

glands. The structure of the filtering apparatus is such that only food strongly reduced in size gets into the digestive glands, at least through the filter almost as a liquid. Particles of food not passed through the filter apparatus remain in the midgut.

The midgut is the longest part of the gut. It is represented by a narrow, straight tube somewhat narrowed at both ends, stretching from the posterior part of the stomach to the rectum; i.e. extending through the entire thorax and the anterior part of the abdomen. The gut walls are represented by muscular layers, a medial basal membrane, and an epithelial layer lined with chitin (Hewitt, 1907). The musculature is represented by a not always well expressed outer layer of longitudinal muscles and an inner layer of circular muscles. The epithelial cells are large and usually form a syncytium (Hewitt, 1907), and thus do not have partitions. Often the midgut wall forms a longitudinal gutter (typhlosole).

The secretory midgut epithelium cells serve only for absorption, while the digestion of food takes place in the midgut through the action of digestive juices entering there from the hepatopancreas (Semenova, 1970). In blood-sucking forms like Aega the midgut is extraordinarily spacious and stretchable. In the parasitic Cymothoidae the filtering apparatus is reduced, the pyloric furrow lacking (Zimmer, 1927). It is worth saying that many embryologists and zoologists have considered the endodermally derived midgut as very small or absent, and the greater part of the so-called midgut is of ectodermal origin and represents an aspect of the hindgut (Goodrich, 1939; Stromberg, 1965, 1967; Holdrich, 1973).

The hindgut or rectum is like a short, thin tube, opening by a slit-like anus at the hind end of the body. The posterior part of the anus is provided with an anal sphincter. The hindgut's epithelial cells do not produce digestive enzymes and do not take part in food absorption or accumulation of glycogen and lipids. One of its functions is the advancement of undigested food to the anal sphincter (Holdich and Ratcliffe, 1970).

There are two pairs of rosette glands, one pair of which are located in the bases of the first maxillae and the other in the upper lip. Each consists of a group of gland cells arranged in the form of a berry (in section they look like rosettes) around a central cell which probably represents the duct cell. Earlier these glands were interpreted as salivary (Hewitt, 1907; etc.) and later an excretory function was most often ascribed to them (Needham, 1942).

The digestive gland, or hepatopancreatic diverticula (earlier they were called hepatic diverticula, but this name, as less correct, is almost unused these days), are represented by wide distally closed tubes or sacs, the proximal ends of which empty into the pyloric part of the stomach. They are arrayed in quantities of a (Paranthura, Epicaridea), 2 (Limnoriidae, Serolidae, Asellidae, a large portion of

Oniscoidea), or 3 (Cirolanidae, Cymothoidae, Idoteide, Ligiidae or the Oniscoidea) pairs along the sides of the midgut (Figure 24) and reach through the greater part of the animal's body. In some Sphaeromatidae, like *Sphaeroma serratum*, there are even 4 pairs, but in this case only 3 pairs are normally developed while the fourth pair is rudimentary, like a small bubble (Tuzet, Manier and Ormiers, 1959). Their wall musculature has a spiral arrangement which undoubtedly constricts to their peristaltic contractions (Hewitt, 1907). The glands are lined with epithelial cells sitting on a thin basal membrane with hollows for muscles (Donadey, 1968). In the epithelium the cells are usually divided into two types: large cells rich in lipids, and small ones poor in lipids but containing lipofuschine (Donadey, 1968; Donadey and Reese, 1972). The cells surface is covered with a brush of numerous microvillae, which considerably increase the absorptive surface (Donadey, 1968, 1969). The epithelial cells of the hepatopancreatic diverticula secrete digestive enzymes of the merocrine type. The predaceous Cirolanidae are provided with the enzymes lipase, acid proteinase and carbohydrase in the digestive glands (Jones, Babbage and King, 1969). Apparently, the hepatopancreatic diverticula serve the functions of secretion of digestive enzymes, absorption, and also excretion. The ultrastructural similarity of the diverticula with the convoluted canals in kidneys speaks of their excretory function (Donadey and Cesarini, 1969). An obvious differentiation of the hepatopancreatic diverticula epithelium into cells secreting digestive enzymes and cells serving an excretory function, is found in sowbugs, Oniscoidea (Semenova, 1970).

#### Circulatory System

The general scheme of the circulatory system in Isopoda is given in Figure 29. The circulatory system is not closed. Characteristically for isopods they differ from the overwhelming majority of crustaceans, so to say, in that the heart is not located in the thorax, but in the abdominal region whereas in many forms it is advanced into the posterior part of the thorax. The heart has the form of a tube or small sac. The blood enters it from a well developed pericardial cavity through 1 or 2 pairs of ostia, which are represented by usually asymmetrically positioned, slit-like openings armed with muscles and small, inturned valves (Hewitt, 1907). The heart walls are muscular. The pericardium is set off from the body cavity by a horizontal septum which supports the heart and is connected with the venous lacunae in the anterior half of the body. Efferent vessels from the gills enter the pericardium. The anterior medial aorta (aorta cephalica) is sent out anteriorly from the heart. This aorta goes into the head. Along the route a few pairs of arteries go out from it, feeding the stomach walls, the hepatopancreatic diverticula, the epimeral region of the thoracic segments, the eyes, the cephalic appendages, etc. (Hewitt, 1907). The anterior aorta gives off vessels to the brain, eyes, and both pairs of antennae. Of the 7 pairs of thoracic arteries, the

posterior three pairs go out from the heart independently while the four anterior ones first arise from a common trunk on each side of the heart (Calman, 1909), which is called the lateral artery and goes out anteriorly and below from the front end of the heart. Rarely all seven pairs start from the anterior aorta. The courses of thoracic arteries I-V are similar to each other. Each of them turns directly downwards, and, finding the dorsal hepatopancreatic tube, gives off a ventral branch providing the latter with blood. Following the curve of the dorsal side of the body, further arteries bend in the ventral direction; reaching the site of limb articulation they divide: the inner branch supplies the ventral surface, the outer branch divides anew, thereby its dorsal branch supplies the epimeral region and the ventral the thoracic limbs. The sixth thoracic artery quickly gives off a branch bending ventrally and connecting with an analogous branch of the opposite side of the body on the mid ventral side of the gut. The subintestinal artery thus formed goes anteriorly and posteriorly giving off branches into the gut wall. The seventh thoracic artery gives off an artery which divides and washes the lateral sides of the gut, and also a large, posteriorly directed abdominal artery which gives off branches supplying blood to the gut, pleopod muscles, and abdominal body wall, and ending in the uropods.

The venous system is lacunar. The blood collects in large thoracic lacunae located between the organs. From there the blood goes through openings into a lateral sinus going along both sides of the body and collecting blood, from the appendages as well. These sinuses unite with the abdominal sinus from below, and from there the blood goes by a lacunar path through the pleopods, where they pass through a complex system of lacunae. After this, when the blood has become arterial, it flows by a special lacunar route into the pericardial sinus. Since the pericardial sinus is connected to the body lacunae, venous and arterial blood get mixed here (Zimmer, 1927).

The blood is colorless and contains variable amounts of ----- (Hewitt, 1907). The blood-producing organs are 2-3 pairs of cellular masses lying on the lower side of the circumcardiac partition in the posterior thorax and usually (but not always) in the anterior abdominal segments.

### Respiratory Organs

In contrast with the majority of crustaceans the respiratory organs, like the heart, are found not in the thoracic, but in the abdominal region. In aquatic isopods pleopods serve as respiratory organs, gills. Sometimes all the pleopods serve both as respirators and as swimming organs, excluding those forms in which one or another pleopods are modified into opercula. Sometimes as well (for example, many Sphaeromatidae) these functions are allotted to different pleopods or even to their rami. In this case the pleopods appearing as gills (usually these are posterior pleopods) are fleshy, inflated, and

lacking natatory setae. The chitinous cuticle is very thin on gill limbs. In the thickness of the limbs are abundant epithelial cells, between which are numerous lacunae filled with hemolymph. In some very large forms (Bathynomus of the Cirolanidae) the pleopods have developed supplementary strongly ramifying projections at the bases of the endopodites, also serving a respiratory function.

### Excretory Organs

The basic excretory organs are the maxillary glands, one pair in number, located in the part of the head corresponding to the segment of the second maxillae (Figure 30). The maxillary glands are homologous to polychaete metanephridia. Each consists of a terminal sac and nephridial canal, the distal part of which is often broadened, forming a urinary bladder. The terminal sac is mesodermal and represents a reduced coelomic sac. The sac walls are formed by a one-layered epithelium located on a basal membrane which is attached to them from the outside. The urinary bladder is connected with the external medium through an opening located at the base of the second maxilla.

Nemec (1896) described a small group of cells located in the body cavity near the bases of the second antenna as rudimentary antennal excretory glands. This cell mass has a small opening but lacks a duct. Later Needham (1942) agreed to homologize Nemec's glands with antennal glands, but considered it more likely that they serve as endocrine glands, at least in adult animals.

Nephrocytes also serve an excretory function, of which the cephalic ones are located in the bases of the first antennae, and the branchial ones for small pairs of groups located in two rows on the sides of the vessels going from the gills to the pericardium.

Finally, as was mentioned above, certain small cells of the epithelium of the hepatopancreatic diverticula serve an excretory function.

### Nervous System

The structural plan of the nervous system is common to all arthropods. It consists of three basic parts: the suprapharyngeal ganglion or brain, circumpharyngeal connectives with a subpharyngeal ganglionic mass, and the ventral nerve chain composed of paired thoracic and abdominal ganglia with longitudinal pairs of trunks of nerve fibers connecting them, the connectives (Figure 31).

The suprapharyngeal ganglion, or brain (Figure 32) is well developed has a considerable size, and consists of three regions: the protocerebrum, deutocerebrum, and tritocerebrum). Of these the protocerebrum and deutocerebrum represent the phylogenetically older

parts of the brain, while the tritocerebrum is the first ganglion of the ventral nerve cord which has shifted forward and fused with the primitive, preordal brain (Henry, 1948). The suprapharyngeal ganglion is located between the eyes, in front of the esophagus and dorsal to it. There are a pair of large blades on the dorsal side of the anterior part of the brain (protocerebrum), from which the eye stalks emerge. On the ventral side are one pair of olfactory lobes, from each of which a large antennal nerve goes to an antenna. Small nerves to the covering of the anterior part of the lateral walls of the head go out from the anterior part of the optic lobes. The deutocerebrum is represented by the two symmetrically positioned ganglionic masses; it innervates the first antennae. The tritocerebrum is usually pear-like; it innervates the second antennae and upper lip, and gives off branches to the gut. The circumpharyngeal connectives of nerve fibers connect the tritocerebrum and the subpharyngeal ganglionic mass, which represents a more or less complete fusion of the paired ganglia connected with the cephalic mandibular and first and second maxillary segments, and innervates the mouthparts and the stomach. The subpharyngeal ganglion is located in the rear part of the head, but sometimes its posterior part lies beyond the limits of the head. The subpharyngeal ganglion is connected with the first thoracic segment's ganglion by a pair of nerve cords, from which nerves go out into the body musculature.

The ventral nerve chain consists of 7 pairs of thoracic and 6 pairs of abdominal ganglia. Each pair of thoracic ganglia are very close to each other. Each ganglion gives off nerves to the thoracic limbs of that side of each segment, and is linked by connectives to the next ganglion and by a commissure to the other ganglion of its pair. Nerves innervating the body musculature go out from the middle of these commissures. The abdominal ganglia are often fused to each other in isopods into a single ganglionic mass. Different stages in the fusion process are encountered in various isopods, from complete isolation of the abdominal ganglia to their complete fusion. Usually this process is tightly connected with the degree of fusion of abdominal segments with the pleotelson. Nerves go out from the abdominal ganglia into the pleopods and the musculature of the abdominal region; a pair of large nerves go out into the uropods from the posterior ganglia or from the rear part of the ganglionic mass, if the ganglia are fused; one long, unpaired nerve goes to the anal opening.

From the subpharyngeal ganglion to the seventh thoracic ganglion a small medial nerve goes between the commissures, which is conventionally called sympathetic (Hewitt, 1907).

### Sense Organs

The sessile, faceted eyes are located on the dorsal surface of the head or on its sides. Each eye consists of 1-2 up to 3000 ommatidia

(in the giant isopod Bathynomus. Each ommatidium consists of its own light refracting (dioptric) and light perceiving apparatus. On the outside an ommatidium is covered with a chitinous, cuticular cornea, the inner surface of which is covered by 2 thin hypodermal cells. Below them are located the set of 2 crystalline cone cells. Each cone cell secretes a transparent mass of semicircular form. In this way 2 transparent segments are formed touching each other along a flat surface, the crystalline cone. The cone cells are surrounded by 2 pigment cells containing grains of dark, distal pigment. The cornea, hypodermal cells and crystalline cone compose the light refracting part of the ommatidium. Found in the proximal part of the ommatidium are from two (Serolis) to 14 (Oniscus) retinal cells forming a retina which serves as the light sensing structure of the ommatidium. The nuclei of the retinal cells are found in their proximal parts. A specially differentiated portion on the inner side of each retinal cell is the rhabdomere. A conjunction of the rhabdomeres forms the rhabdome, which consists of 4-14 rhabdomeres. Proximal pigments is found between the rhabdomeres and retinal cells. Proximal outgrowths of the retinal cells pierce the basal membrane of the ommatidium and, fusing with each other, form a nerve fiber which goes to the distal part of the optic lobe of the brain. In many deep-water, cave-dwelling, interstitial, and parasitic forms the eyes are reduced, even up to complete absence.

The statocysts of many Anthuridea apparently serve as organs of balance. In them the statocysts are represented by bladder-like ? of the covering of the telson, connected by canals with external medium and containing statoliths quiescent on sensory hairs. In some Anthuridea the telson has a pair of such statocysts located on each side of the midline, others have only one unpaired statocyst. Macrostylidae of the Asellota also have statocysts, which in them are like a pair of bladders located at the posterior end of the abdominal region.

The numerous setae of various sorts located on the body and appendages, and discussed earlier, are considered mechanoreceptors; i.e. organs perceiving mechanical stimulation.

Aesthetascs, located predominantly on the first antennae, serve as organs of chemical sense, chemoreceptors. These are setae hollow within. Bipolar nervous cells are located at their base under the hypodermis, and one of the axons of each cell goes into the aesthetasc, and the other to a nerve. In the freshwater asellus Asellus, the aesthetascs of the flagellar joints of the first antennae have the form of overturned bottles, and in many Nannoniscidae the first flagellar segment of the first antennae are armed with very large, balloon-shaped aesthetascs.

## Neurosecretory System and Endocrine Glands

Cells are called neurosecretory which have the morphological appearance of neurons but are capable of producing grains or granules of secretions, substances of high biological activity which can be detected not only in the bodies and axons of these cells but also in the blood channels. Besides, as Carlisle and Knowles (1959) noted, in contrast to other neurons, neurosecretory cells do not innervate muscles or any effector organ at all, and their axons terminate in the walls of blood vessels or sinuses, in systems of other fluid-filled cavities, or even in the epidermis. Usually groups of neurosecretory cells located in various parts of the central nervous system belong to the neurosecretory system (Figure 33), and also neurohaemal structures or organs connected with them which represent the meeting sites of axon termini of one or another group of neurosecretory cells. These axon termini are specialized for storage and regulation of release of the neurosecretion and are intimately connected with a specialized section of a vessel section of corresponding form.

The basic sites of accumulation of neurosecretory cells are the distal lobes of the protocerebrum (medulla terminalis), the optic lobes, and also the posterior region of the protocerebrum. Usually they are differentiated into two to four sorts of cells of various sizes. The basic neurohaemal organ in isopods is the sinus, or blood, gland, characteristic for all Malacostraca (originally in isopods this gland was called the pseudofrontal organ. Later Amar (1948, 1950) homologized it with the sinus gland of other Malacostraca, and Gabe (1952) by a cytochemical method corroborated this homologization). It is located on the optic, or eye, lobe of the protocerebrum below the compound eye (Figure 34) and is represented by a mass of numerous anastomosing ramifications of the inflated ends of neurosecretory cell axons. The neurosecretory product is deposited in an anterior, blind protrusion of the gland (Juchault and Legrand, 1965). Oguro (1959a, 1959b) discovered two pairs of sinus glands in Idoteidae. One pair is located in the central part of the optic lobes and the other near their distal ends directly below the eyes (Figure 32).

Another neurohaemal organ, the organ of Bellonci, is homologous with the X-organ of decapods. This is a sac-like organ composed of a layer of epithelial cells. In the epithelial cells vacuoles and granules are found. In Sphaeroma the organ of Bellonci contains two types of cells, central and peripheral. The central cells are coated by fibers of a diameter 0.1mm and length up to 25mm, grouped into a bundle. A secretion is formed within the central cells. The peripheral cells are provided with platelets that border the central cells (Chaigneau, 1969). In the majority of studied isopods the organs of Bellonci are located below the subpharyngial ganglia, although in the Aegidae they are above them. The organs of Bellonci are connected with the optic lobes by nerve fibers running first from smaller neurosecretory cells, distributed along the medial protocerebrum (Oguro, 1974). Regulations of the important vital functions of the organism occurs with the help

of the neurosecretory system. Neurosecretions participate, in part, in the regulation of the most diverse aspects of metabolism, processes of growth and regeneration, molting, in sex differentiation, gametogenesis, processes of reproduction, adaptive color changes, eye pigment movement for optical adaptation to different conditions of illumination, and so forth.

The Y-organ, or lateral organ, or molt gland is an endocrine structure characteristic of Malacostraca (Gabe, 1953). In isopods it is located in the maxillary segment of the head and participates in regulation of the molting process. Roche (1962) pointed out yet another pair of glands in representatives of the Flabellifera, Valvifera, Tyloidea, Oniscoidea, and Asellota, the anterolateral organs, also located in the head but more ventral and lateral, and in front of the Y-organs, close to the bases of the antennae. Both the Y-organ and the anterolateral organs are attached to the ventral hypodermis. Roche also established that the anterior frontal organs participate in the regulation chiefly of the molting of the anterior half of the animal's body.

Reidenbach (1969) discovered in Idoteidae paired cephalic organs like symmetrical, horizontal plates, which are located at the base of the tritocerebrum. The presence of cellular vacuoles and acidophilic globules, a cyclical secretion pattern, and other signs allow one to assume an endocrine nature for these cephalic organs.

As was already said earlier, the rudiments of the antennal glands possibly also serve a function as glands of internal secretion.

The androgenous gland will be described after the reproductive system.

### Reproductive Organs

In males the paired testes are located in the thoracic region dorsal to the gut. The testes (Figure 35) usually consist of 3 (rarely 1) tubular or pear-shaped lobe, each opening independently into the vas deferens, positioned on the dorsolateral side of the gut and directed posteriorly into the region of the seventh thoracic segment, where they end in a penis, or genital apophysis paired rod-shaped or plate-like chitinous appendages. In some genera (for example *Synidotea*) both genital apophyses are fused into one. Each testes lobe is stretched posteriorly like a thin appendix, which is called a support fiber.

In the females the paired ovaries (Figure 36) have the appearance of two almost straight tubes, usually of the same diameter throughout, located along the sides and dorsal to the gut, most often from the third through the sixth thoracic segment, but sometimes extending into the abdominal region as well. In reproductive periods the ovaries occupy the entire dorsal part of the body cavity. The ovary contains,



on the external side a germinal strip containing oogonia and young oocytes, surrounded by small follicular cell. The part of the gonad adjoining the inner side represents the oocyte maturation zone. A short ooduct goes principally from the outer side of the gonad at the level of the fifth pereopod, on its internal side. The ovaries are provided with four support fibers, three anterolateral and one terminal (Juchault, 1966). The fecundity of free-living isopods fluctuates within wide limits, from one to four in Limnoria and six eggs in Paramunna gaussi up to 982 eggs in Glyptonotus. In the parasitic Cymothoidae it is yet higher and fluctuates from 260 in Ceratothoa oestroides to 2450 eggs in Cymothoa oestrum (Zimmer, 1927).

The vast majority of isopods are separate-sexed animals, but three types of hermaphrodites are encountered among them. Protrandric hermaphroditism, when the animal first functions as a male and later as a female, is found in many parasitic Flabellifera (e.g. Meinertia and Anilocra of the Cymothoidae). More rarely the converse phenomenon is encountered, proterogynic hermaphroditism (Cyathura carinata of the Anthuridea), and in some terrestrial Oniscoidea simultaneous hermaphroditism takes place.

In the isopods the heterogametic is the female sex. Here is sex determination of the type: female XY, Y, male XX (Staiger and Bacquet, 1954). In comparison with many other Malacostraca, the number of chromosomes is remarkably small. The diploid number of chromosomes varies from 10 in Ianiropsis breviremis of the Asellota to 56-62 in certain Oniscoidea (Vandel 1947, Staiger and Bacquet, 1956).

The male and female gonads originate as the result of development of undifferentiated gonad rudiments (Legrand and Vandel, 1948). During this the androgenous gland plays a great role in the process of male sex differentiation. This endocrine structure was first uncovered by Charniaux-Cotton (1956) in amphipods, and was later found in all Malacostraca. The androgenous gland was discovered last of all in isopods chiefly because of its atypical location in this order (Balesdent and Marquet, 1958). Today they are found and described in representatives of seven suborders of isopods. Androgenous glands are located on the vas deferens, most often, in aquatic isopods. It has such a position in Cirolanidae and Cymothoidae of the Flabellifera, and Valvifera and Asellota (Juchault, 1966, 1977; Legrand and Juchault, 1970). The cited authors consider this androgenous gland position the most primitive. In most Sphaeromatidae, Epicaridea, and Tyloidea are attached to the testes. The androgenous gland is composed of mesenchyme cells and is separated from the sexual rudiments during the process of embryogenesis. It is represented by a cord consisting of glandular cells rich in chromatin.

In a young animal the undifferentiated gonads have a generative zone containing gonidia. The androgenous gland hormone is responsible for differentiation of the gonidia into spermatogonia. Without the

androgenous gland the gonads are obliged to become ovaries. In young males removal of the androgenous glands leads to the appearance of a brood pouch and other female characteristics in them. Conversely, implantation of an androgenous gland into a female leads to the appearance of male external sexual characters in it; the ovaries, which are modified into functional testes, are also transformed thereby (Legrand and Juchault, 1970).

The androgenous gland degenerates in the proterandrically hermaphroditic Cymothoidae at the time of sex inversion, while not disappearing completely (Berreur-Bonnenfant, 1962; Trilles, 1963, 1964). In the proterogynic hermaphrodite Cyathura curinata the androgenous gland develops on the gonad at the time of sex change, and its secretion causes the transformation from ovaries to testes (Legrand and Juchault, 1963a). Figures 37 and 38 show the changes that occur with sex change in the proterogynic hermaphrodite Cyathura corinata.

The neurosecretory system, which inhibits or stimulates the androgenous impulse, also exerts an influence on the process of sex differentiation. In particular, it has been shown (Legrand and Juchault, 1970) that removal of the central part of the protocerebrum, results in androgenous gland hypertrophy, and this to its hyperfunctioning. Removal of the optic lobes and the central lobe of the protocerebrum in young males Idotea baltica basteri calls forth premature development in them of morphological characters of adult animals. During the transformation of a male into a female in Cymothoidae, degeneration of the androgenous gland occurs through the influence of hormones discharged by the neurosecretory complex - the X - organs and sinus glands. Transplantation of these glands taken from a male Nerocila into another of the same species already turned into a female, evoked the development of the earlier degenerated testes, and spermatozoid maturation, and also a progressive development of the androgenous gland (Trilles, 1963).

In female the ovary maturation is also controlled by the inhibition of a neurosecretory center located in the medial lobe of the protocerebrum. Removing it from young female Idotea baltica basteri involves premature ovary maturation and sexual maturity (Reidenbach, 1965).

BIOLOGY  
Reproduction

Fertilization is internal. Pairing takes place at the time of the female molt after which the oostegites are formed. The penis, found on the ventral side of the seventh thoracic segment, does not take part directly in copulation. In the vast majority of isopods the role of copulatory organ is occupied by the endopodites of the second pleopods, usually provided with a stiletto-like, rod-shaped, helical, or even more complicated male outgrowth (processus masculinus). The penis still plays a part in delivering sperm into the complete organ. Sometimes (Antarcturus of the Valvifera) the modified first pleopods play a role in fertilization.

An external brood sac or incubatory chamber (Figure 29) develops in females of most isopods after fertilization, composed of paired, overlapping incubatory plates, or oostegites, representing protrusions of the coxal joints of the thoracic limbs. The nursing of the fertilized eggs and embryos goes on within this chamber. Sac ventilation occurs with the aid of thoracic limb movements, directing water into it. In some isopods (e.g. many Sphaeromatidae) an alteration of the female appendages occurs at the time of brooding (appearance of additional lobes on the limb joints, etc.). Thus the females lose their feeding adaptations during the incubation period, but in exchange sac aeration occurs not only from the rear, but also from the front. The number of oostegites varies from 7 pairs in some Cirolanoidea to one pair in a group of species of Arcturidae (Calman, 1909). Sometimes the external brood chamber undergoes reduction to a greater or lesser degree. In these cases development usually occurs in an internal brood chamber formed by paired invaginations of the cuticular covering of the ventral side of the thoracic region (for example, some Sphaeromatidae of the Flabellifera). Thereby, the shortened oostegites only cover the openings of these sacs (Zimmer, 1927). Some Tyloidea also have internal sacs detached from the outside. Here some of the embryos are found in the outer chamber, and some in the inner (Mead, 1963, 1965). Eurydice affinis and E. pulchra (Flabellifera, Cirolanidae) have 5 pairs of oostegites which form a sac, but the young are not brooded in it, but in an internal chamber formed by a pocket of ventral thoracic cuticle. This chamber opens into the pouch formed by the oostegites (Salvat, 1966). Finally, true ovoviviparity is found in Excirolana from the same family Cirolanidae (Davis, 1964; Klapow, 1970). Female Excirolana have three pairs of small, reduced oostegites. The eggs fall from the oviducts into a pair of irregularly formed sacs formed by a single layer layer of cells and located in the thoracic region lateral to the gut. In as much as these sacs do not open externally and the embryos, therefore, are completely isolated from the external environment, this can be said to be typical ovoviviparity. During embryonic development, which lasts three months in Excirolana chiltoni and E. linguifrons, the embryos increase 3 times in volume. Klapow

(1970) showed that the embryos receive supplementary nutrition in these "uteri".

### Development

Eggs in Isopoda are large (up to 11 mm in diameter in *Bathynomus*), rich in yolk, centrolecithal, and oval or almost round, their nuclei are located in the center and surrounded by a mass of cytoplasm, offshoots of which are distributed among the yolk grains. In addition, there is a thin layer of cytoplasm (periplasm) along the periphery of the egg (Ivanov, 1937; Stromberg, 1965). Only in the parasitic Epicaridea, which are not considered in the cited works, are the eggs poor in yolk. The eggs are surrounded by envelopes, one of which, the chorion, is formed by the follicular cells within the ovary and the other, the vitelline membrane is only formed after the introduction of the fertilized eggs into the brood chamber, through the action of the external layer of periplasm.

Cleavage is superficial, only complete in the parasitic Epicaridea (Bonner, 1900; Caullery or Mesnil, 1901). After the third division the nuclei, together with a portion of the protoplasm surrounding them, begin to shift to the surface of the egg, where, fusing with the superficial cytoplasm, they form large, star-shaped cells, which are located on the surface of the yolk (Ivanov, 1937). The cell boundaries appear at the 32-cell stage (Stromberg, 1965). At about this stage, derived cells lying at the vegetal pole become vitellophages; a ring of cells around the group vitellophages represents the embryonic mesoderm and secondary endoderm, i.e., endoderm which goes into part of the animal's gut. Cells of the animal hemisphere give rise to ectoderm (Ivanov, 1937). Gastrulation occurs by epiboly. The process begins by invagination of the vitellophages, after which mesoendodermal mass follows. The germ cells differentiate in the center of this mass. Anterior to them the naupliar mesoderm and mesodermal teloblasts arise. All the postnaupliar (postmandibular) segments are formed by the ectodermal and mesodermal teloblasts (Stromberg, 1965, 1968). In the course of embryonic development there follows the development of a pair of preantennular segments. In each of them a coelomic cavity appears for a short time (Stromberg, 1965). During development the nervous system, a pair of preantennular ganglia and a seventh pair of abdominal ganglia appear. The later, however, quickly fuse with the sixth pair of ganglia (Stromberg, 1968).

Isopods have two types of embryonal dorsal organs, one medial and two dorsolateral ones. Their function is unclear. The medial organ is known in all studied Isopoda, excluding the Epicaridea, and the dorsolateral ones found in Idotea, Sphaeroma, Ligia, and Asellus (Stromberg, 1965).

Authors, having studied isopod marsupial development (Somme, 1940;

Forsman, 1944; Kjennerud, 1952; Naylor, 1955b; Klapow, 1970; etc.), separate it into 3-5 stages (Figure 39). Usually four stages are well distinguished. The first stage occurs within the egg membrane, the chorion. The second, or embryonic stage, occurs within the embryonic membrane. At this stage the embryo has a elongate form, usually curved, straightening out at the end of the stage; a process of segmentation occurs which becomes ever more distinct, developing antennae, mouthparts, and limbs. When the embryonic envelope has ruptured, the animal passes into the third, or larval stage, when it lies free in the pouch; the mouthparts and limbs are completely segmented, although without setae and pressed against the body. Before exiting the pouch (fourth stage, or manca stage) the young are already similar to the adult individuals, but are still lacking the last, seventh pair of pereopods. At this stage the young leave the brood pouch. Besides lacking the seventh pair of pereopods, the young exiting the pouch have a few other differences from the adult state in the proportions of the body, in particular the considerably larger head, and also a lower number of aesthetases on the first antennae, fewer flagellar segments in the second antenna, weakly developed pigmentation, etc. In the course of most marsupial development the animal molts a few times and after each molt becomes more similar to the adult individual(Figure 41).

In Arcturidae part of the postmarsupial development of the young is carried out while clinging to the long, massive second antennae of the mother.

## Growth and Molts

In most isopods growth lasts the whole life, while slowing down abruptly at the onset of sexual maturity. Longevity varies from 1-2 years in many small forms up to 8-9 years and probably more in the large cold water sea roach Mesidotea (Nikitina and Spasskiy, 1963). As in all crustaceans, growth is uneven, which is due above all to the presence of a chitinous external skeleton. Therefore immediately after a molt a considerable increase in body size and weight occurs quickly through an increase in the water content of the animal, and in the course of the rest of the intermolt period, while no increase in body size occurs, a real growth of the organism is found, through the reduction of the organism's water content (Carlisle and Knowles, 1959).

The whole cycle from molt to molt is subdivided into four periods. At the premolt, or preexcysial stage, the organism is prepared for it. Calcium and certain other elements are removed from the skeleton into the organism, thereby increasing their blood concentration. The most stage, or exdysis, elapses in the two steps in the vast majority of isopods. First the skeleton is shed from the posterior half of the body, including the abdominal region and the three posterior thoracic segments, and then, with an interval of a few hours to six days, the anterior half of the body molts (Schoebl, 1879; Herold, 1913; etc.). Molts are uniphasic only in the Antarctic sea roach Glyptonotus (George, 1972). In the post-molting or postecdysial stage, the new skeleton firms up and becomes impregnated with lime. In the molting and post-molt stages the animal usually tries to shelter itself and does not feed. Only in the intermolt stage does the animal enter into a physiological norm, actively feeding, its skeleton becomes completely hardened, and under it a new cuticle forms, i.e. the beginning of preparations for the next molt.

Molt cycle regulation is realized through the participation of the Y-organs, the anterolateral organs, and the neurosecretory system. Longevity in small and medium-sized isopods as a rule does not exceed 1-2 years. In large forms, especially those living in cold waters, life expectancy is considerably greater. For example, even in the Baltic Sea Mesidotea entomon lives up to 8-9 years (Nikitina and Spasskiy, 1963). In the Arctic Ocean the longevity of Mesidotea is apparently even greater.

Sexual dimorphism is the rule in most isopods. Usually immature individuals are externally undistinct, but females with oostegites are usually wider than males and immature individuals in the region of the brood pouch. Males are more often of a somewhat greater size; more rarely females are larger than males. As stated earlier, sexual dimorphism, with a few exceptions, is expressed most of all in the structure of the second, and sometimes the first, pleopods, which in males play a part in aggregating and collecting the sperm into the body of the female. Sometimes a metamorphosis of some of the

mouthparts is found in egg-bearing females, specializations for aeration of the brood pouch. Often dimorphism in the structure of the first or second pereopods is encountered. In this case they are simple in the females and in males are modified into gripping appendages, serving to cling to the female at the time of copulation. Sexual dimorphism is strongly expressed in many Sphaeromatidae (Figure 41). Here the males are larger than the females, the telson planted with bumps or outgrowths, lacking or weakly expressed in the females. Often there are outgrowths on the end of the abdomen and on the free thoracic segments in males. Thus, not uncommonly females and young individual males in the family Sphaeromatidae were assigned to different genera. Finally, sexual dimorphism is very clearly expressed in the parasitic Epicaridea, which we are not concerned with here.

### Feeding

Isopods are extremely variable in the character and method of nutrition. In most free-living isopods the mouthparts are for biting, i.e. adapted for reducing in size practically any kind of food at all. Therefore, among them are a great number of omnivorous forms, although one may still speak of a predominant mode of feeding. For example, species of the genus Idotea of the Valvifera can be considered omnivores, but some species, like I. baltica (Rauschnplat, 1907; Bokova, 1952; Gaerskaya, 1958; Khmeleva, 1973) and I. ochotensis (Kusakin, 1974), feed principally on plant matter, but can also consume animals, or else like I. neglecta prefer animal and often resort to facultative ectoparasitism, clinging to a fish and removing bits of meat from it (Kjennerod, 1952). Many marine isopods, being basically carnivorous, eat not only small, living animals but also carrion (Mesidotea and Glyptonotus of the Valvifera, some species of Excirrolana, Cirolana and Nerocila of the Flabellifera). There are apparently few exclusively herbivorous forms among the aquatic isopods (e.g. Phycolimnoria of the Flabellifera, the water asellus Asellidae of the Asellota). These are joined also by wood-borers (Limnoria and some Sphaeromatidae).

The feeding methods in many isopods, especially among the Asellota, are deposit feeding and detritophagy. Many Sphaeromatidae scrape plants off hard substrates. Species of the family Arcturidae of the Valvifera are filterers.

Typical carnivores are widely represented among the Cirolanidae and families close to it. In a group of families of the superfamily Cirolanoidea, to which belong the Anuropidae, Cirolanidae, Excorallanidae, Corallanidae, Aegidae, and Cymothoidea, one finds a gradual transition from feeding predominantly on carrion in some primitive representatives, to carnivory, and finally to parasitism in the most specialized forms (for example, most of the Cymothoidea). Here one encounters partial reduction of the antennae, gradual

transformation of the walking thoracic legs into clinging organs, and modification of the mouthparts from biting to piercing and sucking. This is usually accompanied by the acquisition of an asymmetrical body form and a transformation from forms into protandric hermaphrodites in the most specialized fish parasites, the higher Cymothoidae. A reorganization of the biting mouthparts into piercing and sucking ones is widely present in the suborder Anthuridae.

Commensals are little distributed among Isopoda. One can count, as commensals, for example, small Asellota of the genus Iais, which live on the ventral side of the body of Sphaeromatidae between the appendages, and Caecijaera, living in the burrows of the wood-borer Limnoria.

As Menzies (1962b) stated, among the deep-water Isopoda, benthic detritophages and to a lesser degree carnivores clearly prevail, filterers consist of less than 1%, and isopods with other feeding modes are absent.

The daily food ration and food assimilation in isopods to a large degree changes in connection with the animals body size, its age, the quality of the food, physiological condition, and also depends on a series of environmental factors. In the predominantly herbivorous Idotea baltica basteri in the Black Sea, its daily food consumption in percentage of weight equals 34% Enteromorpha, 27.3% weaker individuals of its own species, and 26.39% chironomids. The daily consumption of food consists 23% of Enteromorpha, in August 59%, in September 34%, and in October 21% (Bokova, 1952). The mean assimilation of plant food in I. baltica basteri amounts to 63%. Thus food assimilation occurs most effectively in the early period of life, then falls and further on remains level. Thus, young of I. baltica basteri assimilate living Cladophora at 82%, and sexually mature males merely at 58% (Soldatova, Tikhon-Lukanina, Nikolaeva, and Lykashera, 1969). In the smaller crustacean Dynamene versicolor the daily food index changes within limits from 5% in males 5-6 mm long to 45% in crustaceans 2 mm long. According to the data of Tikhon-Lykanina and Lukasheva (1969) on the crustaceans studies by them, Idotea baltica basteri and Sphaeroma pulchellum, 78-84% of the energy absorbed from food goes to satisfy the needs of energy exchange, 12-18% is removed as excrement, 47% is expended in growth, and 10% of the increase is lost with molted skin.

Carnivorous isopods are very voracious. Thus, 3-4 specimens of Eurydice of the Cirolanidae ate an amphipod, Hausterius arenarius, in the space of three minutes, leaving only skeletal fragments of it (Jones, 1968).



## Coloration

Coloration in most isopods is a monotone gray-yellow, green-yellow, or light brown, rarely bright rose, red, or green. In some isopods, for example, species of Jaera, Idotea, Sphaeromatidae, the color is spotted, and a single species has several phenotypes differing in the character of the location of the spots and their color. In a number of cases the animal freely changes its coloration in correspondence with the color of the substrate.

Coloration in isopods is the result of the interaction of cuticular pigments and pigments found in chromatophores. Movable granules of various pigments found in chromatophores evoke adaptive changes in the animal's coloration. The basic pigments belong to the carotenoids and caroteno-proteins. Their composition is very variable and can differ even in species of the same genus. Thus for example, in Idotea metallica the basic pigment is zeaxanthin, with small quantities of idoxanthin, isocryptoxanthin, astaxanthin, beta-carotene, and crustaxanthin. The coloration of this species is the result of the activity of three pigment systems: purple chromatophores, white iridophores, and cuticular carotenoid pigments. Chromatophores are found in the epidermis beneath the cuticle over the whole body and contain pigment, the color of which varies from russet to purple. Iridophores lie in the epidermis over the chromatophores and are encountered predominantly along the midline of the body. They contain small white crystals (Herring, 1969). Idotea resecata, having a brown and green colored variety, had 10 carotenoids extracted: alpha-carotene, beta-carotene, echinenone monoxy-beta-carotene, xanthaxin, 4-oxy-4'-keto-beta-carotene, leutein, zeaxanthin, flavoxanthin, and violaxanthin, and a green carotenoprotein was also found, similar to one extracted from another littoral species of Idoteidae (Lee and Gilchrist, 1972). Beta-carotene, isocryptoxanthin, echinenone, 4-oxy-4'-keto-beta-carotene, isocryptoxanthin, and leutin (Lee 1966a) are found in Idotea granulosa, with red, green, and brown forms. Red, green, and brown individuals were studied in Idotea montereyensis (Lee, 1966b). The cuticle in all three color varieties of this species contains leutein, leuthen-epoide, and canthaxanthin, while their proportions differed in each case. The red cuticle contains predominantly the reddish-producing beta-carotene and anthaxanthin, the green cuticle contains a bluish canthaxanthin-protein complex and a considerably greater quantity of leutein, and the brown cuticle occupies an intermediate position, since it contains a mixture of red and green pigments. Besides carotenoids, in Asellidae and Oniscoidea xanthommatin, ommatin, and ommin are known (Needham, 1970). The chromatophore pigment is a reduced ommochrome in Idotea montereyensis and I. granulosa (Lee, 1966a, b).

Color changes are attained principally by means of pigment granule movement in the chromatophores primarily in melanophores containing dark pigments. The concentration of pigment granules in the

melanophores evokes a lightening of the animal's coloration and their dispersion, on the contrary, its darkening. In the shoreline crustacean Ligia of the Oniscoidea a complete color change following a shift in substrate takes two hours (Green, 1961). In pale specimens of Idotea taken into a dark room, the melanophores began to expand in 15 minutes and in the course of two more hours the color change progressed (Oguro, 1962). In direct sunlight the white pigment grains in iridophores disperse in Idotea metallica, and in darkness opposite movement is found. In this process the iridophore change happens considerably more quickly, 5-10 minutes at the most (Herring, 1969). In Ligia baudliniana introduced to total darkness, a daily rhythm of pigment activity is found, the animal becoming dark by day and light by night (Kleinholz, 1937).

In the same work Kleinholz first described endocrine regulation of color change in isopods. Injection of aquatic extracts of the head of light individuals into dark ones resulted in a concentration of pigment in their chromatophores (Kleinholz, 1937). At almost the same time Stahl (1938a, b) showed that cephalic extracts of the isopods Oniscus ascellus, Porecllio scaber, and Mesidotea entomon evoke a dispersion of the red and yellow pigments in light individuals of the shrimp Palaemon squilla, and Smith (1938) proposed the existence of pigment dispersing and pigment concentrating substances for the melanophores of Ligia oceanica. Enami (1941) and Fingerman (1956, 1963) discovered that injection of sinus gland extracts, superpharyngeal ganglion extracts, and extracts of the ventral nerve chain induced pigment dispersal in the melanophores of Idotea.

Oguro (1959b) showed that the sinus gland in Idotea receives a hormone dispersing the chromatophore pigment, which is produced by the neurosecretory cells of the suprapharyngeal ganglion.

#### On the Evolution of the Isopods

The phylogeny of the Malacostraca can be considered rather well studied at the present time (Siewing, 1956; Birshtein, 1960a; Kaestner et al, 1967), as a result of which we can now with assurance consider isopods as the most specialized representatives of the superorder Pericarida, which in turn is apparently the most specialized among the Malacostraca (Figure 42). Work on the disclosure of phylogenetic relationships within the order, which consists of nine very strongly differentiated suborders, is worse off. Thus carcinologists analysing the degree of primitiveness of one or another suborder usually run across a series of difficulties. First, of all, fossil remains of Isopoda are very scarce and provide little to disclose the time of origin and evolution of this group. The most ancient isopod find is the Upper Carboniferous (middle Pennsylvanian) of North America (Schram, 1970). Representatives of the family Paleophreatoieidae, described earlier by Birshtein (1962) from the Upper Permian stata,

were found here in marine sediments. This family belongs to the suborder Phreatoicidea, nowadays living only in freshwater in India, Australia, Tasmania, and New Zealand. The Flabellifera are known only from the Triassic, the Epicaridea from the Mesozoic, the Oniscoidea and Valivifera from the Oligocene, and the Asellota are unknown in fossil form. However, comparative anatomical data does not allow us to take the Phreatoicidea as the most primitive suborder which, as correctly shown by Nicholls (1943) and Dahl (1954), originated from ancient Flabellifera close to the modern Cirolanidae. Consequently ancient representatives of the Isopoda must have existed, as Schram justly figured, long before the Upper Carboniferous. On the other hand, all the modern isopod suborders, though to differing degrees very strongly specialized, still a greater or lesser quantity of primitive characters.

In order to compare more easily the degree of primitiveness of one or another isopod group, one tries to present what that ancient crustacean must have looked like, still retaining all the primitive characters now scattered among the various suborders and families of isopods, but nonetheless already differentiated from the other orders of Peracarida; i.e., it was already an isopod.

In the evolution of Isopoda the law of integration, or oligomerization, is distinctly displayed (Merezhkovskiy, 1913; Dogel, 1954). A reduction in the number of abdominal segments by fusion with the telson occurs independently in different suborders; within more circumscribe limits is a reduction in the number of thoracic segments by fusion of the most anterior with the head (Serolidae, Arctoridae) or among themselves (Eurycopidae and certain other Asellota). The opposite process, polymerization, is encountered extremely rarely (the presence of multiarticulate, feeler-like pereopods in Chaetilia of the Idoteidae). Therefore, one can say with assurance that the greatest number of free body segments close to the original number of Malacostraca is the original composition in isopods. Furthermore, if in all isopods without exception the thoracic limbs have become uniramous already, still both pairs of antennae retain a rudimentary second ramus in a number of cases. Therefore, the ancestors of the Isopoda still had biramous antennae. In most isopods an alteration of the coxal joint of the first pereopods has occurred into a shield-like epimere grown together with the thoracic segment, and in a number of cases complete fusion without a trace of a seam is encountered. The primitive arrangement is when the coxopodite still looks like a normal segment (in Asellota). The primitive form of the pereopods is a walking leg with more or less cylindrical joints, while all of the pereopods have a similar structure. The pleopods in primitive form also are constructed similarly with an equal degree of development, and the uropods, as in Anuropidae were probably still similar to the pleopods and occupied the same such position, i.e., they were located beneath the abdomen.

Thus the ancestral isopod form could have had the first thoracic

segment already fused with the head, and the appendages of this segment were modified into maxillipeds, seven pairs of similar-looking walking pereopods, and six pairs of pleopods developed alike; the coxal plates still look like limb joints and were not fused with the corresponding thoracic segments. There are no forms among the modern isopods which have retained all these primitive features, but many of them are distributed among the various families and suborders. It is interesting to find out which isopod group retained the greatest number of these characters. Carcinologists determining the phylogenetic interrelationships among the isopods, have most often dwelled on two groups, the Asellota and Flabellifera, in regard to this, and correspondingly, one group of them (Hansen, 1905b, 1925; Monod, 1922; Birshtein, 1951; Zenkevich and Birshtein, 1961; etc.) as very primitive or even the most primitive suborder among the Isopoda, just another (Racovitza, 1912; Menzies and Frankenberg, 1966; Schultz, 1969; Kusakin, 1973) consider such lower Flabellifera as the Anuropidae and Cirolanidae as the most primitive isopods, closest to the ancestral form. The basis for the first point of view was laid out in the work of Schiodte (1866), which considered Cirolana as the most modern type among the isopods. This opinion was accepted by many carcinologists, and the first to point out its mistakenness as Racovitza (1912) who put forth eleven characters by which Cirolanidae must be placed among the most primitive isopods. Here one must note that Schiodte was to some degree correct. Actually, Cirolanidae with their strongly streamlined body, leading a predaceous way of life, and counted the best swimmers among the isopods, are the most modern animals from the point of view of adaptation to the environment they inhabit and the way of life they lead. But this is in no way related to their greater or lesser primitiveness in comparison with other isopods, just like the modern, swimmers-sharks, and modern flyers-eagles are, in their evolutionary relations, very primitive in comparison with many worse swimming fishes or more poorly flying birds.

One can consider similarly the existence of primitive organization features in representatives of the various suborders of Isopoda. However, in doing so, one must take into account that the separation of these suborders occurred very long ago and the suborders have undergone protracted independent evolutions, so the higher representatives in each of the large suborders are already very considerably advanced in comparison with the lower families. The same is found in connection with the various genera in large families.

In isopods integration affects the head and thoracic regions to a small degree, which in most representatives of all suborders have a common structural plan: head, including the first thoracic segment, and seven free pereopodal segments. However, in Bathynomus and Sphaeromides of Cirolanidae, traces of the fusion of the first thoracic segment with the head remain as lateral seams. (Milne-Edwards and Bouvier, 1902; Racovitza, 1912). Pygidization is widely distributed in isopods, i.e. gradual fusion of the abdominal

segments with the telson up to the formation in a number of genera of entire abdomen consisting of a single tagma. The greatest number of free abdominal segments (six), corresponding to the original, number for all Malacostraca, is found in Anthuridea. Only one abdominal segment is fused with the telson in many Isopoda. These are all the Phreatoicoidea and Oniscoidea, the greater part of the Tyloidea, and the superfamily Cymothoidea of the Flabellifera. However, the Asellota are very far along in this regard, since the most primitive of them, the Aselloidea, already all have two free abdominal segments, and all of the rest have one or even an integrated abdomen.

As reported earlier, a rudiment of the accessory flagellum on the first antenna is found in some representatives of the Flabellifera (Bathynomus and young Cirolana of the Cirolanidae, Paralimnoria and many Limnoria of the Limnoriidae), in the genus Mesanthura of the Anthuridea, and also in larval Epicaridea. In all the other isopods, including all the Asellota, the first antenna lacks a supplementary flagellum. The second antenna has a six segmented peduncle only in Asellota, and also in the genus Bathynomus of the Cirolanidae (Cirolana, Conilera, Sphaeromides and Typhlocirolana), and a two-segmented, rudimentary exopodite in some Anthuridea; and some lower Asellota and lower Oniscoidea, the Ligiidae, have a small unsegmented exopodite.

Pereopod differentiation occurs independently in the various suborders of Isopoda. Often the first and rarely the second pair of pereopods are turned into gnathopods; in Aegidae the posterior and in the Cymothoidea all the pereopods are for clinging; in some higher Asellota the posterior pleopods are adapted for swimming. Note that in the lowest Flabellifera, the Anuropidae and Cirolanidae, all the pereopods are of the walking type, and in the lowest Asellota, the Aselloidea the first pereopod is gnathopodal. The exopodite retains a primitive segment-like form in the Asellota; here the ones on the first pereopods are immovable, but on the other pereopods are movably articulated to the corresponding segments. This has to do with the fact that most Asellota do not swim or swim badly. In all other isopods the coxal joint is like a shield-shaped epimere bordering the lateral edge of the segment. The first epimere is completely fused with the segment without a trace of a seam in all isopods, this seam being still seen only in Typhlocirolana of the Cirolanidae (Racovitza, 1912).

Pleopod differentiation takes place in Anthuridea, the higher Flabellifera (Seroloidea, many Sphaeromatoidea), and a number of higher Valvifera (some Arcturidae). In the lower Flabellifera all the pleopods are undifferentiated, of a similar structure. In all Isopoda the uropod sympodite is one segmented and consists of a single basipodite, but in Bathynomus and Sphaeromides of the Cirolanidae rudiments of the precoxal and coxal joints have been found (Milne-Edwards and Bouvier, 1902; Racovitza, 1912). Conversely, in Asellota the pleopods are quite differentiated even in the lower

Aselloidea; in males the first and second pleopods are strongly altered and serve for copulation, and in females the first pleopods are usually absent, and the second pleopods modified into opercula. Finally, all Isopoda, excepting Anuropidae of the Flabellifera, which has all six pairs of abdominal limbs modified into uropods, which have a lateral (Flabellifera, Anthuridea, Valvifera, and Tyloidea) or terminal (Phreatoicoidea, Asellota, and Oniscoidea) articulation. Laterally is considered the more primitive, and Dahl (1954) showed how in the course of development of Phreatoicoidea the latter attachment of the uropods changes into a terminal one. In suborders with a lateral type of attachment, the uropods are strongly specialized in Valvifera and Tyloidea, where they form opercula protecting the pleopods from below, and in the Anthuridea where they hang over the telson, forming together with a tail cup. The most primitive uropod position, is along side the pleotelson and the least altered form of this too is in the Flabellifera.

Even though the Anthuridea retain the greatest number of abdominal segments and in a number of cases retain rudiments of the second branches of the first and second antennae, still one may not consider them the most primitive. The elongate, stick-like body, strongly modified mouthparts and unique uropod aspects testify to the high specialization of this group. The Phreatoicoidea, while retaining many primitive characters, nonetheless cannot be counted the stem group for the Isopoda, since they have specialized uropods, a changed, laterally compressed body form and a series of other specialized features. As was noted above, the Phreatoicoidea are derived from primitive Flabellifera. The Oniscoidea and Tyloidea as well undoubtedly are far removed from the original ancestor, possessing specialized pleopods adapted for aerial respiration, reduced antennules, and an ensuing lack of mandibular palps. Apparently, the Oniscoidea arose independently from the Flabellifera, and Tyloidea from the Valvifera. The latter are also very much deviated from the stem type, possessing a substantially reduced number of abdominal segments and strongly specialized uropods. They arose from primitive Flabellifera. The Asellota and the Microcerberidea, while retaining pretty many primitive organizational features, cannot be considered close to the original form since their abdominal region is highly integrated and consists of not more than two free abdominal segments and besides, the Asellota have strongly specialized first and second pleopods. The structure of the not here considered Epicaridea is so strongly modified in connection with their parasitic way of life that they are considered extremely specialized forms. That is why we join with the point of view of those authors who reckon that the closest to the original type of Isopoda are the primitive Flabellifera like Anuropidae and Cirolanidae, possessing a six-segmented abdomen, a compact, oval body form, and biting mouthparts. In the Anuropidae, besides, the uropods are still similar to the pleopods. Even such primitive forms have specializations mixed in (appearance of epimeres, flat, toothed out growths of the mandibles, etc.), which do not permit them to give rise directly to the other Isopoda.

We present the phylogeny of isopods in the following way. The ancestor of the Isopoda had a oval, compact body, reminiscent of modern Anuropidae and Cirolanidae, but not with their five, rather six free abdominal segments anterior to the pleotelson. It had six pairs of pleopods corresponding to the number of abdominal segments, as in modern Anuropidae. These pleopods fulfilled simultaneous swimming and respiratory functions. The pereopods were of uniform, uniramous, walking type, and probably with natatory setae as in the modern Cirolanidae. The first thoracic segment had already entered the composition of the cephalon, and its appendages were transformed into maxillipeds. The mouthparts were of the biting type usual for crustaceans, but in contrast to the modern Cirolanidae which possess a specialized, flattened, limb-like toothed mandibular protrusion, the latter was probably cylindrical in the ancestral form, as in the majority of modern Isopoda. Both pairs of antennae were with rudimentary exopodites. Judging from the way of life of many modern, primitive Flabellifera, and also by the gill-like pleopod character, serving simultaneously for swimming, one can assume that the ancestral form of the Isopoda led an active nekto-benthic, apparently predaceous way of life.

Very early from such an ancestral form detached a branch adapted to a benthic swarming way of life, the Anthuridea, retaining a free telson. Evolution within this group went basically on a line of specialization from biting mouthparts (Anthuridae) to piercing and sucking ones (Paranthuridae). The Microcerberidae probably also arose from the Anthuridae.

The basal branch first gave off the primitive cirolanoid Flabellifera. From these arose, on the one hand the Oniscoidea, and on the other the Phreatoicidea, and finally the common ancestor of the Valvifera and Tyloidea, apparently independently.

Of the number of families of Valvifera, the most primitive is taken to be the family Idoteidae, and the most specialized the Arcuturidae. The overwhelming majority of Valvifera are benthic animals. Chytrophagous forms predominate among the primitive forms, but predaceous, scavenger, and omnivorous species are also encountered. Ambush predators and filtrators predominate among the most specialized ones.

The evolution of the Flabellifera themselves (not taking into consideration extinct families like Urdacea whose positions are inadequately know) went in three basic directions. One line of development went to the route of transition from a predaceous to parasitic mode of life (Cirolanidae-Aegidae-Cymothoidae). Here the animals remained nekto-benthic. From forms close to the Cymothoidae arose the parasitic Epicaridea. The two other lines gave off benthic herbivores and detritivores, Seroloidea and Sphaeromatoidea. The Asellota apparently originated from ancient Phreatoicidea. Chitton (1894) and Barnard (1927) commented on the closeness of the former to

the Phreatoicidea. Of the four super families of Asellota the most primitive is the fresh-water Aselloidea, and the most specialized the Janiroidea. No less than 16 families are distinguished in the last superfamily, however, the boundaries between them cannot always be clearly outlined, since up till now the range and quantity of the families has been a matter of discussion (Menzies, 1956, 1962b; Wolff, 1962; Birshtein, 1963a; etc.). Without doubt the most primitive is the vast family Janiridae, and the most specialized are the three close families Ilyarachnidae, Eurycepidae, and Munnopsidae, clearly isolated from all the rest. The greater part of the Asellota are benthic detritophages, but some of the higher representatives of the suborder (Munnopsidae and part of the Eurycopidae) have secondarily adopted a pelagic way of life.

Figure 43 is a general view representing the evolutionary scheme of the isopods.



DISTRIBUTION  
DISTRIBUTION BY LATITUDINAL AND VERTICAL ZONES

Isopods have a great quantity of living forms adapted to life either in aquatic (marine, brackish, or even freshwater) media or on land. In the marine environment it would be perhaps difficult to find a biotope in which isopods do not live. Hence they are represented rather richly in all depth ranges in the world ocean and at all latitudes, since in contrast to many other groups, in isopods no clear fall in the number of species is found from tropical latitudes to the poles and from the littoral and upper sublittoral to the maximum depths of the ocean. However, the composition of the isopod fauna is substantially changed from low latitudes to high and from shallow depths to great (Kusakin, 1973).

Flabellifera

The vast majority of species (over 770 out of 1,050) of this most primitive and most species rich suborder of marine Isopoda are accustomed to the shelf zone of warm waters, i.e. tropical and subtropical waters. About 260 species, i.e. about 25%, live in the shelf zones of cold and temperate waters in both hemispheres, and only 19 species, i.e. less than 2% are found at depths greater than 2,000 meters within the entire World Ocean.

In the superfamily Cymothoidea, to which the most primitive family of isopods belongs, out of 596 species only 122 (20%) live in the shelf zone of cold and temperate waters and just 8 species are found at depths greater than 2000 meters.

In the superfamily Sphaeromatoidea out of approximately 400 species just 105 species (about 28%) live in the shelf zones of the cold and cold-temperate waters. Here both species of Plakathriidae live only in the Southern Hemisphere. Only one species of Sphaeromatoidea is found deeper than 2,000 meters.

A different sort of distribution is found in the most highly specialized superfamily in the suborder, the Seroloidea. Out of 54 species, 35 (about 65%) live in cold and cold-temperate waters of the shelf zone, however, only in the Southern Hemisphere, and most richly represented in Antarctica. Only three species of this superfamily, of which one is deep water, penetrated along the American coasts to southern California and Georgia (shelf species) and New England (a deep-water species). Ten species live in depths greater than 2000 meters, and eleven species in subtropical waters.

The reverse of this is the asymmetrical kind of distribution of some predominately tropical families of Flabellifera. Thus, in the Northern Hemisphere the primitive family Cirolanidae is completely absent in the Arctic and penetrates boreal waters to a very limited degree.

Meanwhile in the Southern Hemisphere the Cirolanidae are rather richly represented not only in tropical waters, but also in Antarctica. Six species of this family have been discovered in the latter. Similarly, in the Atlantic Ocean the Sphaeromatidae do not extend north farther than New England and western Norway or in the Pacific Ocean beyond 61 degrees. In the Southern Hemisphere some representatives of this family have a circumantarctic range.

From the foregoing one can propose that the oldest center of isopod fauna formation is the tropical shelf, now still retaining the greatest amount of primitive representatives of this order. One can consider the cold and temperate waters of the Southern Hemisphere as other, younger centers of fauna formation, where the Plakarthriidae and Seroloidea formed, and about which their modern distribution indirectly attests. No analogous center appears in the Northern Hemisphere.

#### Anthuridea

This family, also retaining many primitive features contains about 110 species the greater part of which live in warm waters. Altogether 29 species (about 27%) have been discovered in the shelf zones of cold and cold-temperate waters, and only 7 species (i.e. less than 7%) at depths greater than 2,000 meters. Therefore, for this suborder also the center of formation is to be sought in warm waters.

#### Microcerberidea

In this small suborder most of the species live in subterranean continental waters, and a few species in the seashore, of which only two were discovered in lower boreal waters. That is why we will not mention this suborder any more in the following discussions.

#### Valvifera

Considerably greater complexity is involved with the distribution of this suborder, which apparently got its start from primitive Flabellifera. If one considers that the entire suborder at once, then the greatest number of species (239 of 300; i.e., a little over 70%) live in the shelf zones of cold and cold-temperate waters. Twenty-one species, that is a little more than 6%, are found at depths greater than 2,000 meters. If one considers the distribution individually by family, then for this suborder also a tropical origin follows.

Of the five families in this suborder we consider the most primitive the Idoteidae. In this family the percentage of species living in the shelf zone of warm-water regions is comparatively higher (94 species out of 164; i.e. more than 57%) than the total for the suborder, and

the percentage of deep-water species on the contrary, is lower (3 species, i.e. less than 2%). However, also in the species living in cold and cold-temperate waters of both hemispheres predominate (126 species, or around 77%). (The sum of the percentages are, as in some other cases, surpasses 100% since species exist that on the one hand live in cold-temperate as well as warm waters, and on the other live above as well as below 2,000 meters. In these cases such species are counted not just once.

Of the four subfamilies of Idoteidae, the Mesidoteinae is considered the most primitive, retaining biramous uropods and a seam between the thoracic segments and the epimeres on all pereonal segments, except the first. Nowadays the Mesidoteinae are characterized by an antitropical distribution, since most of the species gravitate toward less saline waters. The genus Mesidotea is widely distributed in the Arctic, and is represented in boreal waters of the Atlantic and Pacific Ocean, and also in the Caspian Sea. The closely related, monotypic genus Saduriella is found in the Lusitanian province. The genus Chiridotea is distributed in subtropical and temperate waters of the Atlantic coast of North America. The Notidotea lives in fresh and brackish waters in New Zealand and the southern tip of American, finally, the genus Austridotea, is in fresh water in New Zealand. The genus Proidotea, also assigned to the Mesidoteinae, is found in Oligocene deposits of Romania and Poland, which allows me to consider Tethys or bodies of water originating from it as the center of the origin of primitive Valifera.

The further evolution of the Idoteidae is connected with moderate and cold waters principally of the Southern Hemisphere. Thus the primitive subfamily Chaetilineae contains three genera of which all (Chaetilia, Chiriscus, and Macrochiridotea) in New Zealand. The subfamily Glyptonotinae is represented by two monotypic genera, of which Glyptonotus is endemic to Antarctica and Symmius is found in subtropical waters of Japan.

The highest subfamily, Idoteinae, represented by the greatest number of genera and species, has a universal distribution and is not found only in the Kerguelen region (Kusakin, 1967). For all the other areas, except the Arctic, endemic genera are characteristic, which is evidence for the existence of a considerable number of comparatively young centers of fauna formation in this superfamily (sic, probably means subfamily).

The family Amesopodidae with a single species is found in the northern part of the Indian Ocean and in the Red Sea and represents a small independent branch taking its origin from the Idoteidae. Another more progressive branch of the Valvifera, including three families, is connected by the roots to cold, temperate, and in part to subtropical waters of the Southern Hemisphere. The most primitive of these three families is the Pseudidotheidae with three genera distributed on the shores of New Zealand, Patagonia, South Africa, and Prince Edward,

Crozet, and Kerguelen Islands. Another family the Xenarcturidae with a single species, is found only along the coast of Patagonia. The most highly specialized family, the Arcturidae has a universal distribution, however, its roots are also to be looked for in the Southern Hemisphere. We count the genus Antarcturus the most primitive in this family (Kusakin, 1972), with its weakly modified anterior pereopods. Species of this genus are widely distributed in the shelf zones of Antarctica, Argentina, South Africa, New Zealand and the southern part of the Indian Ocean. Finally, a set of species in the depths reach into the northern part of the Pacific Ocean, where this genus is known to be typically deepwater and lives at depths of 243 to 7,280 meters. The greatest number of species lives in Antarctic where they are met first at a depth of three to five meters. Only the rather specialized genera Astacilla and Avcturus are endemic to cold and temperate waters of the Northern Hemisphere. The first of these is distributed only in the North Atlantic; most of the species of the second live in the northern part of the Pacific Ocean, but one single species reaches into the Arctic and north Atlantic.

Therefore, for the suborder Valvifera as well we can suppose an origin in tropical waters, probably Tethys. Here the most primitive Valvifera, the Idoteidae, arose and the Amesodidae, departed from them early. Further progressive evolution of the suborder occurred in temperate and cold waters of the Southern Hemisphere. Still younger centers, where the formation of certain phylogenetically younger genera took place, can be revealed in temperate waters of the Northern Hemisphere. Finally, an absolutely recent center, where only the few endemic species of the genus Mesidotea were enabled to form, followed up in the Arctic.

#### Asellota

This suborder in our opinion the most highly specialized existing, differs from the other suborders by a clear predominance in it of cold-water, and also deep-water species. Of altogether 840 species of marine Asellota only 138, i.e. a little more than 16%, live in the shelf zones of warm waters. The other species are almost equally divided between the shelf zones of cold and cold-temperate waters, and depths greater than 200 meters. This notwithstanding, the suborder Asellota also can be shown to have had its origin in the tropical waters of Tethys.

Of the four Asellota super families, the most primitive is the Aselloidea, which populates fresh waters of the Northern Hemisphere. As Birshtein (1951) showed, the most ancient and primitive complex among the Aselloidea is circum-Mediterranean. Of the 35 species of the superfamily Stenetrioidea 27 species live in shelf zones of warm waters, six species in cold-temperate and cold waters of the Southern Hemisphere as far as Antarctica, and two species at depths greater

than 2,000 meters, also in the Southern Hemisphere.

(got bored and stopped, approx. pg. 77).