, the basal one, are directed outward. The internal outgrowth also bears three slmost equal spines. The scaphocerite is a long, slightly curved outgrowth, which bears blunt spines; the third joint of the stalks bears a distal spine on its superior surface; the last long distal joint of the stalk has four spines on its superior edge. The chelipeds and the walking legs are covered with long, soft hairs; the right cheliped is longer than the left. The superior surface of the merus and the carpus of the right cheliped is sparsely covered with strong conical spines, particularly near the internal edges; the longest spine is situated on the inner proximal angle of the carpus; the propodus is broad and spinose, mainly on its internal edge; the dactyli are smooth, and bear tufts of hairs; the movable dactylus has a blunt spine on its external edge near the base; the prehensile edges bear strong white tubercles; the tips have blunt corneous claws. The propodus of the left chela is slightly spinose; the prehensile edges of the dactyli bear a minute denticulation; the tips have spatulate, corneous claws. The meri, the carpi and the propodi of the walking legs have spines similar to those on the chelipeds; the dactyli are markedly flattened, with four basal spines, corneous spinules on the inferior edge, and pointed claws. The second abdominal segment is made up of distinct median, lateral, and marginal plates; the lateral plates have a depression near the internal side. Each of the three subsequent segments is made up of a median plate and a pair of lateral ones; marginal plates are lacking. The telson is short and triangular. The surfaces of all the abdominal plates are covered with fairly large granules; on the lateral plates, particularly on those of the third segment, slight, barely visible depressions are found.

The coloration of the carapace is grayish brown, with orange spots in the depressions on the dorsal surface, on the tubercles of the posterior part of the carapace, on the branchial areas, and on the abdomen. The legs are less brightly colored; they are grayish brown, similar to the general tone of the carapace.

277 Dimensions

Length of carapace	38.0 mm
Maximum width of carapace	47.0 mm
Length of merus of right cheliped	13.0 mm
Length of carpus of right cheliped	10.0 mm
Length of chela of right cheliped	23.5 mm
Length of first walking leg	48.0 mm

Distribution. West coast of North America; Kodiak Island; Port Etches; Sitka; Crescent City, California. Chiefly on rocky bottoms and on shells at depths ranging from 20 to 72 m.

10. Genus SCULPTOLITHODES Makarov

Sculptolithodes Makarov, 1934: 251.

Type species: Sculptolithodes derjugini Makarov.

The carapace has a fairly regular heart-shaped form. The rostrum is clavate, with a blunt, rounded tip. The dorsal surface of the carapace and of the appendages bears a number of outgrowths and prominences of various forms. The lateral edges of the carapace bear blunt spines. The scaphocerites are rudimentary. The walking legs are much longer than the maximal width of the carapace. The plates of the second abdominal segment are fused to form a single plate which covers the whole surface of the segment. Each of the three subsequent segments is composed of a median plate, two lateral plates, and two marginal plates; the lateral plates are strongly calcified, and have a marked central depression.

†1. Sculptolithodes derjugini Makarov (Figure 105)

Sculptolithodes derjugini Makarov, 1934: 251, Figures 1, 2.

The carapace is heart-shaped. The rostrum is massive and clavate, with a blunt, rounded tip and with a depression in the middle of its superior surface; the inferior surface has a fairly regular conical form; its tip is oriented forward and located between the eyes. The superior surface of the carapace has a rich sculpture; the entire gastric area is markedly raised, with a sloping lateral surface and a fairly distinct tubercle on its highest part; at the level of its fusion with the rostrum, this area forms a kind of saddle which covers the anterior part of the carapace. Immediately behind the rostrum, the edge of the carapace is armed with two blunt spines. The remainder of the carapace is markedly depressed, and bears five raised tubercles, disposed as follows: a triangular tubercle on the cardiac area, a pair of heart-shaped tubercles on the branchial areas, and a pair of kidney-shaped tubercles on the metabranchial areas. The lateral edge of the carapace is raised beyond the cervical groove, and bears five
278 or six blunt spines, while in the space between these spines, smaller additional spines may be found. The edge of the carapace bulges markedly on its posterolateral angle and forms a tubercle similar to that described above, and leads directly into the cylindrically thickened posterior edge of the carapace. This edge is interrupted at the level of the intestinal area by a pronounced concavity. The surface of the prominent part of the carapace is relatively smooth, roughly shagreened, while the surface of the depressed

part of the carapace is covered with round granules. The eyestalks reach the tip of the cone on the inferior surface of the rostrum or somewhat exceed it; the corneas are small; the superoexternal distal angle of the stalk bears a few spines. The antennules extend beyond the tip of the length of the distal joint of the stalk; the external flagellum is stout, short and highly pubescent on its inferior side; the internal flagellum is shorter than the external one and almost completely naked; the antennae are slightly longer than the antennules; the scaphocerites are small squamiform outgrowths, each with a terminal spine and a denticulated internal edge. The chelipeds are shorter than the walking legs; both legs have the same structure, but the left leg is slightly smaller than the right. The merus has a triangular cross section, a rounded superior crest, and a marked furrow on the lateral sides, some distance from the distal edge. The inner proximal angle of the carpus bears a platelike prominence which bears four or five denticles on its edges; each of the other angles bears one tubercle; these tubercles may fuse with each other, thus creating a smoother surface. The chela has an evenly swollen superior surface, with a group of spines at the inner distal angle, the dactyli are directed obliquely outward, and are covered with tufts of soft yellow hairs; the prehensile edges bear fairly strong white tubercles; the tips are black and corneous. The superior surface of each joint of the chelipeds is granulated, while the inferior surface is smooth. The first three walking legs are similar in structure and almost equal in length, the second pair, however, slightly longer than the first and third pairs; the fourth pair of walking legs are rudimentary, as in all the genera of this family, and bent under the posterolateral angle of the carapace. Each of the anterior and posterior edges of the merus of the first three pairs of walking legs bears a denticle of an irregular form; the distal end of the merus bears a smooth prominent tubercle on its superior surface; the edges of the superior surface of the carpus are thickened cylindrically, the thickening being imperfectly divided into three tubercles on the anterior edge; the propodus is compressed, with a longitudinal furrow on the superior surface along the anterior edge, and with a roughly denticulated posterior edge; the dactylus is short and compressed, with a longitudinal furrow on the anterior and posterior surfaces, a row of pointed spinules, and a black corneous claw. The entire surface of the legs is granulated, the prominent parts of the meral and carpal joints excepted; the inferior surface is also granulated, but without visible prominences. The first abdominal segment is hidden under the posterior edge of the carapace; all the plates of the second segment are fused; the whole segment thus ap-
279 pears undivided; on both sides of the median line depressions are found. The three subsequent segments have median, lateral and marginal plates (in the female the marginal plates are found only on the right side). The median plates of the fourth and fifth segments are each divided into two. Between the median plates, some small plates and calcified nodules are found. The surface of all the plates is densely covered with round granules; the central parts of the lateral plates are markedly depressed. The telson is semicircular.

Coloration of specimens preserved in alcohol: the prominent parts of the dorsal surface of the carapace, the carpal joints of the chelipeds, and the meral and carpal joints of the walking legs are orange-red; the general color of the chelipeds is pale rose, of the walking legs pale violet. The inferior surface has a lighter coloration.

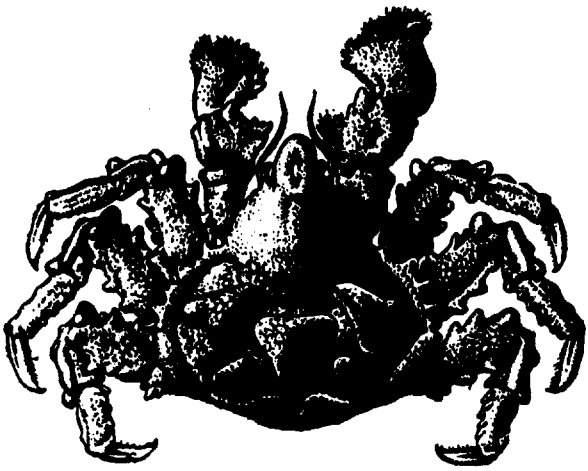


Figure 105. Sculptolithodes derjugini Makarov

As far as sexual dimorphism is concerned, apart from the asymmetry of the abdomen, which is characteristic of the female of this family, the chelipeds are relatively stronger and their dactyli more pubescent in the male; the edges of the abdomen, on the contrary, are more pubescent in the female, and the central part of the lateral plates is less depressed in the female than in the male. The strange sculpture and the color of this species harmonizes amazingly well with the form and color of Lithothamnium, a biotope in which these animals usually dwell; thus, this species is an excellent example of mimicry.

280

Dimensions

Length of carapace.	38.0 mm
Maximum width of carapace.	36.0 mm
Length of merus of right cheliped	14.0 mm
Length of carpus of right cheliped	11.0 mm
Length of chela of right cheliped.	22.0 mm
Length of first walking leg	51.0 mm

Distribution. This species is known at present only from the northern part of the Sea of Japan: near Silant'ev Bay and in the area of Nel'ma Bay. In the collections of the Zoological Institute of the Academy of Sciences, we found a specimen from the area of Andreev Bay (Ussuri Bay) and another from Rishiri Island. It is chiefly encountered on rocky bottoms at depths of 20 to 35 m. This species probably enters the Sea of Japan from the southwestern part of the Sea of Okhotsk.

11. Genus LOPHOLITHODES Brandt

Lopholithodes Brandt, 1849 (1848): 174; Holmes, 1900: 127; Schmitt, 1921: 155. – Echinocerus White, 1848: 47. – Ctenorhinus Gibbons, 1855: 48.

Type species: Lopholithodes mandtii Brandt.

Figure 106. Lopholithodes mandtii Brandt

[Holmes' diagnosis, 1900]

"Carapace broad, pentagonal or hexagonal, convex above; with the margins and upper surface armed with setose tubercles. Rostrum short, spiny. Acicle of the antennae with the margins and generally the upper surface spiny. The terminal joint of the mandibular palp is elongated and flattened, and bent backward so as to lie between the concave inner faces of the mandibles. Chelipeds unequal, tuberculated; carpus with a prominent lobe on the inner side. Ambulatory legs short, tuberculated, and capable of being folded under the carapace. Basal segment of the abdomen entire, the three following segments with lateral plates and also small marginal plates on one or both sides; penultimate joint devoid of lateral plates; telson very small" (Holmes).

1. Lopholithodes mandtii Brandt (Figures 106, 107).

Lopholithodes mandtii Brandt, 1849: 174; Holmes, 1900: 128 (literature); Rathbun, 1904: 164; Way, 1917: 356, Figure 12; Schmitt, 1921: 156, Figure 101, Pl. 21, Figure 1.

[Holmes' description, 1900]

"Carapace strongly convex, wider than long, the whole surface—the large tubercles as well as the intervening spaces—roughened by small, short, setose tubercles which vary greatly in size from low, nearly smooth
282 swellings to rough, subconical projections. Median region very prominent, having a subconical apex a little in front of the middle and a cluster of small, rounded, or subacute tubercles near the posterior end; a large, subconical elevation on the cardiac region in front of which, on either side, is a depressed, comparatively smooth area; median and cardiac areas separated by a comparatively smooth sulcus; a large subconical elevation on the branchial regions and two smaller tubercles on the posterior margin of the carapace. A peculiar smooth wart-like prominence on either side of the median area. Rostrum short and consisting of a strong subconical spine above the base of which is a knob bearing two lateral spines or tubercles with (generally) a spine or tubercle above and below the notch between them. A deep, rounded sinus on either side of the front which serves as an orbit, external to which is an acute spine; beyond this spine is a large spine which extends nearly as far forwards as the rostrum and in the sinus between the latter spine and the postorbital there is generally a small spine or tooth. The antero-lateral margin is armed with a variable number (about eight) of prominent spines and several smaller ones; the middle portion is convex, flattened, and produced. A large, knob-like prominence at the postero-lateral angles which is separated from the last antero-lateral spine by a conspicuous sinus. Ocular peduncles two-jointed, thickly set with spines above, and not nearly reaching the tip of the rostrum. Acicle of the antennae narrow, tapering, much exceeding the tip of the peduncle, and furnished with about thirty strong, smooth, sharp spines. Ischium of the maxillipeds armed within with dark-colored teeth; a tooth on the outer surface near the antero-internal angle; exognath somewhat exceeding the merus. Chelipeds short, the first and second joints with irregular tuberculous projections on

Figure 107. Lopholithodes mandtii Brandt, right scaphocerite

the under side; one or more prominent spines on the antero-internal angle of the merus; the lobe on the inner side of the carpus is very large and acute and margined with sharp, spine-like tubercles; spines on the outer surface of the hands large and numerous; four or five large spines on the upper margin of the larger hand and three or four on that of the smaller. Ambulatory legs subequal, strongly tuberculated, quadrangular at the base; carpi and propodi subcylindrical but very irregular; dactyls short and stout. The basal abdominal segment is strongly concave behind, especially in the female, and nearly at right angles to the carapace; there are two prominent
283 tubercles near the middle and several on the margins; the remaining segments are studded with numerous subconical tubercles; between the median plates there are small, transverse, secondary plates which may be divided by longitudinal fissures; penultimate segment oblong and distally concave. The abdomen of the male is subtriangular behind the basal segment; that of the female rounded at the sides and tip and bent to one side.

"Length, 200 mm; breadth, 245 mm; length of larger cheliped, 202 mm; length of first ambulatory leg, 195 mm. Some specimens are widest between the tubercles at the postero-lateral angles, while others are widest between the tips of the last spines on the antero-lateral margin " (Holmes)

Distribution. From Sitka (Alaska) to Monterey (California).

12. Genus CRYPTOLITHODES Brandt

Cryptolithodes Brandt, 1849: 185; Holmes, 1900: 123; Balss, 1913: 79; Schmitt, 1921: 154.

Type species: Cryptolithodes typicus Brandt.

The width of the carapace exceeds its length; the dorsal surface is smooth, raised in its median part, and broadly produced on either side; thus, the carapace covers all the legs like a roof when they are retracted. The rostrum is usually broad and compressed, with a truncate tip, and is markedly bent downward. The anterolateral edges of the carapace are arcuated and, in most cases, bear small, often hardly visible denticles or tubercles, the edges reaching the posterior edge at an obvious angle; in other cases, the transition is gradual and rounded. The eyestalks are slender at the distal end and broaden markedly at the base. The scaphocerites

are broad and platelike. The chelipeds are unequal and can be retracted under the carapace. The walking legs are flattened, with sharp edges. The abdomen, beyond the second segment, is markedly bent under the cephalothorax; it is triangular, and is closely appressed to a depression formed by the thoracic sternites. The second abdominal segment is either undivided, or composed of two plates. Each of the three subsequent segments is made up of a median plate and a pair of lateral plates; secondary plates may be present or lacking; the marginal plates are lacking. The sixth segment is elongated; the telson is short and triangular. The abdomen of the female is less asymmetrical than in the other genera of this family.

Key to the Species

1 (2). Chelae smooth. Rostrum broadens distally, with distinct anterolateral angles. Abdominal plates smooth. 1. C. sitchensis Brandt.

2 (1). Chelae tuberculated. Rostrum not broadening distally, and with a fairly rounded tip. Abdominal plates with upturned edges.

284 3 (4). Rostrum markedly inclined downward. Lateral lobes of carapace tuberculated. Lateral edges of carapace meet at a distinct angle. Second abdominal segment not divided. In the male an additional plate present between median and lateral plates of third segment and posterior edge of second segment. .2. C. typicus Brandt.

4 (3). Rostrum slightly inclined downward. Lateral lobes of carapace smooth. Lateral edges forming a broad, rounded edge. Second abdominal segment composed of two plates. No additional plates. . . . . 3. C. expansus Miers.

1. Cryptolithodes sitchensis Brandt (Figures 108, 109)

Cryptolithodes sitchensis Brandt, 1853: 245; Holmes, 1900: 125, Pl. 2, Figures 21 to 25; Rathbun, 1904: 164; Schmitt, 1921: 155, Figure 100, Pl. 20, Figures 3, 4; Queen, 1930: 393, Figure 1.

The carapace is transversely oval; the median part is raised, and bordered by a longitudinal ridge or crest which reaches the middle of the rostrum; the hepatic areas bear less marked transverse crests; the cardiac area is swollen. The surface of the carapace is smooth and covered with minute round punctae, visible only with a magnifying glass; the lateral edges are very broad and completely cover the appendages. The rounded anterolateral edge bears from eight to ten blunt denticles, the size of which is very variable; these denticles are sometimes so small that the edge merely appears to be slightly undulated; the lateral angles of the carapace are distinct; the posterior edge of the carapace is rounded, either without denticles, or with one or two small, barely visible ones near the lateral angle. The rostrum is markedly bent downward, distinctly broadening distally and having marked anterolateral angles; the truncate anterior edge of the rostrum bears a small denticle in the middle. On both sides of the rostrum a deep orbital sinus is found. The eyestalks are small,

flattened on their superior side and with a much broadened base; they are completely covered by the rostrum. The second joint of the antennal stalk bears on its internal side a flat outgrowth, directed upward; the external side also bears a plate-like outgrowth, extending both forward and backward; the scaphocerite is a very broad, thin, hard, almost round plate, with a rounded external edge, an undulated internal edge, and a slightly concave superior surface; the superior edge of the last joint of the stalk bears a crest which has the form of a thin plate. The ischium of the third maxillipeds is small and triangular; the external angle bears a small denticle, the internal edge is minutely denticulated, and the external edge bears two round tubercles; the merus is flat, with a very prominent outgrowth on its external edge; the other joints are also flattened and have marginal carinae. The right cheliped is larger than the left, but the structure of both legs is identical. The internal edge of the

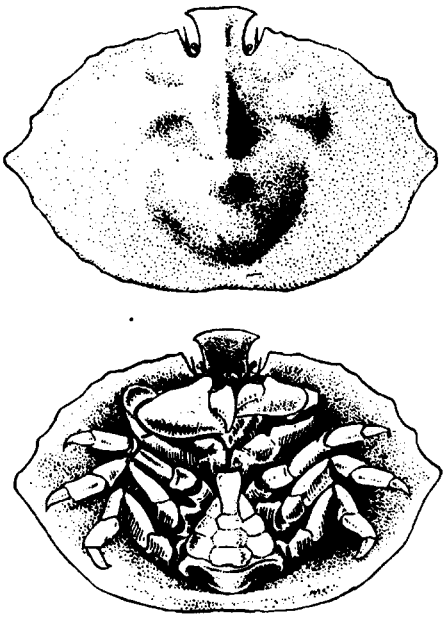


Figure 108. Cryptolithodes sitchensis Brandt, dorsal and ventral views

285 ischium is sharp; the internal edge of the merus bears a flat or almost conical denticle. The superior surface of the carpus bears a crest near its external edge; the rounded anterior edge is sharp; the inner distal angle bears a blunt denticle. The chela markedly broadens distally; the propodus has a slight longitudinal median crest; the internal edge of the propodus is sharp and has a rounded prominence at its distal end; the external edge of the propodus is thick and rounded; the dactyli are short and stout; the external edge of the movable dactylus is crestlike, sharp, and very broad near its proximal end, owing to a rounded prominence; the entire dactylus has a somewhat hook-shaped form; the prehensile edges are concave, often with fused tubercles, and bordered on their external side by tufts of short hairs. The walking legs are smooth, naked, and flattened; the superior edges of the joints are sharp, the inferior side of the merus flattened; the inferior edges of the carpus and the propodus end distally in a small denticle; the dactyli are flat, and are much narrower than the propodus. The second abdominal segment is undivided, with depressions on its lateral parts. Each of the three subsequent segments is made up of one median plate and two lateral ones; the marginal plates are missing. In the male, at the border between the median and lateral plates and the posterior edge of the second segment, a small additional triangular plate is found on each side. The

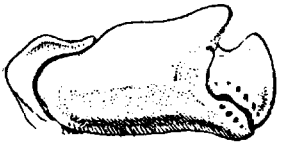


Figure 109. Cryptolithodes sitchensis Brandt, outer surface of right chela

sixth segment is elongated, broadened distally, and concave at its distal end. The telson is small and triangular, often hidden under the distal end
286 of the sixth abdominal segment. The surface of all the abdominal plates is covered with microscopic punctae.

The posterior edge is straighter in young specimens than in adults; the crests on the superior surface of the chela are more distinct, and are sometimes substituted by one or several more or less evident additional crests. The posterior part of the carapace is very swollen in the female, and the posterior edge projects farther backward than in the male.

The color (according to Queen) is dark red; some specimens are brown, while a small specimen was white with brownish-red spots. Holmes (1900) stated, "The males I have seen in a fresh condition were all of a uniform, bright red color. Two females seen were red but with a purplish tinge irregularly marked with blotches of a lighter color. This species is often seen at low tide on the sides of rocks where, at some distance, it might readily be mistaken for a species of bright red incrusting sponge which is found in similar situations."

The specimens preserved in alcohol have a pale-yellow or slightly reddish coloration.

Dimensions

Length of carapace	24.0 mm
Width of carapace	38.0 mm
Length of merus of right cheliped	5.0 mm
Length of carpus of right cheliped	6.0 mm
Length of propodus of right cheliped	10.0 mm
Length of movable dactylus of right cheliped	4.0 mm
Length of first walking leg	18.0 mm

Distribution. From Sitka, Alaska, to Pacific Grove, California. From the littoral to a depth of 13 m.

2. Cryptolithodes typicus Brandt (Figures 110, 111)

Cryptolithodes typicus Brandt, 1849: 185; Holmes, 1900: 124; Rathbun, 1904: 164; Way, 1917: 352, Figure 5; Schmitt, 1921: 154, Plate 20, Figures 1, 2.

The width of the carapace considerably exceeds its length. It has bluntly rounded lateral angles; the posterior edge is not as arcuated as in C. sitchensis; behind the transverse hepatic crests the surface of the carapace is markedly concave; the denticles on the anterolateral and posterior edges are small. The rostrum does not widen distally, and it has rounded anterolateral angles; it is inclined downward and extends considerably beyond the anterior edge of the carapace; because of this the orbital sinuses are very shallow. Near the lateral angles the surface of the carapace is covered with small, low prominences. The scaphocerite is a transverse plate with a straight, truncate anterior edge. The chelipeds differ from those of C. sitchensis in that the superior surface of the propodus

is covered with fairly strong, round tubercles and in particular that of the
287 right chela, and partly the surface of the carpus. The inferior edge of the meral joints of the walking legs bears two crests with a fairly deep furrow between them. The edges of all the abdominal plates are raised, and their surface is covered with small granules. The other characters are identical with those of C. sitchensis. The males bear additional plates between the median and lateral plates of the third segment and the posterior edge of the second abdominal segment; Bouvier (1895) considers that these additional plates are characteristic of the males of all species of this genus.

The coloration (according to Way) is darkish brown on the dorsal side and light gray on the ventral side. Specimens preserved in alcohol are pale yellowish, sometimes with a greenish tint.

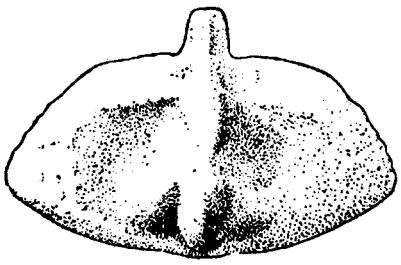


Figure 110. Cryptolithodes typicus Brandt, dorsal view

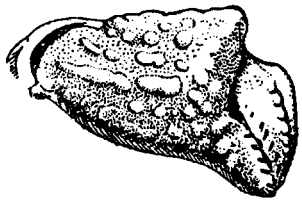


Figure 111. Cryptolithodes typicus Brandt, outer surface of right chela

Dimensions

Length of carapace	14.0 mm
Width of carapace	23.0 mm
Length of merus of right cheliped	4.0 mm
Length of carpus of right cheliped	3.5 mm
Length of chela of right cheliped	8.0 mm
Length of movable dactylus of right cheliped	4.0 mm
Length of first walking leg	12.0 mm

Distribution. From Unalaska (Alaska) to Monterey Bay (California). From the littoral to a depth of 13 m.

3. Cryptolithodes expansus Miers (Figures 112, 113)

Cryptolithodes expansus Miers, 1879: 47; Rathbun, 1902: 32, Figure 1; Balss, 1913: 79, Figure 55; Yokoya, 1928: 759.

The carapace is transversely elongated, with broadly rounded aliform lateral expansions which do not form lateral angles; the surface of the carapace is covered with small punctae from which arise minute setae.

There are larger punctae on the carapace. On the cardiac area a prominent elevation is found. On the branchial area there are two more out-
288 growths (one on each side). The three elevations form a transverse row. A similar elevation is found on the gastric area; a longitudinal median crest extends from the gastric elevation to the distal half of the rostrum. The anterior half of each lateral expansion is occupied by a low, tuberculated prominence (according to Miers the lateral widenings are smooth, and lack tubercles). The edge of the carapace bears some three or four blunt denticles or tubercles, with large, irregular intervals between them. The largest denticles are found on the external angles of the shallow orbital sinuses. The rostrum is inclined slightly downward and, as a rule, extends

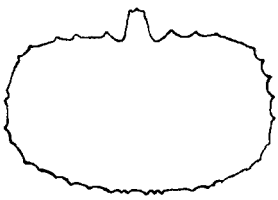


Figure 112. Cryptolithodes expansus Miers, contour of the carapace (From Rathbun, 1902)

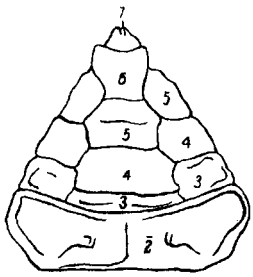


Figure 113. Cryptolithodes expansus Miers, abdomen (From Balss, 1913)

beyond the anterior edge of the carapace. Its edges gradually converge, and are slightly arcuated; the tip is transversely truncate, and bears a small median tubercle. The eyes reach half the length of the rostrum. The second joint of the antennal stalk bears an external crest with two spines, one of which is directed forward and the other backward. The scaphocerite is considerably broader than it is long; its distal edge is concave and has an oblique direction. The basis and the ischium of the left cheliped* are tuberculated on the inferior side; the merus has three crests, the internal one divided into four irregular denticles; a similar crest extends onto the ischium; the superior surface of the carpus is rough, the internal edge blunt. A blunt denticle is found at the inferodistal angle. The propodus and the dactyli are tuberculated on the external and the internal sides. The superior surface of the propodus bears a distinct crest which terminates distally in a pointed, conical denticle. The inferior edge of the propodus bears a blunt crest. The dactyli are much longer than the superior edge of the propodus; their edges almost touch when closed; the movable dactylus bears crests on its superior side, the crest on the proximal end forming a prominence. The ischium of the walking legs bears a denticle on the distal corner of the superior edge; the size of this denticle increases from the first to the third pair of legs. The edges of the subsequent joints are
289 broad and flat; the meri have one superior plate and two inferior ones; the carpi have one superior plate; the propodi and the dactyli each have a superior and an inferior plate. In the natural position the legs are hidden under

* The description is adopted in its main points from M. Rathbun, who studied a specimen whose right cheliped was missing. In his diagnosis Miers states only that "the anterior legs have the palms tuberculated externally."

the carapace, but, when extended, the last joint and half of the penultimate joint extend beyond the edge of the carapace. The length of the abdomen slightly exceeds its basal width. The first segment is very short and transversely elongated. The second segment is made up of two plates separated by a median suture; the edges of both plates are raised. The median plate of the third segment is narrow, with a transverse furrow; the lateral plates are larger. There are no additional plates between the median and lateral plates and the posterior edge of the second segment. The median plate of the fourth segment is broad; the lateral plates are pentagonal. The fifth segment is like the fourth. The sutures between the lateral plates alternate with the intersegmental sutures. On the external edge of the sixth segment is a cavity in which the telson is housed.

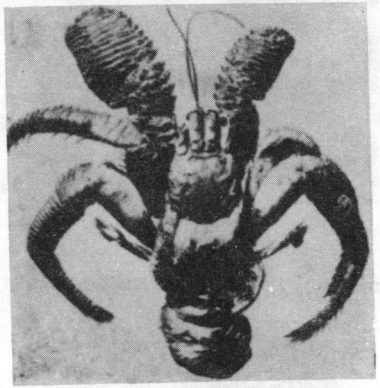
Dimensions

Length of carapace	51.6 mm
Width of carapace	78.9 mm
Length of rostrum	9.5 mm
Length of carapace from external orbital angle to posterior edge	45.0 mm

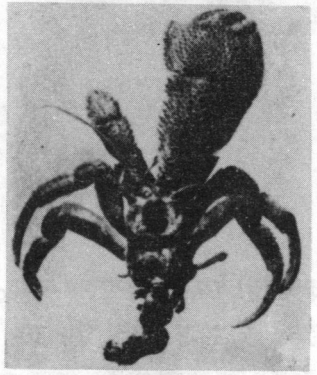
Distribution. Northern Japan (Miers); Minyako, Rikuzen Province (Rathbun); Aomori (Balss); near Hanaguri Cape; between Aomori and Futago Cape and between Benten Island and Cape Kurosaki (Yokoya).

INDEX OF LATIN NAMES

NOTE. This index has been photographically reproduced from the Russian text. The page numbers appearing in the left-hand margin of the translation correspond to page numbers in the Russian text.



Dardanus arrosor (Herbst)



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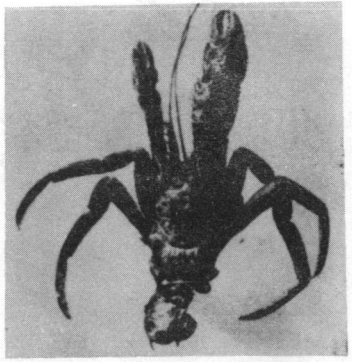
Diogenes edwardsii (de Haan)
(after Stimpson)

Diogenes varians (Costa)



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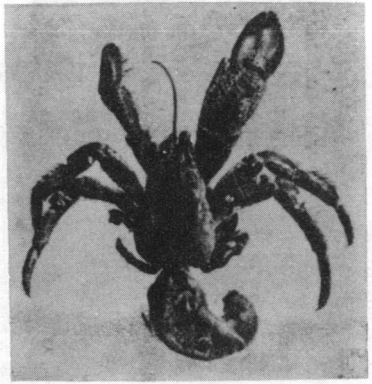

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Clibanarius misanthropus (Risso)

Orthopagurus schmitti (Stevens)

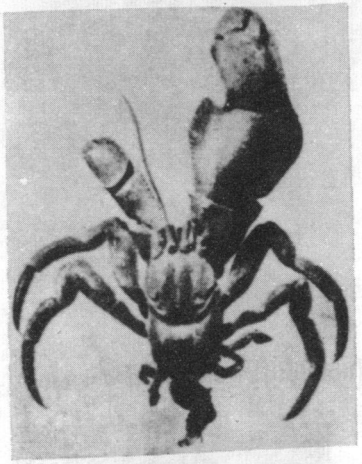
Pagurus ochotensis (Brandt)

Pagurus ochotensis subsp. *aleuticus* (Benedict)

Pagurus armatus (Dana)

Pagurus granosimanus (Stimpson)

Pagurus brachiomastus (Thallwitz)



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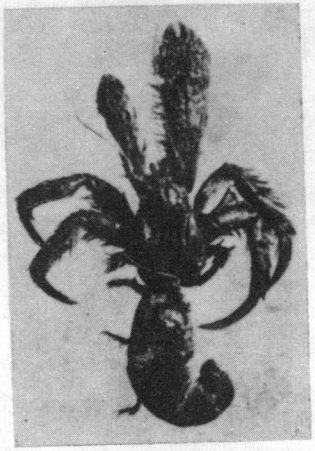

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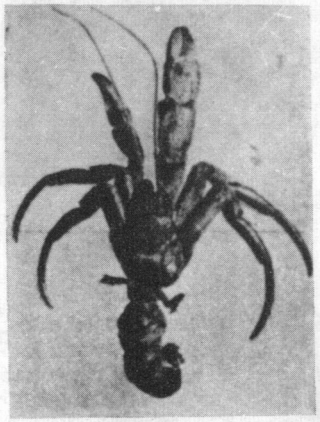

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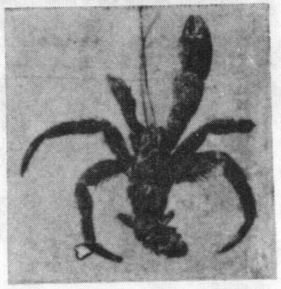

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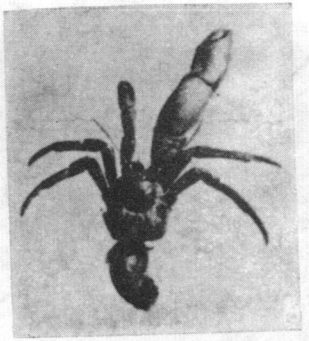

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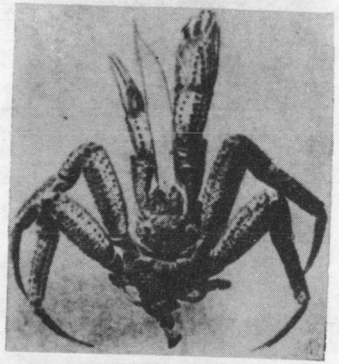
Pagurus pectinatus (Stimpson)



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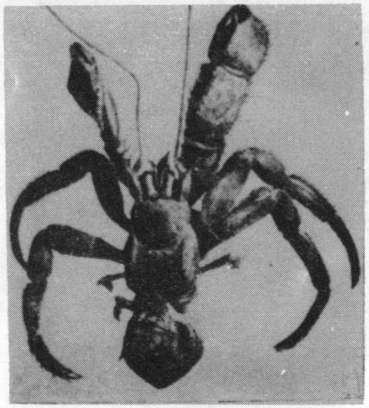
Pagurus bernhardus (Linné)

Pagurus anomalus (Balss)

Pagurus gracilipes (Stimpson)



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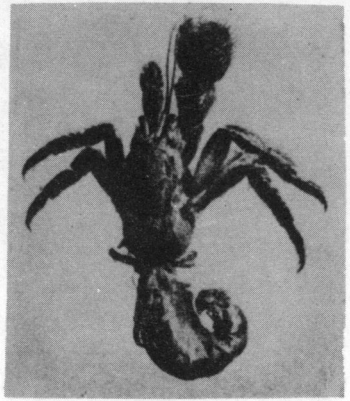

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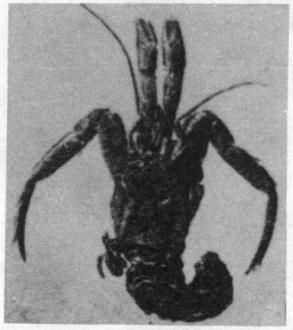

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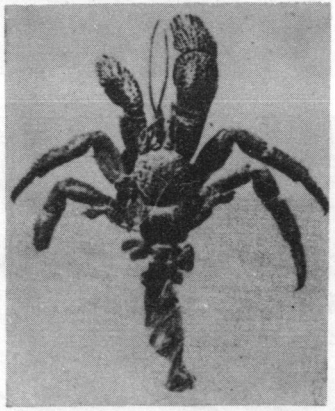

Pagurus beringanus (Benedict)

Pagurus tanneri (Benedict)

Pagurus middendorffii (Brandt)

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