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SOCIETAS PRO FAUNA ET FLORA FENNICA

THE ALIMENTARY CANAL OF BALANUS
IMPROVISUS DARWIN

BY
S. R. TÖRNÄVA

WITH 8 PLATES (72 FIGURES) AND 1 TEXTFIGURE

FROM THE ZOOLOGICAL STATION AT TVÄRMINNE

HELSINGFORSIAE 1948

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Introduction.

The only Cirriped of Finland, *Balanus improvisus* Darwin, has not yet been examined in detail anatomically and histologically. The results of researches upon the intestine tube of the species mentioned as well as of organs and tissues connected with it are presented in this paper.

Historical review.

Of older works treating Cirripeds of the sub-order *Thoracica*, in which the anatomy of the alimentary organs has been studied, those of HOME (1814), CUVIER (1815) and BURMEISTER (1834) may be mentioned, further the works

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of MARTIN-SAINT-ANGES (1835) on *Lepas anatifera* and of KARSTEN (1845) on the shepar of *Balanus tintinnabulum*. DARWIN (1851, 1854) in his great monography and GERSTAECKER (1866) give accounts of all the results attained until then. These studies were mostly morphological, but the later works treat more and more also the histology of the organs. Such are the works of HOEK (1883) (especially noteworthy are his studies on the pancreatic glands of *Scalpellum parallelogramma*, *S. nymphocola* and *Lepas anatifera*); NUSSBAUM (1890) on *Pollicipes polymerus*, *Lepas Hillii* and *Conchoderma aurita*; GRUVEL on *Pollicipes cornucopia* (1893, 1; salivary glands), on *Balanus tintinnabulum*, *Lepas anatifera*, *Pollicipes cornucopia* and *Conchoderma virgata* (1893, 2), on *Coronula diadema* (1904, 2), on the alimentary glands (1904, 1 and 1904, 3) and his monography (1905); HOFFENDAHL (1904) on *Poecilasma aurantium*. — More modern are the works of BROCH (1919) on *Anelasma squalicola* and *Scalpellum Stroemii*; SEWELL (1926) on *Lithotrya nicobarica*; JOHNSTONE & FROST (1927) on *Anelasma squalicola*; MONTEROSSO on *Balanus perforatus* (1923, 1926 and 1927) and on *Chthamalus stellatus* var. *depressa* (1933); PATANÉ (1927) on *Balanus porcatus*, *B. trigonus* and *B. eburneus*; OLGA VIVI (1938) on *Balanus perforatus* var. *fistulosa*. — Finally may be mentioned BROCH's treatise in KÜKENTHAL's handbook (1927), and PAUL KRÜGER's great work (1940, 2) in BRONN's series summing up everything known up to date about the order *Cirripedia* (the digestive organs treated on pp. 93—99).

In the sub-order *Acrothoracica* the alimentary canal has been studied by BERNDT on *Alcippe lampas* (1903, 2) and on *Cryptophilus minutus* subsp. *striatus* (1903, 1; 1907). A summary is given by KRÜGER (1940, 2, pp. 158—160).

Corresponding studies concerning *Ascothoracida* (by KRÜGER considered as a separate order) have been published by LACAZE-DUTHIERS (1880) on *Laura Gerardiae*; KNIPOWITSCH (1892) on *Dendrogaster astericola* and *Laura Gerardiae*; YOSII (1931) on *Baccalaureus japonicus*; PYEFINCH on *Baccalaureus maldivensis* (1934), *B. hexapus* (1936) and *B. torrensensis* (1937). A summary is given by KRÜGER (1940, 1, pp. 24—25).

Technique.

The material used had been collected from the coasts of Helsinki. It was prepared in two different ways, as follows:

A. Most of the investigations were made on serial microtome sections 5 or 10 μ thick. The animals were fixed either in CARNOY's or in GILSON's solution. The sections 10 μ thick were stained in DELAFIELD's haematoxyline and thiazine red, those 5 μ thick in HEIDENHAIN's haematoxyline and thiazine red. In the case of various specimens the sections were cut sagittally, trans-

versally and horizontally. Certain series were marked with lines of soot during the embedding in paraffine, in order to enable reconstructions. Sections parallel to the basis are called horizontal; sections perpendicular to it and to the sagittal direction transversal, in accordance with the natural position of the animal.

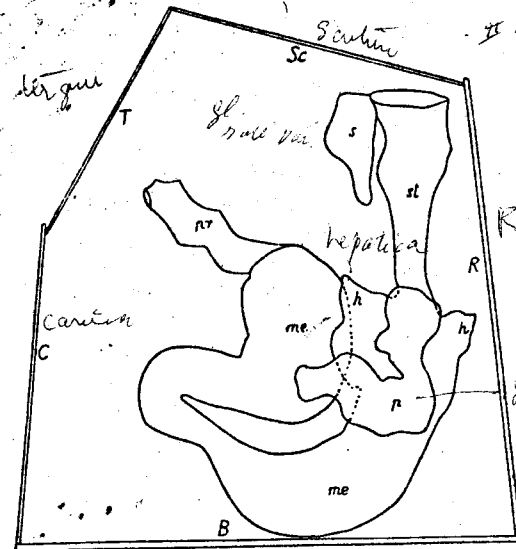
B. Certain investigations were made on total preparations of the intestine, taken out of the animal in physiological salt solution, stained alive in methylene blue, and fixed in a 5% solution of ammonium molybdate, whereupon the preparations were thoroughly washed in tap water, put directly into absolute alcohol, then in xylol, and lastly embedded in canada-balsam.

The structure of the alimentary canal.

The alimentary canal of *Balanus improvisus* consists of three essentially different main partitions (textfigure 1): 1) *Stomodaeum* (st) comprising the foremost, ectodermal

part of the intestine. 2) *Mesenteron* (me), the digestive intestine proper, the epithelium of which is of entodermal origin; the gastric glands are connected with it. 3) *Proctodaeum* (pr), the ectodermal hind part of the intestine.

The whole intestine tube is bent like an irregular U (figg. 1 and 2 and textfig. 1). In young specimens the two shanks of the tube are very near to one another, in older animals with more developed vasa deferentia they are rather widely separated. The mesenteron is much wider than the stomodaeum and the procto-



Textfig. 1. Diagram of the alimentary canal and the shells of *Balanus improvisus*. B = basis, C = carina, R = rostrum, Sc = scuta, T = terga, st = stomodaeum, me = mesenteron, pr = proctodaeum, s = glandulae salivales, h = coeca hepatica, p = glandula pancreatica sinistra.

daeum. The mesenteron is about 3 times as long as the stomodaeum and more than 4 times as long as the proctodaeum.

The following terminology will be used in the description (comp. fig. 1 and textfig. 1). The end of the animal corresponding to the carina shell is called *carinal* (C), the opposite end *rostral* (R) (corresponding to the rostrum shell). The convexity of the intestine sling is directed *basally* (B), its opening *apically* (A). The intestine wall, that forms the outer curve, is called *dorsal* (d), the opposite one *ventral* (v), independent of the direction of the intestine in its different parts. The mouth is situated in the *oral* (o) end, the anus in the *aboral* (a) end of the intestine, independent of their position with regard to the body.

I. Stomodaeum.

The stomodaeum can be divided into three parts: *pharynx*, *oesophagus* and *ventriculus* (fig. 2: a, b, c). Their respective lengths are approximately 3:4:1.

1. Pharynx.

The *mouth* of the Cirripeds opens, as known, at the end of a probosciform protuberance on the apical side of the prosoma. The part of the intestine tube lying inside this *proboscis* I call *pharynx* (fig. 2: a). Its direction is straight basal.

Fig. 3 shows a transverse section of the pharynx. Its walls are more complicatedly folded than those of the *oesophagus* and the *ventriculus* which depends upon its being surrounded by the bases of the mouth parts and the membranes connecting these with one another: dorsally the *labrum*, dorso-laterally the *palpi*, ventro-laterally the *mandibulas* and the *first maxillae*, ventrally the *second maxillae*, also called the *labium*. The aspect of the *lumen* depends also upon the state of contraction or relaxation of the constrictor and dilator muscles and the elasticity of the inner cuticle. As the constrictors of the pharynx are rather weakly developed and the cuticle in places is very thick, the elasticity factor must be considered more important than the muscular constriction, while the dilators are relaxed. In this state the membranes connecting the bases of the mouth parts form 4 longitudinal *furrows*, viz. a dorso-lateral and a ventro-lateral one on each side. — Between the ventro-lateral furrows a high ventral *ridge* rises. Between the dorso- and ventro-lateral furrows there is a pair of smaller lateral ridges. On the dorsal side of the dorso-lateral furrows there is a pair of small dorso-lateral ridges, directly attached to the median dorsal part.

Fig. 4 shows a section through a dilated pharynx from about the same parts as the section in fig. 3. It is seen that the *lumen centrale* (lc) can be widened very much, the four furrows becoming wide and shallow.

EPITHELIUM. The epithelium cells are cylindrical, high and narrow (fig. 5). There is no basal membrane, except in the oral part of the dorsal epithelium, otherwise the epithelium is directly surrounded by a loose irregular connective tissue with large nuclei, through which the muscles run which branch off through the epithelium. Outside the connective tissue there is dorsally a wide lacuna.

Dorsally the full grown *cuticle* is very thick (figg. 3: a, 4: a, b), it is identical with GROVEI's *paragnathes* (1893, 2, p. 434). It consists of two layers, which are differently stained by the dyes. A hook like appendix (fig. 6: h) is seen stretching a short distance into the oesophagus. The cuticle shows a striped structure (fig. 3: a). This may either be due to the cuticle being pierced by fine pores, or the chitin being secreted by the epithelium cells in the form of high and narrow columns; the latter alternative seems more probable (comp. K. C. SCHNEIDER 1902, p. 21).

Laterally and *ventrally* the cuticle is thin, of uniform thickness. It is covered with *bristles* (fig. 3: b); orally there are (fig. 9) longer ones than aborally (fig. 7). Further orally there are both long and straight, and short, forward-bent bristles (fig. 8). Some of the bristles have a basal knob in the cuticle (fig. 9). Regarded under powerful magnification the bristles indistinctly seem to be hollow. It is very probable, that these latter bristles at least are organs of a chemical sense (*tastes*), the basal knobs perhaps being a kind of a nerve-end instruments. This opinion is based on the researches of GROVEI. (1893, 2, pp. 578-579; 1904, 3, pp. 136, 176; 1905, pp. 365, 410).

MUSCLES AND CONNECTIVE TISSUES. Through the epithelium there run thin muscle fibres, which fork and adhere to the cuticle (fig. 10). The epithelium cells obviously have to a great extent changed into muscular substance.

The muscle fibres unite forming the muscles mentioned below (figg. 3 and 4). Since in the literature I have not found any names for these muscles I shall give them as well as those of the other parts of the intestine appropriate denominations.

1) Two strong dilatatory muscles, *one on each side*, originate from the dorsal outer cuticle of the *proboscis*, run, *converging*, to the pharynx and branch off forming some strong fibre-bundles, which insert at the dorso-lateral corners of the dorsal chitin plate (*paragnathe*): *dilatatores pharyngis dorsales* (u₁). Their function is obviously to draw the dorsal wall of the pharynx upwards. In the longitudinal direction of the pharynx they are divided into a number of more or less distinctly separated bundles, which can be grouped in two pairs of series, one median, almost straight dorsally and parallelly running pair, and one lateral more diverging pair. The former is most strongly developed orally, the latter aborally. They end before the transition into the oesophagus.

2) The antagonist of the muscles just mentioned is a very long and narrow muscle (m_2 ; only the right half of it is seen in the section of fig. 3), running from the lateral outer cuticle of the proboscis in a dorsal curve rounding the dorsal epithelium and crossing the dilatator muscles of the pharynx to the other side: *constrictor pharyngis dorsalis*.

3) A narrow paired dilatator muscle (m_3) originates from the lateral outer cuticle, somewhat orally from the origin of the dorsal constrictor, and, crossing the muscle just mentioned, runs, almost horizontally in a slightly ventral direction, and inserts at the dorso-lateral surface of the dorsal chitin-plate. This muscle sends branches into the dorso-lateral ridge and thus also flattens it: *dilatator pharyngis dorso-lateralis*.

4) Somewhat orally from the two last mentioned muscles a dilatator muscle (m_4 , visible in the left side of fig. 3) inserts at the crest of the lateral ridge. It originates from the lateral cuticle of the proboscis, at about the same transversal level as the muscle just described, and runs in a ventro-median direction to the pharynx, whereupon it tapers and runs as a narrow chord bounding the dorsal epithelium of the lateral ridge and finally penetrates in a few branches through the epithelium: *dilatator pharyngis lateralis*. Its function is to draw the lateral ridges sideways and to flatten them.

5) Two narrow dilatator muscles originate from the ventral surface of the proboscis, run in a straight dorso-median direction to the pharynx, and fork into a number of fibre bundles, that insert at the lateral cuticle of the bottom of the ventro-lateral furrows: *dilatatores pharyngis ventro-laterales* (m_5). To these there are attached fibres, which run along the adjoining epithelium dorsally and ventrally of the furrow and branch in through the same (this is seen orally from the section given in fig. 3). These muscles obviously contribute in drawing the lateral ridges outwards and the ventral one downwards.

6) A strong unpaired ventral muscle (m_6) runs transversely from the bottom of the one ventro-lateral furrow to the other; its end-bundles insert at the median cuticle of the furrows. Its function is obviously to bring the two halves of the labium nearer to one another, whereby the median ventral ridge is pushed upwards and the lumen constricted: *constrictor pharyngis ventralis*. This muscle changes aborally into the circular muscle of the oesophagus.

7) Two muscles (m_7) originate from the ventro-lateral surface of the body in the oral part of the thorax, run dorso-orally under the oesophagus and the pharynx converging in a very acute angle, cross through the ventral constrictor, and insert at the cuticle of the crest of the median ventral ridge. Partly they also cross through one another just under the epithelium. Their function is to draw down and flatten the ventral ridge: *dilatatores pharyngis ventrales*.

8) In addition to these larger individualized muscles, muscle-fibres are found, which pass through the epithelium of the lateral ridges and the dorso-lateral furrows and unite forming a number of latero-ventro-aborally running smaller bundles, which join the ring muscle of the oesophagus more aborally.

Longitudinal muscle-fibres are, besides, found outside the epithelium in rather thin bundles; outside them there are clusters of undifferentiated sarcoplasm. In longitudinal sections sarcoplasm is also seen next to the dilatator muscles.

All the muscles of the pharynx are more or less distinctly *transversally striped*.

Between the dorsal epithelium and the constrictor pharyngis dorsalis there is a very compact connective tissue of small cells. Also laterally and ventrally next to the epithelium, filling the space between the muscle-bundles, there are more or less flattened-polygonal cells of connective tissue, somewhat larger than the dorsal ones. I call this tissue and the corresponding tissues in other parts of the intestine the *inner connective tissue*. — The longitudinal muscle fibres run between the cells of this tissue.

On all sides outside the large muscles there is a tissue of large polygonal cells, the *outer connective tissue*. The round or oval nuclei are often close to the cell-boundaries. This connective tissue extends to the dorsal, dorso-lateral, ventro-lateral, and ventral *lacunae*, which surround the pharynx. In the ventral connective tissue the salivary glands (fig. 3:s) are embedded.

2. Oesophagus.

The oesophagus (fig. 2: b) constitutes about one half of the stomodaeum.

Fig. 11 shows a transverse section of the oesophagus with a rather constricted *lumen centrale* (lc). From the lateral sides of the lumen centrale four deep *primary furrows* stretch diagonally, two on each side. From the bottom of each of these, two smaller *secondary furrows* branch off, terminating in two more or less indistinct *tertiary furrows*. A dorsal, a ventral, and two lateral *primary ridges* rise between the primary furrows. Between the secondary furrows smaller *secondary ridges* are seen (figg. 11 and 12).

Fig. 14 shows a section of the oesophagus in a dilated state. Especially the central lumen is dilated, mostly at the expense of the primary furrows.

EPITHELIUM. The epithelium is everywhere covered by a homogeneous cuticle of even thickness, somewhat thinner than the ventral cuticle of the pharynx. In the depth of the furrows it is slightly thinner than elsewhere.

The epithelium cells are mostly high, narrow, cylindrical, with grainy cytoplasm. The cells around the bottom of the furrows are lower, cubical.

When the oesophagus is dilated, also the cells of the ridges become broader and flatter, cubical in form.

There is no basal membrane; the boundary between the epithelium and the inner connective tissue, as well as the boundaries between the epithelium cells, are often very indistinct.

Epithelium cells in different states and aspects are shown in figg. 15—19, 21, 22.

MUSCLES. (Figg. 11—14). 1) The oesophagus is to its whole extent surrounded by a strong circular muscle: *constrictor oesophagi* (mc). Its form in different parts and states of the oesophagus is seen in the figures 11—14. The muscle is more or less distinctly transversally striped. — In longitudinal sections (figg. 16 and 17) the circular muscle fibres are seen to be grouped in bundles, which are arranged in a row along the whole oesophagus at small distances from one another; these distances grow longer near the aboral and most oral parts of the oesophagus. Outside these muscle bundles there are large, polygonal pieces of sarcoplasm (figg. 11, 15—17 : sp) with very foamy and grainy cytoplasm and round nuclei, somewhat smaller than the nuclei of the epithelium cells. Fig. 23 shows a circular muscle in transverse section with its sarcoplasm.

2) *Longitudinal muscle-bundles* are found interspersed in the inner connective tissue inside the circular muscles. They are most abundantly amassed close to the constrictor in the lateral ridges and in two lateral groups in each of the median ridges (fig. 11: ml); further inside the ridges they are more sparse, in small bundles. — In longitudinal sections the longitudinal muscles close to the circular muscle seem to proceed from the latter and to tie its bundles together (figg. 15, 16, 17). Their united contraction would thus simultaneously shorten and constrict the oesophagus. Between the fibrils rather long and flat nuclei are seen (fig. 20: k); these muscle-nuclei prove that the longitudinal muscles are individual and not parts of the constrictor.

3) *Dilatator muscles*. A number of transversally striped dilatator muscles originate from the outer cuticle of the body and stretch to the oesophagus. Near its circular muscle they branch forming fine dilatatory bundles, that run through the circular and longitudinal muscle layers in the spaces between the circular bundles. Inside the inner connective tissue they branch again, forming fine fibres, which run through the epithelium branching dichotomically, and insert at the cuticle of the oesophagus (figg. 15—19 and 21: md). This branching increases the points of insertion and disperses them over a larger surface. — Sections traversing the epithelium cells and the muscle fibrils disclose a very remarkable fact (fig. 24). It is clearly seen, that the *muscle fibrils run inside the epithelium cells* and not between them. This fact has been established with

dorsal and lateral as well as ventral dilatators. The muscle fibrils (m) are in section polygonal, and much thinner in the oesophagus (fig. 24 B) than in the pharynx (fig. 24 A). In some cells the nucleus (k) is seen beside the muscle fibre. In other cells the muscle fibres are missing.

The topography of the dilatators is rather complicated. They are all paired. In fig. 12 the dilatators of the one side are diagrammatically represented, projected on the same level. In reality they are, of course, on different levels all along the oesophagus. Each muscle in the figure thus represents several muscles, situated behind one another along the oesophagus.

The muscles can be grouped in the following complexes, the components of which are marked in the figure with the same letters but with different numbers: *dilatatores oesophagi dorsales* (dd₁, dd₂, dd₃), *dilatatores oesophagi latero-dorsales* (dld₁, dld₂), *dilatatores oesophagi dorso-laterales* (ddl₁, ddl₂), *dilatatores oesophagi laterales* (dl), *dilatatores oesophagi ventro-laterales* (dvl₁, dvl₂), *dilatatores oesophagi latero-ventrales* (dlv₁, dlv₂), *dilatatores oesophagi ventrales* (dv₁, dv₂). — The different complexes are found along the oesophagus in different numbers, varying somewhat in different specimens; here are given the numbers of the specimen, according to which fig. 12 is drawn (in parentheses are given the corresponding numbers for two other specimens): dorsal 6 (4,6), latero-dorsal 1 (1,1), dorso-lateral 4 (3,4), lateral 2 (2,1), ventro-lateral 3 (3,6), latero-ventral 1 (2,3), ventral 7 (5,8). The complexes marked with the same letters are not quite congruent, either as to their number or as to their course, but they correspond, nevertheless, essentially to each other.

Beginning from the oral end of the oesophagus the complexes and the particular muscles were found in the following order in the specimen first mentioned above: dv (one muscle, dv in fig. 11) and ddl₂; dld₂ (visible in fig. 11), dd-complex (dd₃ visible in fig. 11) and dld₁; dv (one muscle); dvl-complex and dlv₁; dv-complex, ddl-complex and dlv₂; dd-complex; ddl-complex, dvl-complex and dv-complex; dvl-complex, dd-complex and dl; ddl-complex; dv-complex and dd-complex; dd and dv; dl (very strong, divided into a dorsal and a ventral half, dl in fig. 13), dd and dv. (For the sake of comparison the succession of dilatators in the two specimens treated within parentheses above may be mentioned. First specimen: dv, dld₂, dld₁, dd-complex, dvl₂, dv, ddl₁, dvl₁, dd, dvl, dv, ddl₁, dl, dlv₂, dd, dld₁; dv, dvl, dd, dl, dv; second specimen: dv, ddl₂, dd, dld₁, dv, ddl₂, dvl, dv, dlv₂, dvl, dv, dd, dv, dlv₂, ddl₂, dvl, dv, dd, dvl, dlv₂, dvl, dv, dd, ddl, dd, dl, dv, dvl). — All the muscles do by no means originate and insert at the same horizontal level; part of them run obliquely orally, others obliquely aborally. The muscles of the ventral complex and dlv₂ originate from a paired ventral pocket at the boundary between the prosoma and the thorax, the ventro-lateral ones and dlv₁ from a lateral pocket of the surface of the body.

CONNECTIVE TISSUES. All the spaces between the epithelium of the primary ridges and the circular muscle not occupied by radial or longitudinal muscles are filled with an *inner connective tissue* (fig. 15: bvi), which, nevertheless, is almost totally lacking in the secondary ridges and around the secondary furrows, where the epithelium directly touches the circular muscle.

The inner connective tissue consists of small, tightly packed cells. In the longitudinal sections one can see, that they have the form of flattened, longitudinally directed spindles. Here and there fine threads penetrate through the tissue in different directions. It is thus an intermediate form between a cellular and a fibrillary connective tissue (figg. 16 and 17).

Outside the circular muscle and its sarcoplasm there is a cellular *outer connective tissue* (fig. 15: bvy). Its cells are larger than those of the inner connective tissue, but smaller than the sarcoplasm-cells. Their cytoplasm is much more homogeneous than the sarcoplasm. The nuclei are round, flat, or irregular in form, seated near the cell-boundaries, somewhat larger than those of the myoblasts and only slightly larger than those of the inner connective tissue. The contours of the cells are wavy. — The outer connective tissue passes gradually outwards into the common interstitial connective tissue of the body, which tissue consists of larger polygonal cells and is very loose and lacunous.

3. Ventriculus.

The last part of the stomodaeum must for theoretical reasons be called *ventriculus* (fig. 2: c). In its dilated state it is difficult to determine its boundary towards the oesophagus. It has then the form of a funnel (fig. 25), open towards the mesenteron. In the wall of the ventriculus two dorsal transversal furrows (f_1 and f_2) are seen; by the former the stomodaeum bends in an angle carinally; in *Balanus improvisus* this angle is very obtuse and little conspicuous (comp. BROCH 1919, pp. 16—17). A third circular furrow (f_3) forms the boundary between the ventriculus and the mesenteron; here the epithelium rolls itself somewhat backward, orally.

In its constricted state the ventriculus is, on the other hand, a distinctly limited part of the intestinal canal (fig. 26). The boundary between the oesophagus and the ventriculus may be called *cardia*, the boundary between the ventriculus and the mesenteron *pylorus*. Both at the oral and at the aboral end of the ventriculus the intestine is constricted by a strong muscle, orally by the *sphincter cardiacus*, (ms_1 , comp. fig. 13), aborally by the *sphincter pyloricus* (ms_2) (both seen also in fig. 25). Between these muscles the stomach has a fairly round outline; the ventral curvature is somewhat stronger than the dorsal. Behind the sphincter pyloricus the aboral end of the ventriculus protrudes into the wide oral end of the mesenteron in the manner described by GRUVIL (1905, p. 385).

In transversal sections the same ridges and furrows are found as in the oesophagus; with the exception of the tertiary furrows, which are entirely missing in the ventriculus (fig. 27). The lumen in the middle part of the ventriculus does not change; the stomach may be open or closed. — In fig. 28 the end protrusion of the ventriculus (v) is seen. The cuts connecting the lumen centrale with the lumen of the mesenteron are continuations of the primary and secondary furrows; in the pictured section only the primary furrows are seen dorsally; ventrally the secondary furrows disappear more aborally.

EPITHELIUM. The epithelium is essentially of the same type as in the oesophagus (fig. 29). The cells are mostly lower than there, more or less cubical. In the secondary ridges and around the secondary furrows they are, however, high, cylindrical cells; the furrows being here much shallower than in the oesophagus. The cytoplasm is foamy, with some threads or rows of granules running zigzag or spirally. The cuticle is of uniform thickness, its thickness depending upon its age. The epithelium is pierced by sparse radial muscle fibres.

INNER CONNECTIVE TISSUE. The inner connective tissue (fig. 29 A: bvi) is rather weakly developed; especially in the vicinity of the sphincter muscles, but not around them. It penetrates into the primary ridges as a narrow wedge and extends at their base. In places it is separated from the epithelium of the ridges by the radial muscle fibres, which run along the base of the epithelium (fig. 27: md). Nearer to the sphincter muscles and in the secondary ridges the inner connective tissue is pressed between the epithelium and the muscle-layer and resembles a basal membrane; a real basal membrane is, however, lacking, as elsewhere in the ectodermal parts of the intestine. The sphincter muscles are surrounded by a thick layer of inner connective tissue.

MUSCLES. Besides the two sphincters already mentioned, the musculature contains the same components as in the oesophagus, but is much weaker. The circular and the longitudinal muscles together form a very thin layer (fig. 29: mc-1). The circular bundles are prolonged in the longitudinal direction of the stomach and are rather sparsely seated (fig. 25: mc). Flattened and lengthened sarcoplasm-cells (fig. 29 A: sp) are seen outside the muscle bundles. The circular muscles together compose the *constrictor ventriculi* (fig. 27: mc). The *sphincters* are seated in the inner connective tissue inside the constrictor proper and the longitudinal fibres. In fig. 13 the constrictor ventriculi is seen contracted together with the sphincter cardiacus ($ms_1 + mc$), forming a thick homogeneous layer. Also around the pylorus the whole muscle layer is thick; elsewhere it is thin. In the aboral protrusion of the ventriculus the circular muscles are lacking.

The *longitudinal muscles* form weak bundles partly in the inner connective tissue of the primary ridges, partly alongside the circular muscle in its whole length between it and the epithelium (fig. 27: ml).

Dilatators. The most aboral of the previously mentioned *dilatatores oesophagi* (fig. 13:dl) function as antagonists of the sphincter cardiacus; some dilatatory bundles are, besides, seen radiating in different directions from the oral end of the ventriculus. Further aborally the dilatators at first become very sparse, but increase again still further aborally. They run from the cuticle through the epithelium cells, gather in bundles, which in the primary ridges run alongside the base of the epithelium cells (fig. 27: md), and break then through the circular muscle, radiate in numerous small bundles in every direction and are lost in the surrounding outer connective tissue. The number and thickness of these bundles in the different directions varies somewhat in different specimens.

Outside the circular muscle and its sarcoplasm there is a typical, very lacunous *outer connective tissue*, which nearest to the ventriculus is composed of flat cells.

4. *Glandulae salivales.*

In connection with the stomodaeum a group of glands seated on the ventral side of the *pharynx* may be treated: the *glandulae salivales* (figg. 1 and 2:s). They consist of a conglomeration of monocellular glands, that open laterally on the inner (dorsal) surface of the palpi labiales and extend in a curve under the pharynx, near the median level also somewhat under the oesophagus (fig. 31, fig. 3:s). They fill the labium wholly (fig. 32:s, salivary glands dotted). They lie in the connective tissue under the ventral epithelium of the pharynx and ventrally in regard to the musculus constrictor pharyngis ventralis (m, in figg. 31 and 3). The cells are not tightly packed together, but arranged in groups, which are somewhat apart from one another. Nearer the orifices they are more tightly packed.

In the section pictured in fig. 3 (the level of the aboral part of the constrictor pharyngis ventralis) the salivary glands (s) are most densely grouped laterally. Further orally they touch each other also medially, and where the mouth parts begin to part they form a compact mass, that almost wholly fills the space between the oral part of the ventral constrictor and the ventral lacuna. Further orally they part again from the median level and open laterally (fig. 32: m).

The gland cells are large, bottle-like in form. Their inner part is very wide; toward the orifices they gradually become narrower and open through ex-

ceedingly narrow canals in the cuticle of the labium (fig. 31 A). Two or more cells appear at least in places to have a common outer orifice. — Their cytoplasm contains numerous fine grains or drops, most numerous in the bottom part of the cells. Besides, the cells are pierced by sparse threads in different directions.

The nuclei display in different specimens different aspects. In the two specimens, pictured in figg. 31 and 32, the nuclei are rather small, irregular in form with a strongly stained chromatic content and an indistinct membrane; sometimes they contain a clearer rounded body. They are mostly seated by the cell-boundaries in the pouch-part of the cells. — But in the specimen pictured in fig. 3 the nuclei (ks, more powerfully magnified in fig. 30) are quite different. They are here large, rich in achromatic nucleoplasm, have a thick membrane, 1 or 2 roundish nucleoli, and a great number of chromatic grains most densely situated around the nucleoli and alongside the nucleomembrane. In some cells the nucleus is distinctly round, in others it has a more irregular form (comp. also fig. 33). Some nuclei are almost wholly filled with chromatic grains and several larger chromatic bodies. The nuclei are in this specimen situated more or less far from the cell-boundaries.

How is this difference in the aspect of the nuclei to be explained? It cannot depend on the fixation technique, since the two first mentioned specimens were fixed in different solutions (CARNÓV and GILSON), the last mentioned specimen in the same solution as the second one (GILSON). All these specimens were stained in DELAFIELD's haematoxyline. It must be supposed, that the nuclei, which, as known, are of great importance for the secretion in gland cells, are in different physiological phases. This is also supported by the fact, that, when small, compact, and consisting of almost only chromatic, they are situated by the boundaries of the cells, obviously at rest, and when swollen and showing a distinct structure, they are seated in the interior of the cells, where they appear to be very active.

Fig. 33 shows a part of a gland cell, powerfully magnified, of another specimen with obviously active nuclei (fixed in GILSON, stained in HEIDENHAIN's haematoxyline). The cytoplasm is filled with rather large secretion grains, of which those near the throat of the cell unite forming large drops (sd). Nearer the bottom of the cells the secretion grains are much more sparse.

II. *Intestinum entodermale.*

The entodermal part of the intestine consists of 1) the mid-gut proper, *mesenteron*, and 2) the glands attached to it, the *glandulae gastricae*. The mesenteron can be divided into two portions, between which, however, no real boundary can be ascertained in *Balanus improvisus*, viz.: 1) *pars anterior* s.

glandularis, into which the gastric glands open, and 2) *pars posterior s. nutritoria*. The latter is about five times as long as the former. The gastric glands are of two kinds: 1) *coeca hepatica* (textfig. 1: h) and 2) *glandulae pancreaticae* (p). Since the former glands have essentially the same histological structure as the mesenteron and in the species in question neither morphologically nor physiologically can be distinctly bounded from the *pars anterior mesenterii*¹, I shall treat them in connection with it. The strongly differing pancreatic glands shall be treated separately.

1. Mesenteron.

PARS ANTERIOR S. GLANDULARIS. The lumen of this foremost sixth part of the mid-gut is always very capacious and has, if one disregards the hepatic coeca, roughly the form of a pear or a hen's egg with the broader end turned orally (fig. 2: d). It lies in the same direction as the aboral end of the ventriculus or bends somewhat rostrally. It differs morphologically from the *pars posterior* by the gastric glands opening into it, and physiologically by its strong secretion. In other respects it is essentially similarly built as the latter portion.

COECA HEPATICA. The hepatic coeca (seen in the plastic reproduction fig. 1 but mostly invisible in the median section fig. 2) are wide appendices, opening into the *pars anterior* without any marked boundary. As their orifices are very wide, they do not prevent the food from entering the coeca, which probably serve the purpose of secretion as well as of resorption. The coeca have numerous more or less shallow side-pockets and protuberances.

There are altogether 7 coeca, which I have named as follows (figg. 28, 34 and 35). The unpaired *coecum ventrale* (cv) stretches from the middle of *pars anterior* in an oral direction a long way under the ventriculus (in the aboral section in fig. 35 it is seen only as a narrow furrow, fv). — Almost as far orally the paired *coeca latero-dorsalia* (cld) stretch in a dorso-latero-oral direction, to the dorso-lateral sides of the ventriculus; their wide orifices extend somewhat further aborally than the wide proximal part of the ventral coecum (the aboral furrow disregarded). — The paired *coeca ventro-lateralia* stretch somewhat less orally and open into the oral end of the *pars anterior* (cvl, seen only at the one side in fig. 28); they stretch in a more markedly oral and only slightly ventro-lateral direction to the ventro-lateral sides of the ventriculus. — The paired *coeca latero-ventralia* (clv) start from the same parts but more ventrally, and more orally seem to proceed from the ventral wall of the ventro-lateral coeca (fig. 28, right side); their wide orifices extend along almost the whole

¹ Genitive of the latin form *mesenterium*.

of the *pars anterior*. These coeca stretch from the ventro-aboral corner of the *pars anterior* quite a distance in the latero-ventro-aboral direction (fig. 36).

PARS POSTERIOR S. NUTRITORIA. This long portion of the mesenteron differs from the *pars anterior* partly by the lack of separate glands, partly by its weaker secretion. It follows the dorsal curve of the body and has thus a nearly U-formed course with the convexity dorsally, in this species, nevertheless, with the exception mentioned below. The *pars posterior* can be divided into four parts, which, however, are not distinctly bounded from each other and do not really differ from one another (see figg. 1 and 2). 1) The first part runs at first in the same direction as the *pars anterior*, but is narrower. Having run almost basally, it bends gradually and passes at last almost directly carinally. 2) The second part runs straight in an almost carinal direction, but slightly apically. 3) The third part begins in the carinal end of the prosoma, at the point where the intestine bends in a sharp curve rostrally, and runs almost parallel with part 2, diverging from the dorsal wall of the body. 4) The intestine bends in a right angle apically and passes into the thorax. In the specimen given in figg. 1 and 2 this part is exceedingly dilated, its ventral wall approaches part 1 and the *pars anterior*, while the latero-ventral hepatic coeca even embrace it laterally. In other specimens part 4 is much narrower (fig. 40). — The parts 3 and 4 form together a curve with the convexity ventrally; this is the exception, in which the course of the intestine of *Balanus improvisus* differs from the typical one of the *Cirripedia*, where the mesenteron forms an only dorsally convex curve. In older specimens with developed vasa deferentia part 4 is pushed more carinally, whereby the last mentioned curve as well as the sharp curve between the parts 2 and 3 become less marked and the course of the intestine approaches the typical form. — The three aboral parts are almost equal in length, part 1 about one and a half time longer than the others. — The rectum starts from the carino-apical end of part 4.

Transverse sections of the *pars posterior mesenterii* are shown in figg. 36—40 (figg. 36, 37, 39 and 40 from the same specimen in equal magnification; figg. 36 and 37 with the dorsal side, figg. 38—40 with the ventral side upwards). It is seen, how the outline of the section differs in different parts of the intestine, being oval in some places with the long axis in different directions, more or less circular in others, and more or less triangular in others with the apex turned either dorsally or ventrally. Following the intestine section by section one can see how the different forms gradually pass over into each other, how for instance the intestine seems to exhibit a torsion, the long axis of the oval figure gradually changing from horizontal into perpendicular. All these forms, as well as the differences in width, are probably dependent on the peristaltic movement of the intestine. — From the sections one also sees,

that the epithelium presents numerous small, longitudinal furrows along the entire mesenteron, which in some sections, however, are less distinct and sparser. Also numerous small, more or less marked transversal furrows (fig. 46: f) are discernable in several parts of the epithelium of the mesenteron. All these furrows are probably due to muscular contraction (comp. NUSSBAUM, pp. 52—53).

EPITHELIUM. In every part of the mesenteron there are two kinds of epithelium cells, viz. cells showing *balloon secretion* and cells without it. The former are dominating in the pars anterior and in the coeca hepatica, the latter in the pars posterior. The other kind of cells, none-the-less, are not lacking anywhere, so that the names *pars glandularis* and *pars nutritoria* only designate a relative difference. It is, besides, certain, that the same cells at times have balloon secretion and at other times are without it. This is proved partly by the fact, that the corresponding cells in different specimens show the one or the other aspect, and partly by the existence of intermediate forms, in which the cells show a weak balloon secretion but otherwise are more like the cells without it. All the epithelium cells of the mesenteron and the coeca are thus really of the same kind. — The resorption of nourishment thus takes place through the same cells as secrete digestive secretions, a common feature with the evertbrates; the cells resorb the nourishment, while at rest in regard to the secretion.

Samples of epithelium from different parts of the mesenteron and in different states are shown in figg. 41—53 (the figures are from 5 different specimens). Cells with balloon secretion (bs) are seen in figg. 41 and 42. The «balloons» have mostly the form of a pear (fig. 41) or smaller drops (fig. 42) with a basal, narrow «stem», that breaks off, when the secretion falls into the lumen. — The cells are generally high, cylindrical cells, in places with a convex apex (figg. 43 and 47). Under the furrows (fig. 46: f) and in places, where the intestine is widely dilated (fig. 45), they are flattened and more or less cubical. Thus, the different height of the epithelium of part 4 of the pars posterior ventrally (g) and dorsally (h) in fig. 2 proves, that the intestine in this case is dilated only on the ventral side. Here the cells are arranged in groups of a few cells, so that groups with broader apices and cell boundaries diverging toward the lumen (fig. 45) and groups with narrower apices and converging cell-boundaries lie beside one another by turns.

The distal end of the epithelium cells is covered by a typical *brush-border* (sb) (Stäbchensaum, «striped cuticle»); in fig. 41 it is invisible on account of the secretion.

The cytoplasm is foamy and presents zones of different affinity to the staining dyes (comp. fig. 47). The zone containing the nucleus is characterized by granules showing strong affinity to haematoxyline. The nuclei are seated

in the central zone, sometimes somewhat nearer the apex, in other cases nearer the base of the cells. — In some cases the cells seem to contain vacuoles (fig. 52: v). The cytoplasm is also pierced by a network of threads with a stronger affinity to the staining.

The epithelium of the hepatic coeca (fig. 52) has the same structure as in the mesenteron proper; its balloon secretion is more plentiful.

Fig. 49 shows a piece of epithelium of somewhat differing appearance from the bottom of a longitudinal furrow (beside the ridge shown in fig. 48). Here the epithelium cells are small and lie in several layers. They are obviously young cells, originating from a mother cell, that has divided both radially and tangentially (comp. MONTEROSSO 1923 and 1926).

The epithelium cells of the mesenteron stand on a thin, compact *basal membrane* or *membrana propria* (figg. 48, 52, 53: mp).

MUSCLES. Outside the *membrana propria* the mesenteron is surrounded by a rather thin *tunica muscularis*, consisting of *plain* (unstriated) muscles. It is divided into two layers (figg. 42 and 48). The inner layer consists of longitudinal muscle bundles, *musculi longitudinales mesenteri interni* (ml), the outer one of circular ones, *musculi circulares mesenteri* (mc). The circular bundles are small and arrayed along the intestine at short distances from one another (fig. 42). Also the longitudinal bundles are small and arrayed around the intestine at certain distances from one another (fig. 48). In fig. 51 the contraction of the longitudinal muscles obviously gives the basal membrane its wavy form.

Along the aboral part of the pars posterior, embracing part 4 and the aboral half of part 3, a ring of stronger outer longitudinal muscle bundles, *musculi longitudinales mesenteri externi* (fig. 40: me), is found at a small distance outside the circular muscle layer, running in the innermost layer of the common connective tissue of the body. These muscles are arrayed around the intestine rather far apart from one another. They do not all begin at the same transverse level, but some of them start more orally, others more aborally. All of them extend to the end of the mesenteron and are obviously differentiated by the cells of the connective tissue, in which they lie. They start from the *membrana propria* of the mesenteron and insert at the oral end of the rectum, where they penetrate through the epithelium.

Regarding the intestine on a total preparation, the *tunica muscularis* looks like a network with rectangular meshes (fig. 54); in which the more outstanding, superficial circular muscles (mc) cross the less prominent, deeper lying inner longitudinal ones (ml). The muscle bundles have a slightly wavy course. Aborally the external longitudinal muscles are also seen as thicker longitudinal stripes.

STRATUM PERINTESTINALE. Around the entire mesenteron and the coeca hepatica, but not around the pancreatic glands, there is a particular layer, *stratum perintestinale*, which according to MONTEROSSO (1927) serves to prepare the resorbed nourishment. It is shown in figg. 36—39 and 48 (spi). It consists of one layer of cells, which rest directly on the outer surface of the basal membrane of the epithelium projecting between the muscle bundles of the tunica muscularis. The cells project in all directions and in transverse sections form a regular wreath around the intestine. They have generally the form of a high and narrow club; their basal part is narrow and the distal part thick. — In some cases (fig. 55) the form differs from the one just described. The cells are then relatively low and broad, almost cylindrical in form; the proximal part is, however, always narrower. — The cell boundaries are somewhat wavy. In the basal part of the cell the cytoplasm contains very fine threads (*proximal filaments*). The nucleus, mostly seated in the distal half of the cell, is irregularly oval with the long axis in the longitudinal direction of the cell. A roundish body, *parasoma* (fig. 55: p), is sometimes found on the distal side of the nucleus. The cytoplasm contains, besides, round or irregular bodies or drops (*granula, corpuscula, vacuoles*). (Comp. MONTEROSSO 1927, pp. 407—413).

In certain specimens the cells of the stratum perintestinale contain a number of round, yellow, strongly refractive drops (fig. 55: d). These are most numerous around the oral parts of the mesenteron (pars anterior, coeca hepatica, and part 1 of pars posterior), and decrease gradually toward its aboral parts. Where they are most abundant, the cells are almost crammed with them. These drops are evidently resorbed nourishment, and their occurrence shows, that the resorption is strongest in the oral parts of the mesenteron, taking place also in the hepatic coeca.

2. *Glandulae pancreaticae.*

A pair of large glands, *glandulae pancreaticae* (fig. 1: p), open into the pars anterior mesenteri. They vary in form in different specimens and are not strictly symmetrical. Each gland can, however, be divided into two lobes, a medio-oral and a latero-aboral one. Each gland evacuates its secretion through a duct of its own, *ductus pancreaticus* (fig. 57: dp), the orifice of which opens into the mesenteron in its latero-oral wall, ventrally from and close to the orifices of the latero-dorsal coeca hepatica, at the level of the orifice of the ventriculus.

The lobes have numerous protuberances and branches, their form being thus rather complicated. In most cases the medio-oral lobes have 3 and the latero-aboral lobes 2 branches, besides a varying number of minor protuberances. The latero-aboral lobes are generally larger than the medio-oral ones

(fig. 1), but, for instance in the specimen shown in fig. 57, the former were much less developed. — The lumen is very irregular on account of folds projecting from the walls of the glands; generally it is narrow at the end of the branches, which here have the form of round tubes, and wider in the central parts of the glands, which parts have the form of bags.

In fig. 1 the pancreas (p) of the left side is represented plastically. Sections through different parts of the pancreatic glands (p) are shown in figg. 56, 57, and 28 (medio-oral lobes) and in fig. 35 (latero-aboral lobes, just dividing into two branches each). The different parts of the glands embrace the pars anterior mesenteri laterally, dorsally and orally; their most oral branches stretch somewhat more orally than the ventriculus on the dorso-lateral side of the stomodaenum.

EPITHELIUM. The epithelium cells of the pancreatic glands are exceedingly large. Their form is irregular; in the end tubes (fig. 58) they are cubical or conical with the apex toward the lumen, in the wider parts they are often flatter, rectangular in section. No brush-border can be discerned. Between the cells there are often more or less deep intercellular secretion capillaries (is), which enlarge the secreting surface. The cytoplasm shows a structure of very densely arrayed fine basophile grains, stained strongly violet by the haematoxyline. These are obviously secretion grains. Some times a vacuole (v) is seen. The boundary of the cells toward the lumen often looks very ripped; the fringes evidently consist of secretion leaving the cells.

The nuclei are exceedingly large, irregularly oval, seated near the base of the cells; their long axis is often parallel to the cell basis. They mostly contain several chromatine bodies irregularly polygonal in form; some times there is only one large oval nucleolus.

What is the strong basophilia of the pancreas-cells due to? It is easy to suppose, that the reaction of the secretion grains is acid. After having fed living specimens with litmus-powder I found that the colour of the mesenteron changed into red, which proves that the contents of the intestine are acid (comp. GRUVEL 1893, 2, pp. 553—554).

The epithelium cells of the pancreas stand on a rather thin *membrana propria*. Close to it there is a weak *circular muscle* (fig. 58: mc). Weak *dilatatory muscle bundles* (md) are also found here and there, which branch just outside the circular muscle and insert at the basal membrane. The glands are wholly surrounded by the common connective tissue of the body; the cells of this tissue are much smaller than the pancreas-cells.

DUCTI PANCREATICI. From the central part of the medio-oral lobe of each pancreatic gland an evacuation duct, *ductus pancreaticus*, sets out, opening

into the pars anterior mesenteri, very close to the fold formed in its latero-oral wall by the ventriculus protruding into the mesenteron (fig. 57: dp). A highly magnified drawing of the right pancreatic duct is given in fig. 59. The duct runs in a medio-aboral direction and is bent like an S with the first (distal) convexity turned aboro-laterally and the second (proximal) one oro-medially. It is very narrow (in the specimen pictured, about 20μ thick).

As no section has gone through the middle of the lumen of the duct, it is difficult to get an exact picture of its *epithelium*. One sees only very densely seated nuclei, which proves, that the cells are small and low. The nuclei are irregularly oval with the long axis generally in the longitudinal direction of the duct. They are smaller than the nuclei of the gland epithelium.

Muscles. The ducti pancreatici are richly provided with muscles. Outside the epithelium there are rather strong *longitudinal muscles* (fig. 59: ml) along the whole length of the duct; they continue in the circular muscle layer surrounding the pancreas and in the muscles of the mesenteron. — From the median side of the distal end of the duct some *oblique muscle-bundles* (mø) stretch latero-aborally and partly disappear into the outer connective tissue, partly join the intestine muscles further aborally. They evidently function as constrictors. Their antagonists are *dilatatory muscle-bundles* (fig. 57: md₁), which run from the latero-oral wall of the duct in a latero-aboral direction. — A number of *constrictors* (mc) traverse the aboral and middle parts of the duct. Also these have *dilatatory* antagonists, which partly run laterally, slightly orally from the latero-aboral wall of the duct (fig. 59: md₃), and partly medially, from the median wall, inserting in the middle of the convexity of the proximal curve (md₂). — Also on the dorsal and ventral sides of the duct more or less *oblique constrictors* cross the duct obliquely, and *dilatators* radiate from it.

Laterally and medio-aborally the ductus pancreaticus is surrounded by the common connective tissue of the body, medio-orally only by one layer of cells of connective tissue, outside which there is a large *lacuna* (fig. 59: l) situated in the angle between the pancreas and the median convexity of the ductus pancreaticus. On the median side of the lacuna there is again connective tissue.

III. Proctodaeum (Intestinum rectum).

The proctodaeum, which is much narrower than the mesenteron, consists entirely of the *intestinum rectum* (fig. 2: i), which runs through the 4 aboral segments of the thorax. It can be divided into 4 parts, which more or less correspond to the segments (fig. 60: I—IV). Their position is, of course, dependent on the actual position of the thorax. At the transition from part III to part IV there is a pair of deep *ventral diverticles* (fig. 64: r₂, laterally), the

distal ends of which bend orally. At this point the rectum forms an angle with the apex ventrally and passes to the *anus* (figg. 60, 64 and 65: a), which is dorsally situated at the base of the penis.

The *lumen* of the rectum, which is much narrower than the lumen mesenteri, resembles orally on the whole that of the stomodaeum. In the transverse sections (fig. 61) one sees the *lumen centrale* (lc), the primary (1) secondary (2) and tertiary (3) *furrows*, and also small *quarternary furrows* (4, not everywhere visible), and between these primary, secondary, tertiary and low quarternary *ridges*. The lumen is not strictly symmetrical and varies somewhat in different parts of the rectum (figg. 61—63) and in different specimens, depending upon the physiological states of the rectum.

When the rectum is closed, only parts I—III are constricted, while part IV is strongly contracted lengthwise and the anus kept wide open (fig. 64). When the rectum is open, part IV is much longer, while the anus and the most aboral part are narrower than the oral main part of part IV (fig. 65). — Part IV has two lateral pockets, *coeca analia* (figg. 64 and 65: ca) close to the anus.

EPITHELIUM AND INNER CONNECTIVE TISSUE. The epithelium and the inner connective tissue (figg. 66 and 67) of the proctodaeum are of the same type as in the stomodaeum.

The *epithelium* is covered by a homogeneous *cuticle* (fig. 66: cut), the thickness of which depends on its age. The cells are relatively small, cylindrical. The basal membrane is lacking, the boundary between the epithelium and the connective tissue being difficult to discern. — The cytoplasm contains numerous grains, which give it a foamy appearance; they are most abundant in the apical half of the cells. Here and there vacuoles (fig. 67: v) are seen. Thin fibrils or rows of granules run through the cells in different directions, often zigzag or in spirals. — The nuclei often (but not always) appear to be seated nearer the apical end of the cell (fig. 67), but as the base of the epithelium cells is difficult to detect, it is possible, that the cells are in reality lower than they seem and that the nuclei are seated basally as in epithelium cells of the same type in the stomodaeum. — Muscle fibres (fig. 67: md) run through the epithelium to the cuticle; they are weaker than in the stomodaeum.

Fig. 68 shows the place, where the rectum starts from the mesenteron. The rectal epithelium (er) is easily distinguished from the more deeply stained mesenterial epithelium (emi). Also the difference between the cuticle of the rectum and the brush-border of the mesenteron is distinct. — At the boundary there is a deep furrow (f), which does not seem to have any epithelium or only a very low one. — Besides the dilatatory muscle fibres (md), also *longitudinal epithelium-muscle fibrils* (me) are found inside the epithelium cells near the cuticle, a feature lacking in the stomodaeum.

The inner connective tissue consists of small, irregular cells; their cytoplasm has almost the same structure as the plasma of the epithelium cells, but is somewhat more homogeneous. The nuclei (fig. 66: kh) are rather large, irregularly spindle-like in form.

MUSCLES. A diagrammatic sketch of the rectal muscles discernible in sagittal sections is given in fig. 60.

Longitudinal muscles. 1) Alongside part I of the rectum one dorsal, one ventral, and, on each side, 3 lateral longitudinal muscles stretch, forking at the oral end of part II, running through the inner connective tissue and the epithelium, and inserting at the cuticle; orally they continue directly as muscles of the mesenteron: *musculi mesenterio-rectales* (fig. 60: ml₁). Their function is obviously to shorten part I and simultaneously dilate the oral end of part II, which is adapted to forward the contents of the intestine. The ventral muscle also sends a branch somewhat further than the middle of part II. — 2) In parts II, III, and IV of the rectum small, sparse, short inner longitudinal muscle-bundles run close under the epithelium and through it to the cuticle: *musculi longitudinales recti interni* (fig. 66: mi). Such muscles are found dorsally and ventrally as well as laterally. — 3) Dorsally, outside the inner muscles, there is a muscle, divided into several rather weak bundles, which runs alongside part II and inserts at the cuticle of the transition to part III: *musculus longitudinalis recti dorsalis* (fig. 60: ml₂). Its function is evidently analogous with that of the mesenterio-rectal muscles. — 4) Ventrally, alongside the aboral part of part II and the whole of part III there is a stronger muscle, which runs outside the *musculi interni*, but also in some places near the epithelium; it originates with several branches from the aboral half of part II and inserts at the ventral diverticles between parts III and IV: *musculus longitudinalis recti ventralis* (fig. 60 and 66: ml₃); during its course it splits into several bundles. — 5) A very strong, paired lateral muscle originates ventro-laterally (with regard to the intestine, but on the dorsal side of the body) from the outer cuticle on the caudal side of the anus, runs obliquely in several bundles along the rectum, and inserts dorso-laterally at the aboral half of part II: *musculus longitudinalis recti lateralis* (fig. 60: ml₄). It originates with several small branches from a rather lengthened surface. It shortens the whole aboral half of the rectum. — 6) A broad, paired latero-ventral muscle runs in many bundles from the distal end of the diverticle at the boundary between parts III and IV to the latero-ventral edge of the anus: *musculus recto-analis* (fig. 60 and 65: ml₅). It shortens part IV and simultaneously dilates the anus.

The inner longitudinal muscles are directly differentiated in the inner connective tissue and in the epithelium of the ridges. The outer ones, on the other hand, have separate *sarcoplasm* cells (fig. 69: sp).

Radial muscles. The radial muscles pierce the epithelium of the rectum and insert at the cuticle in the same manner as in the stomodaeum. In transverse sections (fig. 61) one sees, how the muscle fibres running through the epithelium in the crests of all the larger ridges unite in fine bundles (md), which run along the base of the epithelium on both sides of the ridges and break through the circular muscle. — The following dilatatory muscles are found: 1) A short and thick, paired dorsal dilatator originates from the bottom of a pocket in the dorsal wall of the body, runs to the rectum in a slightly oral direction, and inserts with several branches at the cuticle of the dorsal ridge of the aboral half of part II: *dilatator recti dorsalis anterior* (fig. 60: md₁). It is a synergist of the aboral branch of the ventral *musculus mesenterio-rectalis*. — 2) A long, paired ventral dilatator, synergist of the one just mentioned, originates from the ventral surface of the thorax and runs almost perpendicularly toward the rectum; it divides into two branches, of which one inserts at the cuticle of the ventral ridge of the aboral half of part II and the other similarly in part III; they run in several fine branches through the inner connective tissue and the epithelium: *dilatator recti ventralis* (md₂). — 3) A series of short dorsal and latero-dorsal muscle-bundles run from the dorsal cuticle of the thorax and the above mentioned pocket to the cuticle of parts III and IV of the rectum: *dilatatores recti dorsales posteriores* (md₃). They dilate these parts of the rectum and the anus. — 4) Three pairs of lateral dilatators run from part I in an oro-lateral direction, the first pair from its oral end around the aboral part of the mesenteron, the second pair from the middle and the third pair from the aboral part of part I to the lateral walls of the thorax: *dilatatores recti laterales anteriores*. The oral end of part I is also dilated by the *musculi longitudinales mesenterii externi*. From parts II and III lateral dilatators run in an oro-lateral direction: *dilatatores recti laterales medii*. From parts III and IV lateral dilatators run aboro-laterally: *dilatatores recti laterales posteriores*. They form bundles, which insert at surfaces of the rectal cuticle situated in a row at equal, small distances from one another, and run, more or less parallel to one another, to the aboral, lateral surface of the body.

Circular muscle bundles surround the rectum similarly to the stomodaeum and form the *constrictor recti* (fig. 61—63 and 66: mc). The bundles are densely arrayed along parts I and II, more sparsely along part III, but lacking in part IV. They are much weaker than in the oesophagus, almost as weak as in the ventriculus; they are narrow in the longitudinal direction of the intestine, thus differing from the circular bundles of the ventriculus. The sarcoplasm cells (fig. 61: sp) are also much smaller than in the oesophagus, about the same as in the ventriculus. Most orally the constrictor recti passes over into the muscles of the mesenteron (fig. 68: mc).

I have not found any *sphincter ani* in *Balanus improvisus*; the analogous

function is performed by the constrictor at the aboral end of part III. Also the musculi longitudinales recti laterales (figg. 60, 64, 65: ml₄) may contribute in constricting the aboral part of the rectum, whereas the anus itself always remains open. When the anus is not dilated (as it is in fig. 64) it obviously takes the form shown in fig. 65 in consequence of the elasticity of the cuticle.

In fig. 68 some of the longitudinal musculi mesenterio-rectales (ml₁) are seen in transverse section outside the circular muscle (mc). Somewhat further aborally one after the other enters inside the circular muscle through the spaces between the bundles. In fig. 62 the ventral and lateral longitudinal muscles (ml) run inside the constrictor; on the left side the lateral muscle is just entering inside it.

All the larger muscles of the rectum are distinctly *transversally striped*.

Outside the circular muscle and its sarcoplasm there is a typical, lacunous *outer connective tissue*. Around the last part of the rectum the connective tissue is very sparse and the lacunae are large.

IV. The innervation of the intestine.

GRUVEL has made clear, which nerves innervate the intestine (1893, 2, 1904, 2, 1904, 3, 1905). But I have not found any statements concerning the *peripheric end instruments of the intestine nerves* in the literature.

I have examined the end parts of the nerves, such as they are seen in total preparations of the intestine made as described in the introduction (Technique: B). In these preparations the nerves were highly coloured, the muscle fibres weaker.

In figg. 70—72 nerves from different parts of the intestine are shown. At regular distances there are groups of longitudinally running *nerve fibres* (in one case 8 groups on one side). The nerves run in irregular, spirally twisted curves; they often branch and anastomose. At longer or shorter intervals they form knoblike, thickened end instruments, partly seated at the ends of the branches, mostly at the ramifications, but sometimes anywhere on the nerve-fibres. — Between these parallel main trunks there is a network of much finer fibres, forming irregular, larger and smaller polygonal meshes (fig. 71: right side).

In the pars anterior mesenterii (fig. 70) the nerve-fibres are thicker and the end knobs more numerous than in the pars posterior (fig. 71). In the rectum (fig. 72) the nervature, as a whole, is weaker than in the mesenteron, but the fibres of the network between the longitudinal main trunks are relatively thicker in proportion to the fibres of the main trunks.

Discussion of the results.

I. General.

Regarding the *division* of the alimentary canal of the *Cirripedia* different authors have had different views. CUVIER (MARTIN-SAINT-ANGE, p. 517), MARTIN-SAINT-ANGE (pp. 527—530) and GERSTAECKER (pp. 471—472) divide it into oesophagus, stomach, intestine proper and rectum. Their «stomach» corresponds to the pars anterior mesenterii. — DARWIN's division is amazingly «modern»; he divides the digestive canal into oesophagus, stomach and rectum (1854, p. 14), which partitions correspond to the stomodaeum, mesenteron and proctodaeum. — NUSSBAUM divides the alimentary canal into 4 parts: oesophagus, stomach, intestine, and anus with its vestibulum (p. 50). He also calls the pars anterior mesenterii «stomach»; although he points out (p. 56), that it is not homologous to the stomach of the Decapodes, he does not lit upon the idea of considering the aboral part of his «oesophagus» as stomach. He also counts the pars posterior mesenterii and the rectum as one main partition, the «intestine», which he later on, however, divides into the intestine proper and the rectum. — Also BERNDT (1903, 1, pp. 433—440), KNIPOWITSCH (pp. 144—145) and GRUVEL (1893, 2, pp. 436, 484, 527) make use of the old division: oesophagus, stomach, mid-gut and rectum, wherein «oesophagus» corresponds to stomodaeum (excl. pharynx) and «stomach» to pars anterior mesenterii. KNIPOWITSCH (p. 140), however, admits that the «stomach» embryologically belongs to the mid-gut. In a later work (1905) GRUVEL inconsistently divides the digestive apparatus into the following main partitions: mouth with chewing apparatus, stomach, intestine opening through the anus, and the adjoining glands (p. 386). — HOFFENDAHL unites ventriculus and pars anterior mesenterii under the name «stomach», although he points out their histological difference; the oral part, which corresponds to the ventriculus, he calls «Oesophageal aussackung» (pp. 375—377; comp. also NUSSBAUM, p. 56). — BROCH (1919, p. 6) divides the digestive canal into 4 parts: oesophagus, stomach, the digesting intestine, and proctodaeum. But his «stomach» corresponds to the ventriculus and his «digesting intestine» to the mesenteron (comp. his discussion). His division thus differs from the one used in this paper only by the stomodaeum being divided into two parts. Later (1927, p. 517) he, nevertheless, unites the oesophagus and the stomach under the name stomodaeum.

JOHNSTONE & FROST (pp. 57—63) correctly divide the alimentary canal into stomodaeum, mid-gut and proctodaeum, but they incorrectly call the digestive intestine (which together with the digestive glands composes the mid-gut) «stomach». — YOSII (pp. 171—172) divides the canal into «mouth» (corresponds to the pharynx), «oesophagus» (= the rest of the stomodaeum), «stomach» (= pars anterior mesenterii), and «intestine», which is divided in

two — the anterior part (= pars posterior mesenteri) and the posterior part (= proctodaeum). He is corrected by PYEFINCH, who quite correctly divides the gut into «fore-gut» (consisting of pharynx and oesophagus), mid-gut and hind-gut (1934, pp. 230—235; 1936, pp. 664—668; 1937, pp. 355—360). — MONTEROSSO (1933, pp. 121—123) also correctly divides the digestive canal into «oesophagus», «intestino medio (mesenteron)» and «intestino terminale». VIVI, although correctly dividing it into 3 main parts, «intestino boccale», «intestino medio» and «intestino terminale» (p. 112), incorrectly calls the anterior part of the mesenteron «stomach» and the posterior part «intestine proper». — All these authors include the ventriculus in the «oesophagus».

The only correct division from the point of view of morphology, comparative anatomy and embryology is the one into three main parts: stomodaeum, intestinum entodermale (mesenteron and the gastric glands), and proctodaeum. KRÜGER is of the same opinion (1940, 2, p. 93). He calls the entodermal part «Mesenteron»; he also quite correctly calls the small aboral part of the stomodaeum stomach («Magen»).

II. Stomodaeum.

According to DARWIN (1851, p. 40) the mouth parts confine a cavity, the «supra-oesophageal cavity», in the middle of which, between the mandibles, the oesophagus opens. This cavity I have called *pharynx*, and I have examined it in detail, whereas previous authors have treated it only in connection with the mouth parts. — According to GRUVEL (1893, 2, p. 436) the pharynx consists of the hind bottom of the mouth cavity.

DARWIN (1854, p. 74) mentions also, that in *Balaninae* a «sub-triangular portion of the inner fold of the labrum, that hangs over the oesophagus» is thickened and yellowish; it has patterns, which he supposes to give a hold for the muscles that open the upper end of the oesophagus. This supposition cannot be correct; as we have seen, all the dilators of the oesophagus run radially to the outer cuticle of the body. DARWIN also mentions, that some fine muscles insert at the membrane forming the supra-oesophageal cavity (p. 40). These are evidently the dilatores pharyngis, although he does not mention anything about their course.

The thickened part of the inner fold of the labrum, mentioned by DARWIN, is the thick dorsal chitin piece described above («paragnathe», see figg. 3:a and 6), which according to DARWIN is typical for *Balaninae*. He also mentions, that it shows a central junction-line (1851, p. 322). Also GRUVEL has paid attention to this chitin piece (1893, 1, pp. 859—860) and names it «paragnathe» (1893, 2, p. 434). In *Balanus tintinnabulum* it is formed by two symmetrical parts, joined together at the median line (1893, 1, p. 859). — In my trans-

verse sections on the contrary no such junction-line can be seen in the structure of the chitin plate.

The proboscis is of different length and form in different species (comp. GRUVEL 1893, 2, pp. 432, 482; BROCH 1919, pp. 6, 13). In *Balanus improvisus* it is relatively large, which also appears, from the fact, that the pharynx is three fourths as long as the oesophagus.

BROCH's assertion (1927, p. 517), that the folds of the ventriculus do not correspond to the folds of the oesophagus, and that the ventriculus in transverse sections displays a «star-formed» aspect, does not hold good with *Balanus improvisus*; as we have seen (fig. 27), the longitudinal furrows and ridges correspond to those of the oesophagus.

According to NUSSBAUM (p. 51) the epithelium cells of the stomodaeum («matrix cuticulæ») are low, cubical, in the species examined by him. As I have pointed out, the form of the epithelium cells depends upon the state of dilation or constriction of the intestine, being mostly high, cylindrical, when the lumen is narrow, and vice versa.

In a cypris-stage of *Poecilasma aurantium* HOFFENDAHL (p. 376) has found a membrana propria in the ventriculus («Oesophagealaussackung»). BROCH (1919, p. 17) has found a weakly developed basal membrane in the ventriculus of *Scalpellum Stroemii* and BERNDT (1907) in *Cryptophialus striatus*. In *Balanus improvisus*, however, a basal membrane is wanting in the ventriculus, although the inner connective tissue in some places resembles one (comp. chapter «Ventriculus»).

Concerning the muscles of the stomodaeum NUSSBAUM (p. 51) has generally made similar observations as I. He has not, however, studied the dilators in detail nor has he denominated any muscles. — The muscles of the oesophagus in *Anelasma squalicola* have been briefly described by JOHNSTONE & FROST (pp. 54—55).

GRUVEL (1893, 2, p. 437) is of the opinion that in *Balanus tintinnabulum* the dilatatory muscle fibres run between the epithelium cells. In *Balanus improvisus* they certainly pass through the cells, as I have pointed out. Since there is no reason for supposing that it would be different in two species so closely related, it is probable, that GRUVEL has made a mistake. In the usual longitudinal sections through the epithelium the muscle fibres often seem to run between the cells, and GRUVEL has evidently not examined transverse sections of the cells. Neither have BROCH (1919, pp. 8, 14) nor VIVI (pp. 113—114) discovered the real position of the radial fibres.

BROCH's observations concerning the difference between these fibres, which he calls the connective parts, and the muscle tissue proper (1919, pp. 14—17)

are interesting. Although I have not used the same fine staining methods as BROCH, I can assure, that I have not found any transversal striation in the finest bundles, not even before their forking and penetrating into the epithelium and that the connective fibres are stained by the thiazine red much more brilliantly than the muscle-substance proper. BERNDT (1903, 2, pp. 415—416) has made similar observations. Also KRÜGER (1940, 2, p. 95) suggests, that these fibres are connective (»bindegewebig»).

A common condition in *Cirripedia* is evidently, that the muscles weaken more or less when approaching the aboral parts of the stomodaeum (comp. HOFFENDAHL, p. 50; BROCH 1919, pp. 8—9). This is also the case with *Balanus improvisus* and is noticeable already before the end of the oesophagus.

I have not found the sphincters at the two ends of the ventriculus mentioned anywhere in the literature.

The GLANDULAE SALIVALES were at first discovered by NUSSBAUM, who did not, however, detect their glandular character, and called them »the indefinable organ 2» (pp. 41—42). — GRUVEL has examined them in detail in a number of species (1893, 1, pp. 860—861; 1893, 2, pp. 441, 427, 528, 543; 1904, 3, pp. 134—137). He is of the opinion, that they are salivary glands, as were HOFFENDAHL (p. 384) and BERNDT (1903, 2, pp. 419—420). — BROCH (1919, pp. 15—16), on the other hand, thinks that they are *poison glands*, basing his opinion on researches on *Scalpellum Stroemii*. — Lacking further evidence I think it better to call them *glandulae salivales* for the present. — BROCH mentions, that the nucleoli of the gland cells are not at all stained by DELAFIELD's haematoxyline. In my preparations they were, however, distinctly stained.

BROCH (1927, p. 518) asserts, that the glands in question are generally seated in the basal joint of the first pair of cirri and only exceptionally (in some *Scalpellidae* and *Lepadidae*) behind the labium. In *Balanus improvisus* they are, however, seated in the labium, as we have seen. GRUVEL (1893, 2, p. 441) has found them in the labial palpi of *Balanus tintinnabulum*, in the same manner as some of the glands of *Pollicipes cornucopia* (p. 528). Also NUSSBAUM (p. 42) has found them in the labium of *Lepas Hillii* and HOFFENDAHL (pp. 347, 384) in that of *Pocillasma aurantium*. BROCH's way of summarizing the facts is thus incorrect.

In this connection it may be mentioned, that in *Balanus improvisus* I have not found any organ corresponding to NUSSBAUM's indefinable organ 1» (see NUSSBAUM, p. 41; GRUVEL 1904, 3, pp. 144—147).

III. Intestinum, entodermale.

According to GRUVEL (1893, 2, p. 140) only non-assimilable chitin pieces of the food are left in the »mid-gut» (= pars posterior mesenterii); this is in accordance with my supposition, that the resorption takes place chiefly in the pars anterior.

According to VIVI (pp. 114—115) the »stomach» (= pars anterior mesenterii) of *Balanus perforatus* var. *fistulosa* is orally and aborally bounded by valves. Her »*valvola cardiaca*» corresponds to my »pylorus»; in *Balanus improvisus* there is nothing corresponding to her »*valvola pilorica*».

It can be gathered from the literature, that the *Cirripedia* may be divided into two groups, one in which the »cirriped-stomach» consists of a stomodaeal and an entodermal part, and another in which it is purely entodermal. *Lepas Hillii* (NUSSBAUM, p. 56), *L. anatifera* (GRUVEL 1893, 2, pp. 485—486), *Pollicipes cornucopia* (GRUVEL 1893, 2, p. 528) and *Pocillasma aurantium* (HOFFENDAHL, pp. 375—377) belong to the former and *Pollicipes polymerus* (NUSSBAUM, p. 56), *Balanus tintinnabulum* (GRUVEL 1893, 2, pp. 439—440), all the species examined by later authors (see »Introduction»), and *Balanus improvisus* to the latter.

EPITHELIUM. DARWIN's statement concerning the »cuticle» of the mesenteron (1851, pp. 45—46; 1854, p. 86), also mentioned by GERSTAECKER (pp. 472—473) refers to a »membrane» surrounding the contents of the mesenteron. VIVI (p. 116) calls this membrane »peritrofica». NUSSBAUM (pp. 51—52) states, that the tube mentioned by DARWIN is not a cuticle but a mucous covering, secreted by one of the two kinds of cells, which form the epithelium of the mesenteron. The other kind of epithelium cells are covered with a brush-border. — NUSSBAUM's observations of two kinds of epithelium cells are not in accordance with mine as to *Balanus improvisus*. I have not been able to find any special gobletlike secretory cells nor any of another form. Certainly cells with and cells without balloon secretion are found, but all the cells are equally built and capable of secreting; on cells, where the secretion is weak, the brush-border is clearly visible, whereas according to NUSSBAUM it is missing on the mucous cells. Unfortunately NUSSBAUM does not give any drawings of either kind of these epithelium cells. There is, nevertheless, no reason for doubting the existence of this differentiation in the species examined by him, which all are *Lepadomorpha*, but it is not a common condition in the *Cirripedia*. Also JOHNSTONE & FROST (p. 61), BERNDT (1903, 2, pp. 417—418; 1907) and PYERFINCH (1934, pp. 230—231; 1936, p. 666) have found differentiations among the epithelium cells. — It is also very likely, that the secretion of the mesenterial epithelium cells of *Balanus improvisus* is at least partly mucous. —

Concerning the secretion of the mesenterial epithelium comp. also GRUVEL (1893, 2, pp. 439—440, 485—486, 528), HOFFENDAHL (pp. 376, 377) and PYEFINCH (1936, p. 666). PYEFINCH's description and figures resemble the balloon secretion in *Balanus improvisus*.

JOHNSTONE & FROST in their paper on *Anelasma squalicola* (p. 61) assert, that the oesophagus, stomach and intestines are lined throughout with a chitinous cuticle, and only the tubules of the digestive gland lack this layer, inferring therefrom, that the mid-gut is therefore represented by the digestive glands. Later on (p. 62) they, nevertheless, state that the epithelium in the mesenteron has a »striped cuticle» or »Stäbchensaum». Thus it is not correct to call this »cuticle» chitinous, nor does the mid-gut in the species in question fundamentally differ from that in other cirripeds. — According to SEWELL, the mesenteron is not lined with chitin (KRÜGER 1940, 2, p. 94).

JOHNSTONE & FROST (p. 61) also assert, that there is no »basement membrane» anywhere in the intestine. So far as the epithelium of the mid-gut is concerned, this is probably a mistake. According to BROCH (1919, p. 9), the same species has a distinct basal membrane.

FILATOWA (1902, pp. 380—381) has shown through staining experiments, that certain cells in the »stomach» of the larvae of *Balanus improvisus* have an excretory function; their histological structure differs also from the rest of the stomach wall (comp. GRUVEL 1905, p. 449).

MUSCLES. According to DARWIN (1854, pp. 85—86) each coecum hepaticum in species of the genus *Balanus* must have a sphincter muscle at the place, where they open into the »stomach», judging from their way of detaining liquid. I have not, however, found any special sphincters of the coeca in *Balanus improvisus*; their orifices are, on the contrary, so wide that the coeca pass into the intestine without any distinct boundary. Naturally the common tunica muscularis of the mesenteron may serve as sphincters in this case.

DARWIN's statements on the structure of the wall of the mesenteron (1854, p. 86) do not in every respect agree with the results of later investigations. His »cellular mucous layer» is the same as the epithelium. He has quite overlooked the inner longitudinal muscle layer, the fibres of which are still finer than those of the circular layer. His »longitudinal layer» refers evidently to the outer, stronger muscle bundles, which in *Balanus improvisus* surround only the aboral part of the mesenteron. The latter, on the other hand, have been overlooked for instance by MONTEROSSO (1923), unless they are lacking in *Balanus perforatus*, and by GRUVEL (1893, 2, pp. 439—440, 486).

NUSSBAUM mentions a »dilator ventriculi» (his »ventriculus» = pars anterior mesenterii). The arrangement of the muscles of the mesenteron in the species examined by him differs from that in *Balanus improvisus*, the longi-

tudinal muscles lacking, while their function is performed by oblique muscle bundles connecting the circular muscles with one another (pp. 24, 52, 54 and pl. V fig. 3). — As it appears from the above description, I have not found any dilators attached to the mesenteron. The elasticity and cohesion of the tissues are the only factors that can restore the form of the mid-gut after a contraction.

According to NUSSBAUM (pp. 28, 52) and HOFFENDAHL (p. 378) all the muscles of the digestive organs are transversally striped; NUSSBAUM, however, admits, that he did not see the striation in the mesenteron (pp. 29, 52). DARWIN (1851, p. 45) and GRUVEL (1904, 3, pp. 138—139) on the contrary assert, that the muscles of the mesenteron are plain. I have not in *Balanus improvisus* been able to discover any transversal striation in the muscles of the mesenteron, whereas it is in many places very distinct in the muscles of the stomodaeum and the proctodaeum, although less so in other places. NUSSBAUM's view, however, is in accordance with the general rule, that all the muscles of the *Arthropoda* are transversally striped. Compare also JOHNSTONE & FROST (pp. 55—57) on the »pseudo-striation» of the »muscle-fibres» and the histology of the muscle bundles.

According to BROCH (1919, pp. 9, 17), the digesting intestine is destitute of muscles in the species examined by him. Also JOHNSTONE & FROST (p. 61) mention the absence of a muscular layer in *Anelasma squalicola*.

STRATUM PERINTESTINALE. DARWIN's »hepatic layer» (1854, pp. 86, 547, 578) is obviously the stratum perintestinale, which was afterwards overlooked until MONTEROSSO discovered it (1923) and described it in detail (1927), at first calling the layer »peritoneal» (1923) but later on »perintestinal» or »perienteric» (1927). According to PATANÉ (pp. 126—130) it shows specific morphological and structural differences in the different species.

GLANDULAE CASTRICAE. As to erroneous notions of older authors concerning the *glandulae pancreaticae*, see HOEK (pp. 33—34), DARWIN (1851, pp. 57—58; 1854, pp. 100, 128—129) and GERSTAECKER (pp. 487, 490). The true nature of these glands was discovered by HOEK (pp. 34—36), who proposed that they should be called pancreatic. — What MARTIN-SAINT-ANGES (pp. 528—529), KARSTEN (pp. 301—302), and LAÇAZE-DUTHÈRES (pp. 560—562) describe as liver (*hepar*), corresponds evidently to the pancreatic glands. — JOHNSTONE & FROST's »digestive glands» (p. 62 and fig. 38) resemble histologically most nearly the pancreatic glands.

As to the *coeca hepatica* GERSTAECKER (p. 472) at first suggested, that they were some kind of a liver-organ (comp. also HOEK, p. 37).

NUSSBAUM simply calls the hepatic coeca »brown glands» and the pancreatic glands »white glands» (pp. 53—55). — GRUVEL classifies the gastric glands as »hepatic» or »gastro-hepatic», »hepato-pancreatic», and »pancreatic» glands;

the *hepato-pancreatic* glands are an intermediate form between the two others and are found in certain species (1893, 2, pp. 441—443, 487, 531, 544—545). As a fourth category he mentions «stomachal glands», which are epithelium cells of the «stomach» (1904, 1, p. 174).

Later on GRUVEL (1934, 3) published some new points of view concerning the differentiation of the gastric glands based on studies on *Balanus psittacus*. In this species the pancreatic glands open into the hepato-pancreatic ones; these in their turn open into the hepatic glands, which communicate directly with the stomach-cavity. This proves, that the pancreatic glands are not individual ones, but only deep coeca with specialized cells of the hepato-pancreatic glands, which in turn only are differentiated diverticles of the hepatic coeca; besides, all intermediate forms are found when passing from one element to another (pp. 133, 139—142).

GRUVEL asserts, that he has found the greatest conformity to exist with regard to these circumstances in all the *Pedunculata* and *Operculata* examined by him, which fact he generalizes in his monography (1905). This generalization is, however, unwarranted. HOEK (pp. 34, 36), NUSSBAUM (pp. 53—55) and BROCH (1919, pp. 6, 13—14) have shown the existence of differing conditions. My researches on *Balanus improvisus* also prove, that the pancreatic glands in this species open through the ducti pancreatici into the pars anterior mesenterii quite independently of the coeca hepatica. — KRÜGER (1940, 2, p. 94) criticizes GRUVEL's terminology of the digestive glands.

FILATOWA (p. 385) describes something in *Balanus improvisus*, that she calls the «Organe de Knipowitsch», seated «between the thorax and the abdomen on both sides of the digestive apparatus». It resembles the organ in *Dendrogaster astericola* that KNIPOWITSCH has described and drawn, with the difference that KNIPOWITSCH describes evacuation-ducts, which are absolutely lacking in *Balanus improvisus*. — FILATOWA's drawing corresponds exactly to the aspect of the pancreatic glands, but the position that she mentions is strange. If she refers to the boundary between prosoma and thorax, she has probably pictured an unusually far carino-apically stretching branch of the latero-aboral lobe of the pancreatic gland. No special «KNIPOWITSCH's organ» without evacuation-duct can be found there nor anywhere else in the species in question. — KNIPOWITSCH's drawing (pl. I, fig. 32) also resembles a pancreatic branch.

IV. Proctodaeum.

NUSSBAUM (p. 53) mentions a «vestibulum» of the anus. This refers evidently to what I call part IV of the rectum or, perhaps, rather to its most aboral part. — MONTEROSSO's (1933, p. 123) «ampolla rettale» (pictured in his pl. 3, fig. 4) also resembles part IV.

VIVI (pp. 116—117) divides the rectum of *Balanus perforatus* var. *fistulosa* into two regions, of which the oral one is characterized by oblique muscles, while the aboral shows special folds called «villi ad armatura chitinosae», which are longitudinal ridges of the wall. Since VIVI does not publish any drawings, it is impossible to ascertain how these regions correspond to the 4 parts described in this paper; possibly VIVI's second region is homologous to my part IV.

HOFFENDAHL mentions (p. 378) that the chitin layer lining the «intestine» is not pierced by canals but shows a smooth surface. It is very likely, that he refers to the rectum; otherwise the statement would be strange. — The «intestine» mentioned by HOEK (p. 6) in the cypris of *Lepas australis* is evidently also the rectum.

NUSSBAUM mentions a paired muscle, «dilator vestibuli ani» (p. 28 and pl. V fig. 9 and 5), and an unpaired dorsal muscle, «levator ani» (p. 52 and pl. V fig. 5). It is difficult to decide, whether they can be considered homologous to any of the muscles described in *Balanus improvisus*. — JOHNSTONE & FROST (p. 61) have found only a few, radially placed muscle bundles belonging to the proctodaeum. KRÜGER's account (1940, 2, p. 96), that these muscles belong to the mid-gut, is probably due to a misunderstanding.

DARWIN (1854, p. 87) and GRUVEL (1893, 2, pp. 440—441) talk about a «sphincter ani», the latter in *Balanus tintinnabulum*. I, nevertheless, maintain my opinion, that at least in *B. improvisus* there is no real sphincter.

Summary.

The digestive canal of *Balanus improvisus* Darwin is of the same type as in other *Cirripedia thoracica*. It differs from the type principally by the aboral part of the mesenteron forming a secondary curve, the convexity of which is directed ventrally. The ectodermal parts, stomodaeum (pharynx, oesophagus and ventriculus) and proctodaeum (intestinum rectum), are of the same structural type, sharply differing from the «intestinum entodermale» (mesenteron and glandulae gastricae).

The pharynx occupies a comparatively great part of the stomodaeum. The ventriculus comprises a small part, the boundaries of which in its dilated state are difficult to determine exactly; in its constricted state it is orally bounded by the sphincter cardiacus, whereas a small knob of it protrudes into the mesenteron on the aboral side of the sphincter pyloricus.

The lumen of the pharynx differs rather from that of the oesophagus and the ventriculus, which are of the same type. The lumen of the proctodaeum

is mainly of the same type as that of the oesophagus, but strongly modified in its aboral parts. The lumen of the mesenteron is much wider and simple in form.

The mesenteron comprises, as commonly among the cirripeds, the greater part of the alimentary canal. It is indistinctly divided into two parts, which I call *pars anterior* and *pars posterior mesenteri*. From the *pars anterior* 7 *coeca hepatica* proceed, which do not differ from the rest of the mesenteron in structure and without sharp boundaries pass into it through wide orifices. The *coeca* have been denominated in this paper. There is, besides, one pair of pancreatic glands, which have a quite specific structure; each of them is divided into a medio-oral and a latero-aboral lobe. Each gland opens through a particular ductus pancreaticus directly into the *pars anterior mesenteri* and not through the *coeca hepatica*. Hepato-pancreatic glands are missing in *Balanus improvisus*.

The epithelium of the ectodermal parts of the intestine is covered by a *cuticle* of chitin, which is a direct continuation of the outer cuticle of the body and is moulted together with it. In the pharynx it shows certain modifications (bristles, paragnathe). — The entodermal epithelium is lined with a *brush-border*, excepting the pancreas-cells, which appear to be uncovered.

The *epithelium* is mostly cylindrical when the lumen is constricted, cubical when it is dilated. All the cells of the mesenteron and the hepatic *coeca* can have balloon secretion. The nuclei in the ectodermal epithelia are mostly seated in the basal half of the cells, in the entodermal epithelia more often in the apical half. — The epithelium cells of the pancreatic glands differ from the other cells. They are exceptionally large, irregular in form, and strongly basophilic. Their large nuclei are seated basally and contain irregularly arranged chromatine. Between the cells there are intercellular secretion capillaries.

In the entodermal parts of the intestine the epithelium stands on a *membrana propria*, which, on the contrary, is missing in the ectodermal parts, excepting dorsally in the oral part of the pharynx.

Immediately outside the epithelium of the ectodermal parts there is a special *inner connective tissue* of small cells, an intermediate form between cellular and fibrillary connective tissue.

The *muscles* of the digestive canal have been described in detail and denominated. The tunica muscularis of the mesenteron is unitary and weakly developed. The muscles of the stomodaeum and the proctodaeum, on the contrary, are strong and consist of a great number of individual muscles. There are circular (constrictor), longitudinal, and radial (dilatator) muscles. In certain cases they can have combined functions. A great number of muscle fibres insert at the intestine by means of particular, branched, connective fibrils. These fibrils pass in the ectodermal parts through the epithelium cells

and attach to the cuticle. In the rectum there are, besides, longitudinal epithelium-muscle-fibrils. In the entodermal parts the muscle fibres insert at the *membrana propria*. — The ducti pancreatici have a number of particular muscles.

The muscles of the ectodermal parts of the intestine are transversally striped, those of the entodermal parts are plain. The smaller muscles are directly differentiated in the connective tissue, through which they run, while the larger ones have a special sarcoplasm. The end parts of the connective fibrils in stomodaeum and proctodaeum are differentiated by the epithelium cells.

With the exception of the glandulae pancreaticae the intestinum entodermale is surrounded by a special *stratum perintestinale*, consisting of one layer of cells, which stand on the outer surface of the *membrana propria* and show particular histological and physiological characteristics.

Farthest off the intestine is surrounded by the common cellular connective tissue of the body changing around the ectodermal parts nearest to the intestine into a special *outer connective tissue* with more or less flattened cells.

Salivary glands (or poison glands) are found in *Balanus improvisus* only in the labium, from where they extend a short distance under the oesophagus. They show two functional phases, the one with swollen nuclei, seated in the interior of the cells, the other with shrunk nuclei, seated close by the cell-boundaries.

The *end-nervature* of the intestine has been examined on total preparations stained alive.

To Professor ALEX. LUTHER, who has lead and advised me in accomplishing his work, I hereby express my sincerest thanks.

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EXPLANATION OF THE FIGURES.

The figures, except those drawn from vitally stained total preparations, are drawn from the following six specimens, the numbers of which are mentioned (in parentheses) at the end of the explanation of each figure:

Specimen N: r	Fixation	Sections	Staining
1	Carnoy	sagittal 10 μ	Delafield + thiazine red
2	Gilson	" 5 μ	Heidenhain + "
3	Gilson	horizontal 10 μ	Delafield + "
4	Gilson	" 5 μ	Heidenhain + "
5	Gilson	transversal 10 μ	Delafield + "
6	Carnoy	" 5 μ	Heidenhain + "

The second number in the parentheses refers to the approximate magnification (for instance 500 \times).

Plate I.

Fig. 1. Plastic reconstruction of the digestive organs of a young *Balanus improvisus*. C = carinal, R = rostral, B = basal, A = apical side of the animal; d = dorsal, v = ventral side, o = oral, a = aboral end of the intestine; the thick line of dashes = the median outline of the body; s = glandulae salivales, p = glandula pancreatica of the left side; the thin lines of dashes = the outlines of the different sections of the intestine, the thin dotted lines = the corresponding outlines of the glandula pancreatica. (N:r 1, 80 \times).

Fig. 2. Semi-diagrammatical sagittal section through the intestine tube, combined from several sections. Stomodaeum: a = pharynx, b = oesophagus, c = ventriculus; mesenteron: d = pars anterior, e, e', f, g, h = pars posterior; proctodaeum: i = intestinum rectum; s = glandulae salivales (N:r 1, 80 \times).

Plate II.

Fig. 3. Transverse section of pharynx, 40 μ from transition to oesophagus; lumen constricted. a = paragnathe, b = bristles, lc = lumen centrale, s = salivary glands (dotted), ks = nucleus of salivary gland, lat = lateral ridge, d-lat = dorso-lateral ridge, m₁ = dilatator pharyngis dorsalis, m₂ = constrictor pharyngis dorsalis, m₃ = dilatator pharyngis dorso-lateralis, m₄ = dilatator pharyngis lateralis, m₅ = dilatator pharyngis ventro-lateralis, m₆ = constrictor pharyngis ventralis (aboral part), m₇ = dilatator pharyngis ventralis. (N:r 3, 250 \times).

- Fig. 4. Transverse section of pharynx in dilated state. a = paragnathe, lc = lumen centrale, m₁ = dilatator pharyngis dorsalis, m₂ = dilatator pharyngis lateralis, m₃ = constrictor pharyngis ventralis, m₄ = dilatator pharyngis ventralis. (N:r 4, 100 \times).
- Fig. 5. Ventral epithelium of oral part of pharynx. n = nucleus, x = vacuole, c = cuticle. (N:r 1, 1000 \times).
- Fig. 6. Paragnathe in sagittal section; fully developed, just moulted. g = yellow-stained layer, r = red-stained layer, h = hook-like aboral appendix. (N:r 1, 250 \times).
- Fig. 7. Piece of old ventral cuticle from aboral part of pharynx with short bristles. (N:r 2, 500 \times).
- Fig. 8. Piece of new ventral cuticle from oral part of pharynx with a long and a short bristle. (N:r 2, 500 \times).
- Fig. 9. Piece of old ventro-lateral cuticle from oral part of pharynx; bristles with basal knob. (N:r 2, 500 \times).
- Fig. 10. Dorsal pharynx-epithelium with radial muscle fibres (m). c = young cuticle, k = nucleus, n = nucleolus. (N:r 2, 500 \times).

Plate III.

Fig. 11. Transverse section of oral part of oesophagus in constricted state, 40 μ from transition to pharynx. lc = lumen centrale, sp = sarcoplasm, mc = constrictor oesophagi, ml = longitudinal muscles, dv = dilatator oesophagi ventralis n:r I, dld₂ = dilatator oesophagi latero-dorsalis 2, dd₂ = dilatator oesophagi dorsalis 3 n:r I. (N:r 3, 250 \times).

Fig. 12. Transverse section of a more aboral part of oesophagus with a diagram of the dilator muscles. mc = constrictor oesophagi, ml = longitudinal muscles, dd₁ = dilatator oesophagi dorsalis 1, dd₂ = dilatator oesophagi dorsalis 2, dd₃ = dilatator oesophagi dorso-lateralis 1, dld₁ = dilatator oesophagi dorso-lateralis 2, dld₂ = dilatator oesophagi dorso-lateralis 3, dld₃ = dilatator oesophagi dorso-lateralis 4, dld₄ = dilatator oesophagi dorso-lateralis 5, dvl₁ = dilatator oesophagi ventro-lateralis 1, dvl₂ = dilatator oesophagi ventro-lateralis 2, dvl₃ = dilatator oesophagi ventro-lateralis 3, dvl₄ = dilatator oesophagi ventro-lateralis 4, dvl₅ = dilatator oesophagi ventro-lateralis 5, dv₁ = dilatator oesophagi latero-ventralis 1, dv₂ = dilatator oesophagi latero-ventralis 2, dv₃ = dilatator oesophagi latero-ventralis 3. (N:r 3, 125 \times).

Fig. 13. Transverse section from the boundary between oesophagus and ventriculus (cardia); lumen totally constricted. dl = dilatator oesophagi lateralis n:r II, ms₁ = sphincter cardiacus, mc = constrictor ventriculi. (N:r 3, 250 \times).

Fig. 14. Transverse section of oesophagus in dilated state, 50 μ from transition to pharynx. lc = lumen centrale, mc = constrictor oesophagi, dd = dilatator oesophagi dorsalis, dvl₁ = dilatator oesophagi ventro-lateralis 1, dvl₂ = dilatator oesophagi ventro-lateralis 2, dv = dilatator oesophagi ventralis. (N:r 4, 100 \times).

Fig. 15. Piece of dorsal wall of oral end of oesophagus; lumen dilated, epithelium: cells cubical, md₁ = fine dilatatory muscle fibres, md₂ = thicker dilatatory muscle bundle, mc = constrictor oesophagi, ml = longitudinal muscle, bvi = inner connective tissue, bvy = outer connective tissue, sp = sarcoplasm. (N:r 1, 1000 \times).

Fig. 16. Pieces of dorsal and ventral wall of oesophagus (b in fig. 2); median sagittal section. sp = sarcoplasm, mc = constrictor oesophagi, ml = longitudinal muscle, md₁ = fine dilatatory muscle bundle, md₂ = thicker dilatatory muscle. (N:r 1, 500 \times).

Fig. 17. Piece of ventral wall of oesophagus, from sagittal section next to the one in fig. 16. md₁ = fine dilatatory muscle bundle, ml = longitudinal muscle, mc = constrictor oesophagi, sp = sarcoplasm. (N:r 1, 500 \times).

Plate IV.

Fig. 18. Dorsal and ventral piece from wall of oesophagus; cuticle recently moulted. k₁ = strongly differentiated epithelium nucleus, k₂ = weakly differentiated epithelium nucleus. (N:r 2, 500 \times).

Fig. 19. Piece of ventral epithelium in fig. 18. c₁ = old cuticle, c₂ = new cuticle. (N:r 2, 1000 \times).

Fig. 20. Muscle nucleus (k) in longitudinal muscle (ml) of oesophagus. (N:r 2, 1000 \times).

Fig. 21. Piece of epithelium from top of primary ridge of oesophagus; lumen not much dilated, epithelium cells high, cylindrical. cut = old cuticle, still connected with the epithelium by thin threads; md = radial muscle fibre. (N:r 4, 1000 \times).

Fig. 22. Piece of epithelium from the same section, from the deepest part of a furrow; epithelium cells lower, almost cubical, mc = constrictor oesophagi. (N:r 4, 1000 \times).

Fig. 23. Muscle fibres and sarcoplasm of oesophagus. ml = longitudinal muscle, mc = circular muscle, sp = sarcoplasm, v = unstained cytoplasm, k = nucleus, n = nucleolus. (N:r 2, 1000 X).

Fig. 24. Section traversing ventral epithelium of stomodaeum; A from pharynx, B from oesophagus. m = muscle-fibril, k = nucleus of epithelium cell. (N:r 5, 500 X).

Fig. 25. Sagittal section through ventriculus in dilated state (c in fig. 2). f₁ and f₂ = dorsal transversal furrows, f₃ = circular furrow at the boundary between ventriculus and mesenteron, mc = circular muscles, ms₁ = sphincter cardiacus, ms₂ = sphincter pyloricus, em = epithelium of mesenteron. (N:r 1, 250 X).

Fig. 26. Sagittal section of ventriculus in constricted state; section somewhat laterally from the median level. ms₁ = sphincter cardiacus, ms₂ = sphincter pyloricus. (N:r 2, 250 X).

Fig. 27. Transverse section through middle part of ventriculus. lc = lumen centrale, mc = constrictor ventriculi, ml = longitudinal muscles, md = radial muscles. (N:r 3, 250 X).

Fig. 28. Transverse section through oral end of pars anterior mesenteri, end knob of ventriculus (v) in constricted state, and medio-oral lobes of glandulae pancreaticae (p). cld = caecum latero-dorsale, cvl = caecum ventro-laterale, clv = caecum latero-ventrale, cv = caecum ventrale. (N:r 3, 50 X).

Plate V.

Fig. 29. Sagittal sections of ventriculus, near cardia; A piece of dorsal wall, B piece of ventral wall. bvi = inner connective tissue, mc-l = circular and longitudinal muscles, sp = sarcoplasm. (N:r 2, 1000 X).

Fig. 30. Nucleus of salivary gland, n = nuclei. (N:r 3, 500 X).

Fig. 31. Glandulae salivales; sagittal section. m_s = constrictor pharyngis ventralis, transversely cut. (N:r 1, 250 X).

Fig. 31 A. Orifices of salivary glands. (N:r 1, 500 X).

Fig. 32. Longitudinal section of labium. s = glandulae salivales, m = their orifices; salivary glands dotted. (N:r 5, 100 X).

Fig. 33. Part of a salivary gland cell; sagittal section. k = nucleus, n = nucleolus, sd = secretion drop. (N:r 2, 500 X).

Fig. 34. Transverse section through middle part of pars anterior mesenteri. cld = caecum latero-dorsale, clv = caecum latero-ventrale, cv = caecum ventrale, 47 = place of epithelium shown in fig. 47. (N:r 3, 50 X).

Fig. 35. Transverse section through aboral part of pars anterior mesenteri and latero-aboral lobes of glandulae pancreaticae (p). clv = caecum latero-ventrale, fv = aboral furrow of caecum ventrale. (N:r 3, 50 X).

Fig. 36. Transverse section through most oral part of pars posterior mesenteri. clv = caecum hepaticum latero-ventrale, spi = stratum perintestinale, 48 = place shown in fig. 48. (N:r 3, 100 X).

Fig. 37. Transverse section of pars posterior mesenteri, part 1; somewhat more aborally than fig. 36. (N:r 3, 100 X).

Plate VI.

Fig. 38. Transverse section of pars posterior mesenteri, part 2; ventral side upwards. spi = stratum perintestinale, 55 = cell shown in fig. 55. (N:r 5, 100 X).

Fig. 39. Transverse section of pars posterior mesenteri, part 3; ventral side upwards. (N:r 3, 100 X).

Fig. 40. Transverse section of pars posterior mesenteri, part 4; ventral side upwards. ml = musculi longitudinales mesenteri externi. (N:r 3, 100 X).

Fig. 41. Piece of dorsal wall of pars anterior mesenteri (d in fig. 2); epithelium cells with balloon secretion. bs = secretion balloon. (N:r 1, 500 X).

Fig. 42. Piece of ventral wall of pars posterior mesenteri, part 1 (e in fig. 2); balloon secretion weaker than in fig. 41. bs = secretion drops, sb = brush-border, ml = musculi longitudinales mesenteri interni, mc = musculi circulares mesenteri. (N:r 1, 500 X).

Fig. 43. Piece of dorsal wall of pars posterior mesenteri, part 1 (e' in fig. 2); epithelium cells without balloon secretion. sb = brush-border. (N:r 1, 500 X).

Fig. 44. Piece of ventral wall of pars posterior mesenteri, part 2 (f in fig. 2). (N:r 1, 500 X).

Fig. 45. Piece of ventral wall of pars posterior mesenteri, part 4 (g in fig. 2); lumen very much dilated, epithelium flattened. (N:r 1, 500 X).

Fig. 46. Piece of dorsal wall of aboral end of pars posterior mesenteri (h in fig. 2). f = small transversal furrow. (N:r 1, 500 X).

Fig. 47. Epithelium of ventral wall of pars anterior mesenteri (47 in fig. 34). 1-4 = differently stained zones of the epithelium cells (1 = pink, 2 = darker red, 3 = violet zone containing the nucleus, 4 = brilliant red zone). (N:r 3, 1000 X).

Fig. 48. Piece of ventral wall (48 in fig. 36) of pars posterior mesenteri, part 1. ep = epithelium, mp = membrana propria, ml = musculi longitudinales mesenteri interni, mc = musculus circularis mesenteri, spi = stratum perintestinale, bv = common connective tissue of the body. (N:r 3, 500 X).

Fig. 49. Epithelium from bottom of a longitudinal furrow in pars posterior mesenteri (to the left of the ridge in fig. 48); young cells, dividing both radially and tangentially. (N:r 3, 500 X).

Fig. 50. Epithelium of oral wall of pars anterior mesenteri; cells without balloon secretion. sb = brush-border. (N:r 2, 1000 X).

Fig. 51. Ventral epithelium from pars posterior mesenteri, part 1; longitudinal section. (N:r 2, 1000 X).

Fig. 52. Epithelium of a caecum hepaticum, near its orifice. sb = brush-border, s = fringed substance, probably fixed secretion, v = vacuole, mp = membrana propria. (N:r 4, 500 X).

Fig. 53. Dorsal epithelium of pars posterior mesenteri, part 2. lc = interstice between two cells, mp = membrana propria. (N:r 6, 1000 X).

Plate VII.

Fig. 54. Muscles of mesenteron, seen from the outside. mc = musculi circulares mesenteri, ml = musculi longitudinales mesenteri interni. (Total preparation, 250 X).

Fig. 55. Cell of stratum perintestinale (55 in fig. 38) of pars posterior mesenteri, part 2. k = nucleus, d = refractive drops, p = parasoma, mc = musculus circularis mesenteri. (N:r 5, 1000 X).

Fig. 56. Transverse section through ventriculus (v) and medio-oral lobes of glandulae pancreaticae (p). (N:r 3, 100 X).

Fig. 57. Section through medio-oral lobes of glandulae pancreaticae (p), ducti pancreatici (dp), ventriculus (v) and oral end of pars anterior mesenteri. mc = constrictor muscles of ductus pancreaticus, md₁ = dilatatory muscle of ductus pancreaticus. (N:r 5, 100 X).

Fig. 58. Transverse section of a tubular branch-end of latero-aboral lobe of pancreatic gland. is = intercellular capillary, v = vacuole, mc = circular muscle, md = dilatatory muscles, md₁ and md₂ = dilatatory muscles. (N:r 3, 250 X).

Fig. 59. Right ductus pancreaticus of fig. 57. ml = longitudinal muscles, mo = oblique muscles, md₁ and md₂ = dilatatory muscles, l = lacuna. (N:r 5, 250 X).

Fig. 60. Sagittal section of intestinum rectum with diagram of its muscles. I-IV = the different parts of the rectum, part I quite constricted, part II rather narrow, parts III and IV dilated; a = anus, ml₁ = musculi meso-rectales, ml₂ = musculus longitudinalis recti dorsalis, ml₃ = musculus longitudinalis recti ventralis, ml₄ = musculus longitudinalis recti lateralis, ml₅ = musculus recto-analis, md₁ = dilatator recti dorsalis anterior, md₂ = dilatator recti ventralis, md₃ = dilatatores recti dorsales posteriores. (N:r 1, 100 X).

Fig. 61. Transverse section of intestinum rectum, oral end of part II; constricted state; ventral side upwards. lc = lumen centrale, 1 = primary furrow, 2 = secondary furrow, 3 = tertiary furrow, 4 = quaternary furrow, l = lacuna in inner connective tissue, ml = longitudinal muscle, mc = constrictor recti, md = dilatatory muscle-bundle, sp = sarcoplasm. (N:r 4, 250 X).

Fig. 62. Transverse section of intestinum rectum, aboral end of part II; rather dilated state; ventral side upwards. ml = longitudinal muscles, mc = constrictor recti. (N:r 4, 250 X).

Plate VIII.

Fig. 63. Transverse (probably oblique) section of intestinum rectum, aboral end of part III; very dilated state; ventral side upwards. mc = constrictor recti. (N:r 4, 250 X)

Fig. 64. Horizontal section of aboral end of intestinum rectum; closed state. r₃ = constricted part III with its two ventral diverticles, r₄ = part IV of rectum, a = anus, ca = coeca analia, ml₄ = musculus longitudinalis recti lateralis. (N:o 3, 250 X).

Fig. 65. Horizontal section of part IV of intestinum rectum; open state. r₄ = part IV, a = anus, ca = coeca analia, ml₄ = musculus longitudinalis recti lateralis, ml₃ = musculus recto-analis. (N:r 4, 100 X).

Fig. 66. Piece of ventral wall of intestinum rectum, part III; sagittal section. cut = cuticle, kb = nuclei of inner connective tissue, mc = constrictor recti, ml₃ = musculus longitudinalis recti ventralis, mi = muscoli longitudinales recti interni, md₂ = dilatator recti ventralis. (N:r 1, 500 X).

Fig. 67. Dorsal epithelium and inner connective tissue of intestinum rectum, aboral end of part II. v = vacuoles, md = radial muscle fibres, kr = chromatine grains of nuclei of inner connective tissue, l = unstained cell resembling a lacuna. (N:r 2, 1000 X).

Fig. 68. Section from transition between mesenteron and proctodacum. er = epithelium of rectum, emi = epithelium of mesenteron, f = furrow at the zone of transition, md = dilatatory muscle fibres, me = longitudinal epithelium-muscle fibrils, mc = constrictor recti, ml = muscoli mesenterio-rectales. (N:r 5, 250 X).

Fig. 69. Transverse section of latero-ventral musculus mesenterio-rectalis (ml₁), showing its sarcoplasm (sp). k = nucleus, n = nucleolus. (N:r 6, 1000 X).

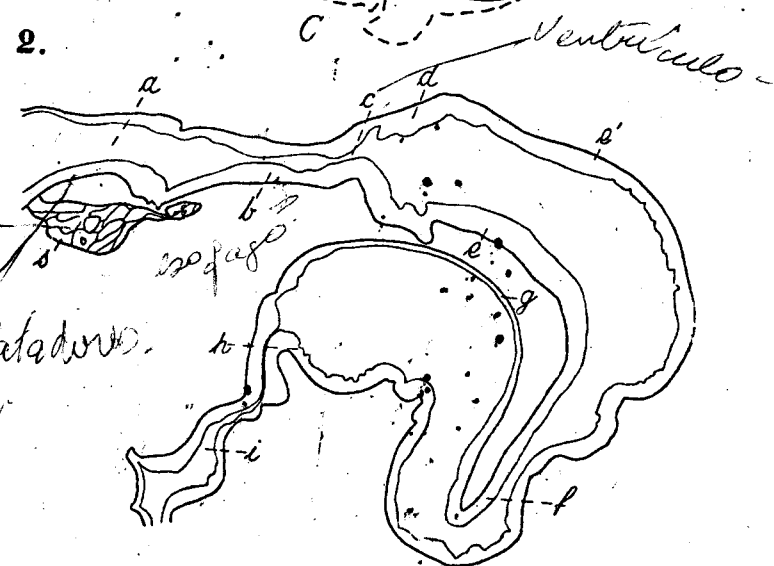
Fig. 70. Nerves of pars anterior mesenteri. (Total preparation, 250 X).

Fig. 71. Nerves of pars posterior mesenteri. (Total preparation, 250 X).

Fig. 72. Nerves of intestinum rectum. (Total preparation, 250 X).



2.



el. radior.

*musculus dilatatorius
da faringe*

PLATE II

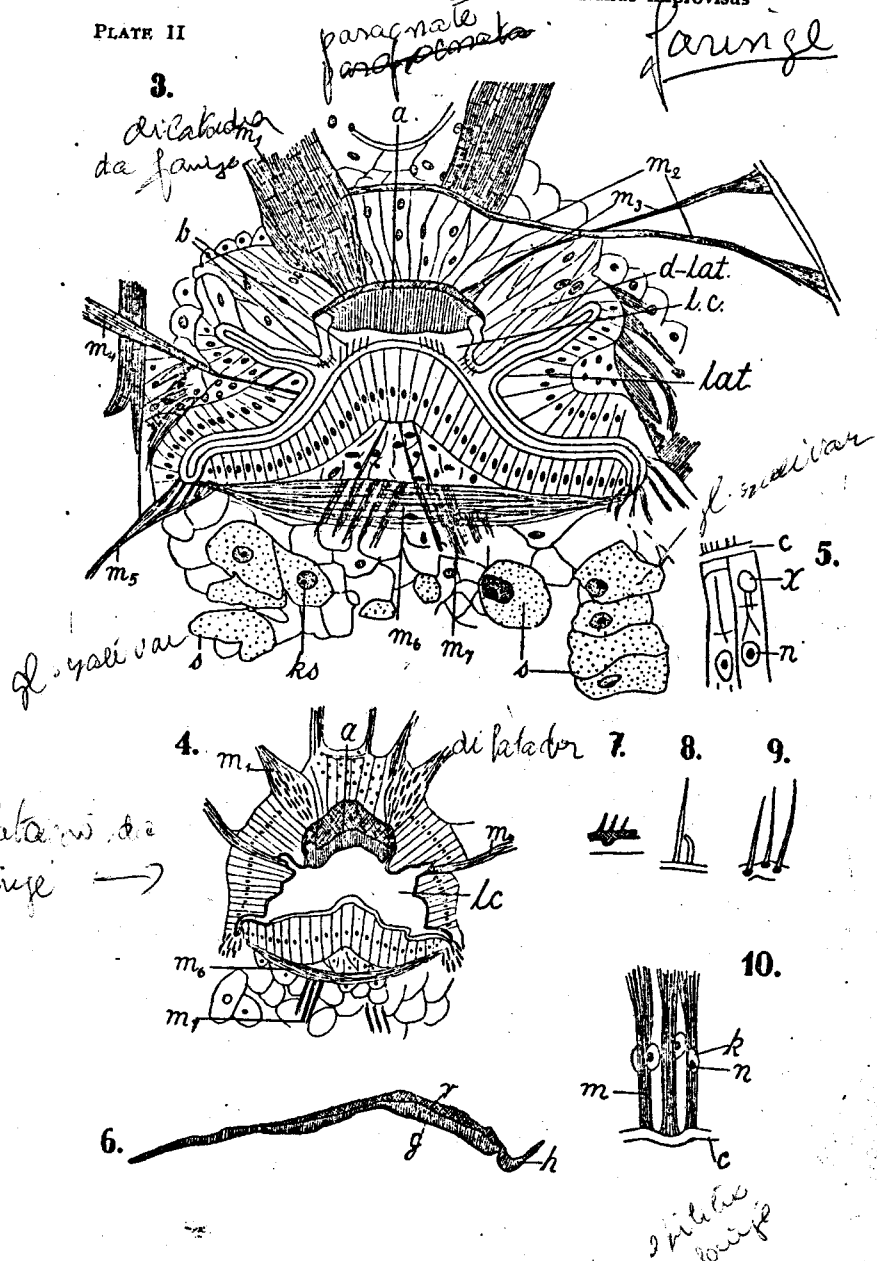
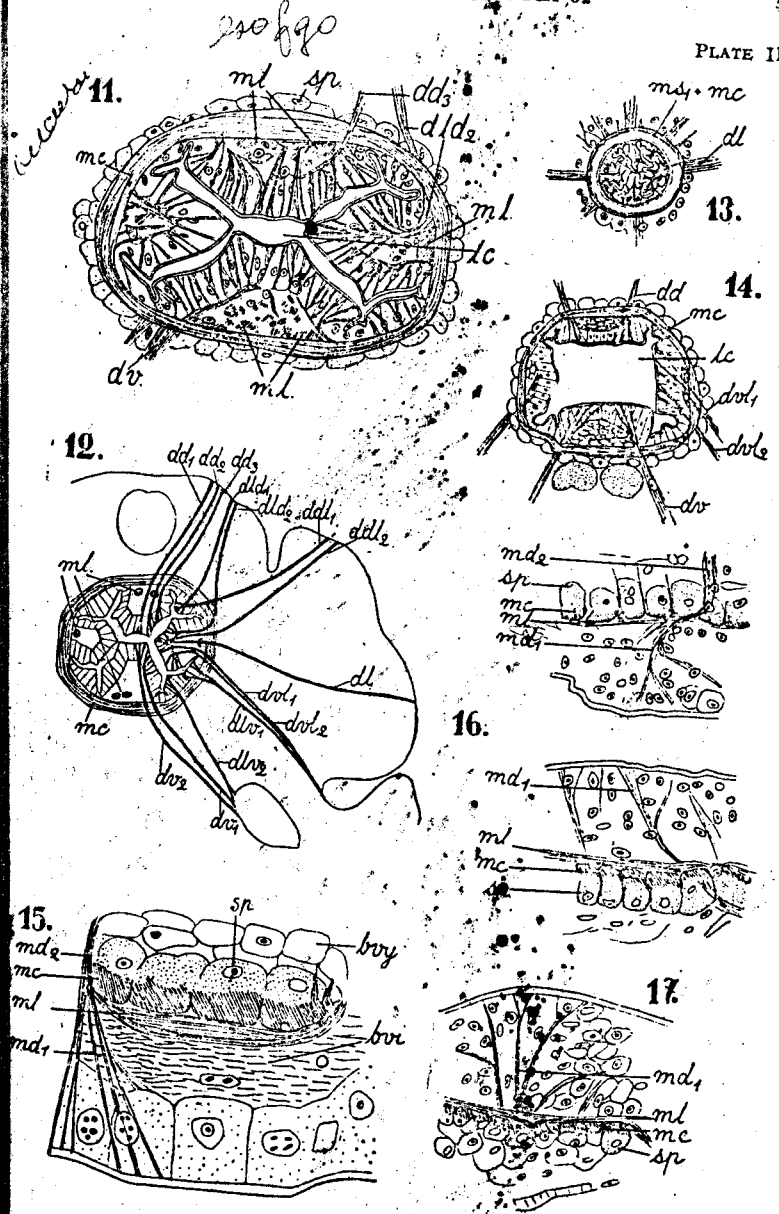
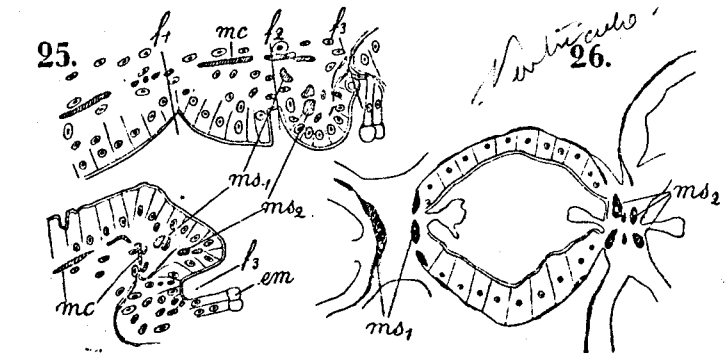
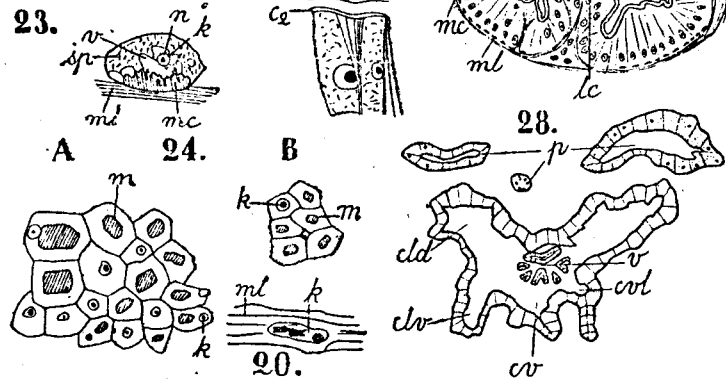
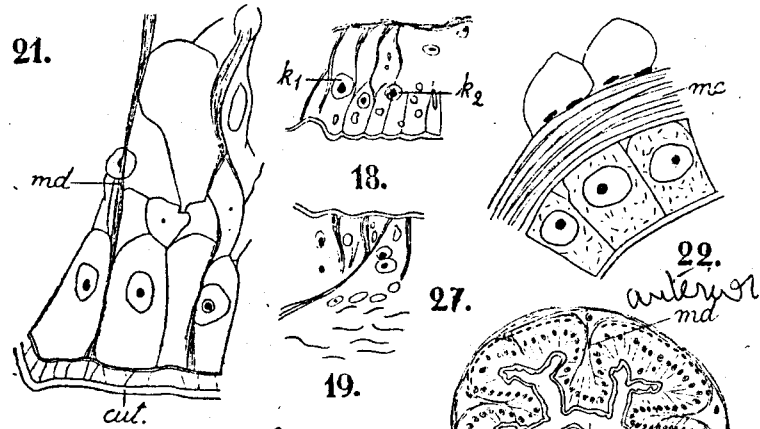


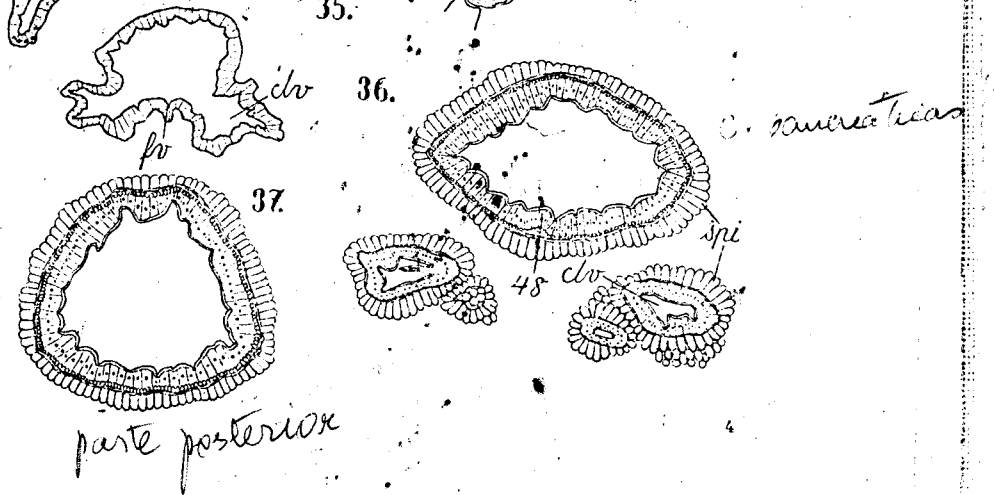
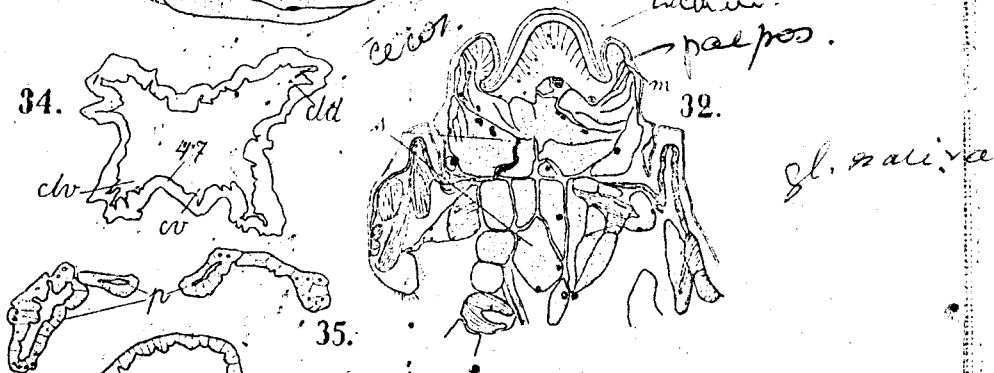
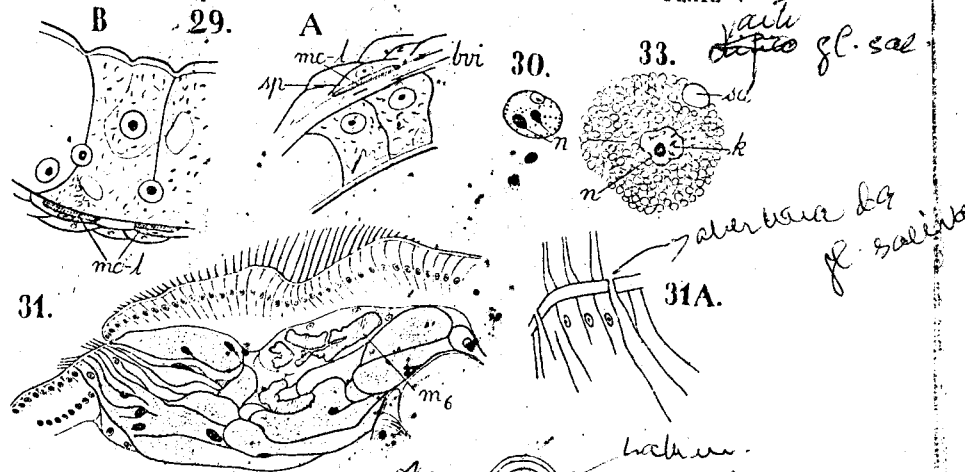
PLATE III



esofago



esofago e ventriculo = cardia



parte posterior

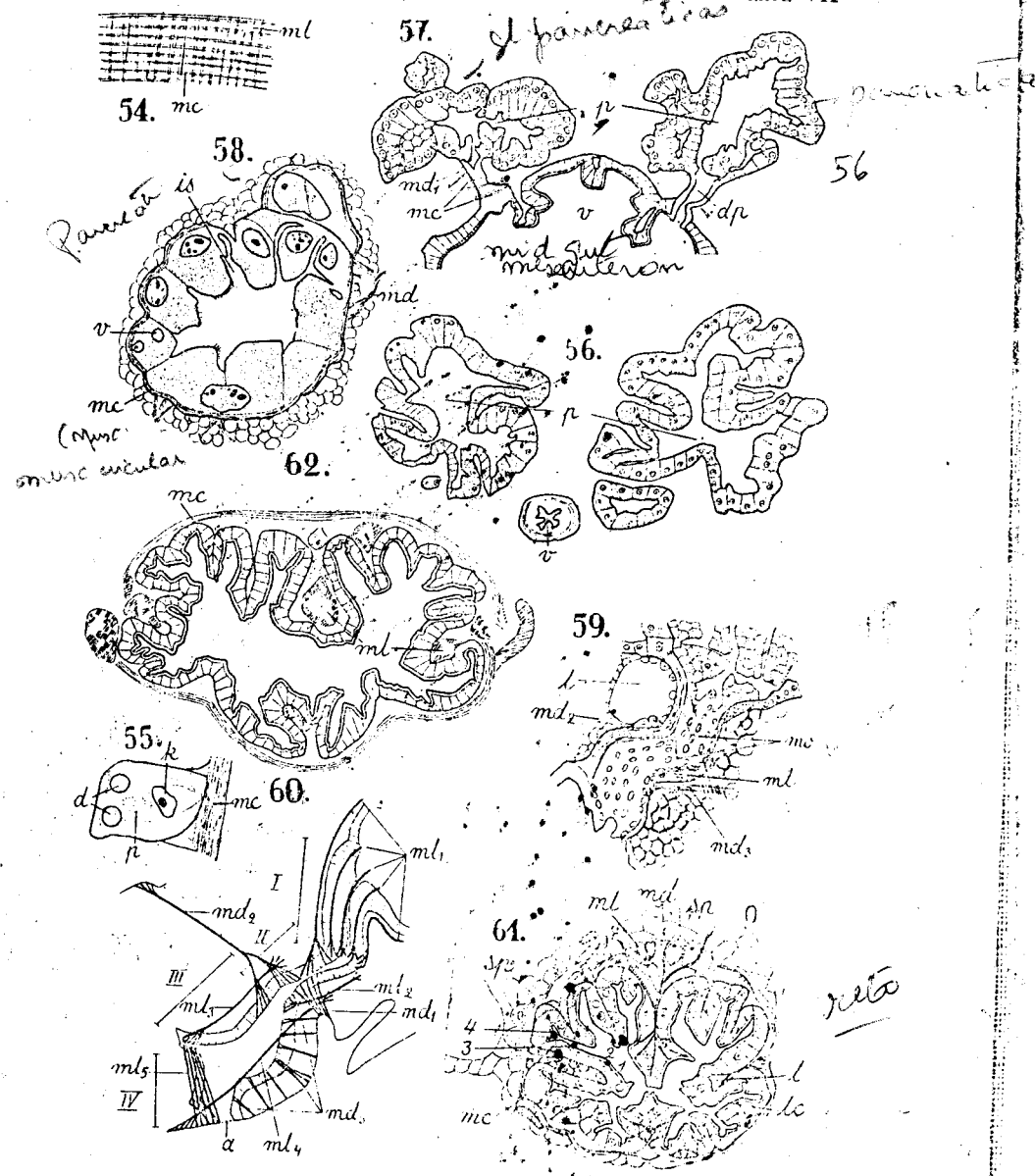
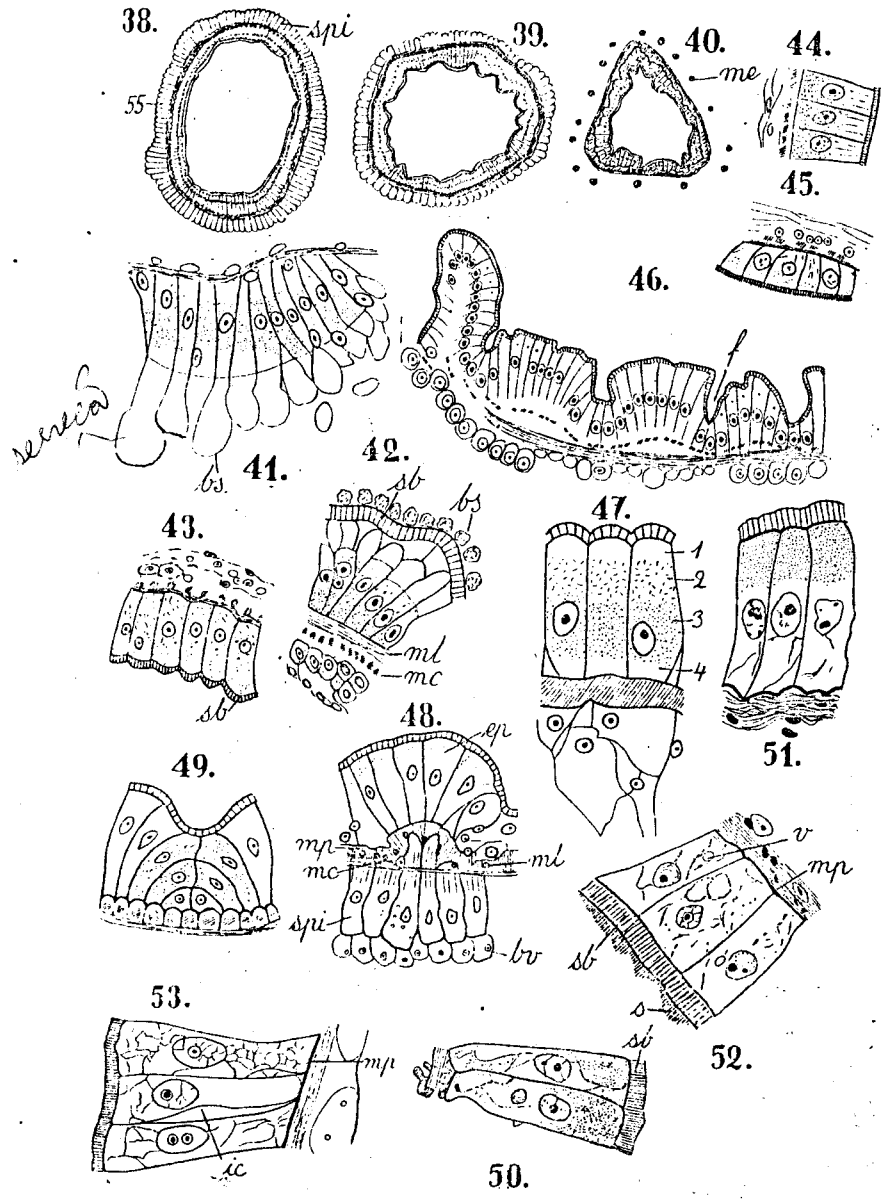
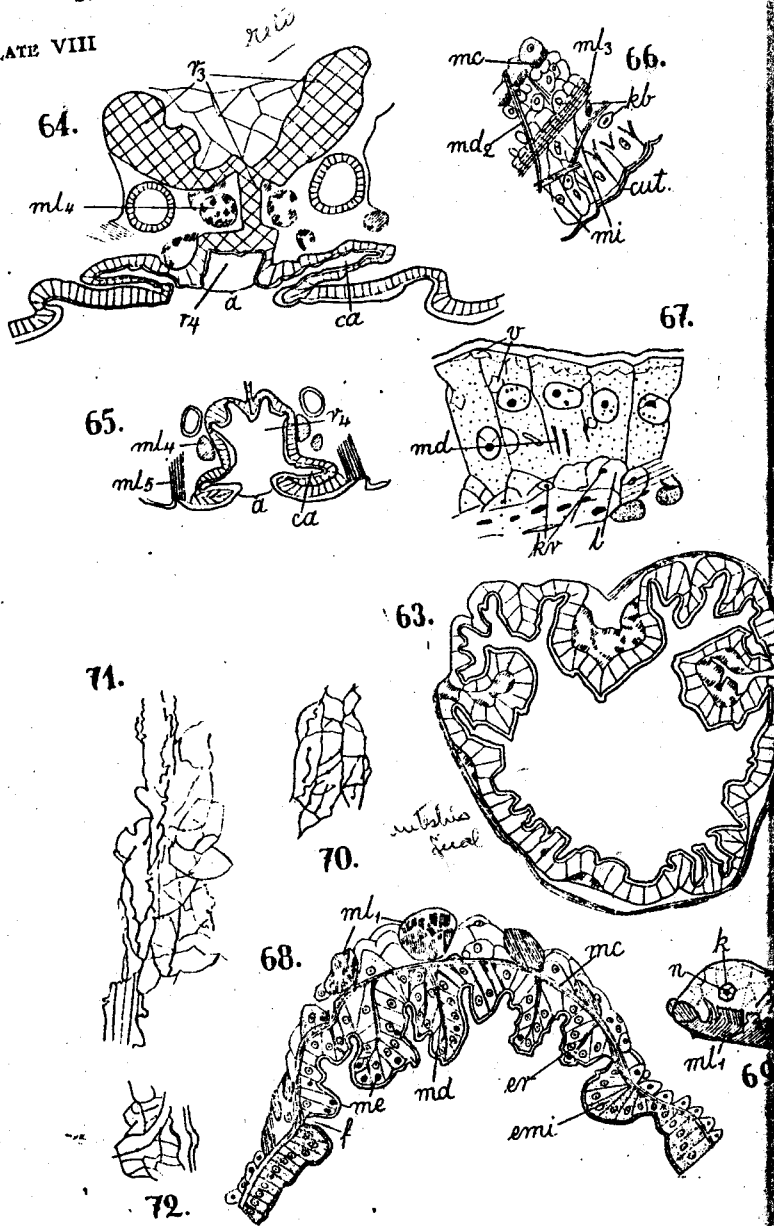


PLATE VIII



26. **Tor G. Karling:** Zur Morphologie und Systematik der Allococlea cuneata und Rhabdocoela lecitiphora (Turbellaria). Mit 20 Abbildungen im Text und 17 Tafeln. Helsingforsiae 1940. S. 1-260.
27. **Jorma Soveri:** Die Vogelfauna von Lammi, ihre regionale Verbreitung und Abhängigkeit von den ökologischen Faktoren. Mit 31 Tabellen, 21 Diagrammen und 52 Karten im Text sowie 4 Lichtbildbeilagen, 2 Kartenbeilagen und einer Diagrammbeilage. Helsingforsiae 1940. S. 1-175.
28. **T. H. Järvi:** Über den Maränenbestand im Pyhäjärvi (SW-Finnland). Mit 9 Tafeln, 6 Textfiguren und 1 Karte, sowie 24 Lichtbildern. Helsingforsiae 1940. S. 1-38.
29. **T. H. Järvi:** Sea-Trout in the Bothnian Bay (Salmo Trutta). With eight illustrations. Helsingforsiae 1940. P. 1-28.
30. **Elvi v. Pfaler-Collander:** Vergleichend-karyologische Untersuchungen an Lygaeiden. Mit 49 Abbildungen im Text und 2 Tafeln. With an English Summary. Helsingforsiae 1941. S. 1-119.
31. **Päiviö Kuusisto †:** Studien über die Ökologie und Tagesrhythmik von Phylloscopus trochilus-acredula (L.) mit besonderer Berücksichtigung der Brutbiologie. Helsingforsiae 1941. S. 1-120.
32. **T. H. Järvi:** Die Bestände der kleinen Maränen (Coregonus albula L.) und ihre Schwankungen. 1. Pyhäjärvi (Süd Karelien). Mit 13 Tafeln. Helsingforsiae 1942. S. 1-89.
33. **T. H. Järvi:** Die Bestände der kleinen Maränen (Coregonus albula L.) und ihre Schwankungen. 2. Ober- und Mittel-Keitele. Mit 12 Tafeln. Helsingforsiae 1942. S. 1-144.
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35. **Harry Federley:** Zur Zytologie einer semisterilen Population von Pygaea pigra. Mit 16 Abbildungen im Text. Helsingforsiae 1942. S. 1-21.
36. **Pontus Palmgren:** Die Spinnenfauna Finnlands. II. Pisauridae, Oxyopidae, Salticidae, Clubionidae, Anyphaenidae, Sparassidae, Ctenidae, Drassidae. Mit 115 Figuren, 2 Tabellen und 27 Karten. Helsingforsiae 1943. S. 1-112.
37. **Tor G. Karling:** Studien an Halammovortex nigrifrons (Karling) (Turbellaria Neorhabdocoela). Mit 7 Abbildungen im Text und 2 Tafeln. Helsingforsiae 1943. S. 1-23.
38. **Alex. Luther:** Untersuchungen an rhabdocoelen Turbellarien. IV. Über einige Repräsentanten der Familie Proxenetidae. Mit 6 Tafeln und 121 Abbildungen im Text. Helsingforsiae 1943. S. 1-95.
39. **Lars von Haartman und Göran Bergman:** Der Herbstzug an zwei Orten in Südfinnland und seine Abhängigkeit von äusseren Faktoren. Mit 1 Tabelle und 14 Diagrammen. Helsingforsiae 1943. S. 1-33.
40. **T. H. Järvi:** Zur Kenntnis der Coregonen-Formen Nord-Finnlands insbesondere des Kuusamo-Gebietes. Mit 28 Tafeln. Helsingforsiae 1943. S. 1-61.
41. **Håkan Lindberg:** Ökologisch-geographische Untersuchungen zur Insektenfauna der Felsenkümpel an den Küsten Finnlands. Mit 10 Karten, 14 Tabellen und 7 Abbildungen im Text sowie 4 Tafeln. Helsingforsiae 1944. S. 1-178.
42. **Martta Heinäjoki:** Die Opilionidenfauna Finnlands. Mit 29 Figuren, 2 Tabellen und 9 Karten. Helsingforsiae 1944. S. 1-26.

43. **Hilma Alarotu:** Untersuchungen über die an Fischen in Finnland monogenetischen Trematoden. Mit 17 Abbildungen im Text und 1 Tafel. Helsingforsiae 1944. S. 1—52.
44. **Lars von Haartman:** Zur Biologie der Wasser- und Ufervögel im Meer Südwest-Finlands. Mit 31 Tabellen, 12 Diagrammen, 12 Abbildungen und 1 Kartenbeilage. Helsingforsiae 1945. S. 1—77.
45. **Håkan Lindberg:** Die Biologie von *Pipunculus chlorionae* Frey. Einwirkung von dessen Parasitismus auf Chloriona-Arten. Mit 12 Abbildungen und 5 Tabellen. Helsingforsiae 1946. S. 1—50.
46. **Alex. Luthers:** Untersuchungen an rhabdocoelen Turbellarien. V. Einige Typhloplaniden. Mit 60 Abbildungen im Text. Helsingforsiae 1946. S. 1—56.
47. **Göran Bergman:** Der Steinwälder, *Arenaria i. interpres* (L.), in Beziehung zur Umwelt. Mit 7 Tabellen, 8 Diagrammen, 17 Figuren, 10 Tafeln und 14 Abbildungen sowie 6 Karten. Helsingforsiae 1947. S. 1—151.
48. **T. H. Järvi:** Über den Kleinmaränenbestand (*Coregonus albula* L.) in Keshjärvi (Südfinland). Mit 4 Tafeln. Helsingforsiae 1947. S. 1—15.
49. **Alex. Luthers:** Untersuchungen an rhabdocoelen Turbellarien. VI. Mollusken aus Finnland. Mit 62 Abbildungen im Text. Helsingforsiae 1947. S. 1—40.
50. **Tor G. Karling:** Studien über Kalyptorhynchien (Turbellaria). I. Die Placorhynchidae und Gnathorhynchidae. Mit 20 Abbildungen im Text und einer Tafel. Helsingforsiae 1947. S. 1—64.
51. **Enzio Reuter:** Index generalis seriei Acta Zoologica Fennica 1—50 (1947). Helsingforsiae 1948. S. I—VII+1—75.
52. **S. R. Törnävä:** The Alimentary Canal of *Balanus improvisus* Darwin. 8 plates (72 figures) and 1 textfigure. Helsingforsiae 1948. P. 1—5.