

# The Morphology of the Nudibranchiate Mollusc *Melibe* (syn. *Chioraera*) *leonina* (Gould)

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With Plates 27 to 37.

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## I. INTRODUCTION.

A CONSIDERABLE part of this work was done under the direction of Professor Trevor Kincaid, at the University of Washington (Seattle), 1914-15. It was continued at Columbia University, 1918-20, and at Woods Hole, 1919 (summer). Dr. T. C. Frye, the Director of the Puget Sound Biological Station at Friday Harbour, Washington, had some new material collected during the summer of 1919, and sent to me at Woods Hole. Upon this material, and the previous data together with new material collected at Friday Harbour, during the summer of 1921, this paper is concluded.

In three previous communications (1919, 1921) I described the method of feeding, the kind of food, method of swimming (1922), and the colour, of *Melibe leonina* (Gould) as well as the distribution of the family *Tethymelibidae*<sup>1</sup> Bergh (1890, 1892: 1039-43). I also made an extensive review of the literature on the nudibranchiate molluscs, particularly the *Cladohepatica*. Several misprints, relative to year, volume, and page, occurred in the literature. These have been corrected. I hope that the references as printed in my papers may be of help to other workers in this field on the molluscs.

<sup>1</sup> Attention should be called to the fact that the name *Tethys* as applied to a Nudibranch is incorrect. This was established in 1895. (Vide H. A. Pilsbry, "Classification and Phylogeny of Tectibranchiata", 'Manual of Conchology', 16: i-vii, 1-262, 74 plates.) The name *Tethys* was first given to a Tectibranch by Linnaeus. (Vide 'Systema Naturae', 10th Edition, 1758, p. 653.) Consequently the family name *Tethymelibidae* must be rejected from the nomenclature of Nudibranchiata. The Nudibranch '*Tethys*' has apparently no name of its own.



## II. ACKNOWLEDGEMENTS.

The writer wishes here to express sincere thanks to Professor Trevor Kincaid for helpful suggestions during the first period of this work ; to Dr. H. L. Osterud for collecting and fixing new material in 1916 ; to the Curator of Books and Literature, Dr. R. W. Tower, of the American Museum of Natural History, for unfailing kindness during the review of the literature ; and to the Director of the Puget Sound Biological Station, Dr. T. C. Frye, for every co-operation and assistance while at the station, in the summer of 1921.

## III. ON THE STATUS OF CHIORAERA GOULD.

Bergh's description of various species of *Melibe* (1875*b*, *Melibe capucina*, *M. rangii*; 1879*a*, *M. vexillifera*; 1884, *M. papillosa*; 1888, 1890*b*, *M. ocellata*; 1902, *M. bucephala*; and 1908, *M. rosea* Rang), emphasizes the following as Melibeian characteristics: 'Bulbus pharyngeus cum mandibulis ut in Phylliroidis; margo masticatorius mandibulae fortiter dentatus' (1875*b*: 362). Perhaps the only exception to this may be found in the species collected at the mouth of the Columbia River, in the State of Washington (1904), in which case the author is not sure of the mandibles. He says: 'Bulbus pharyngeus lingua destitutus. . . . Die Mundröhre und der Schlundkopf schienen sich wie sonst bei den Meliben zu verhalten. . . .' I have previously called attention (1919, 1921) to the possibility that this species may be the same as the one described by Gould (1852) from the Puget Sound region. Not all *Melibes* have the same characteristics, as indicated by Bergh; this is also shown by Alder and Hancock (1864), and substantiated by Eliot (1902). The generic characteristics as enunciated by Bergh (1875*b*) do not necessarily hold, even though this author thinks that Hancock's (Alder and Hancock, 1864) description is incorrect. Bergh (1875*b*: 363, 364) says: 'Es kann kaum bezweifelt werden, dass die von Hancock untersuchte Form mit der von mir besprochenen congenerisch ist. Es werden sich daher die bei



dem englischen Verf. vorkommenden, von den untenstehenden abweichenden anatomischen Angaben wahrscheinlich als unrichtig erweisen . . . Besonders wird solches wohl der Fall sein, wo Hancock den Anfang des Verdauungskanals bespricht : "The buccal organ is provided with neither tongue, jaws nor collar ; it is not by any means very distinctly marked, formed as it were by a mere enlargement of the oesophagus, and having little or no increase of muscular power." "

But Eliot (1902) verifies Hancock's claim when he writes : 'I also found Alder and Hancock's description of the internal anatomy correct, particularly as regards the absence of jaws. . . . Mr. Crossland and I have . . . dissected several specimens of *Melibe fimbriata*, and in all failed to detect any trace of jaws.'

Gould's *Chioraera leonina* (1852) corresponds very closely in the general anatomy to that of *Melibe fimbriata* Alder and Hancock, (1864) ; this is also true in regard to the species discovered by Rang (1829) and subsequently described by Bergh (1863, 1871, 1875 *b*, 1879 *a* 1884, 1888, 1890 *b*, 1902, 1904, and 1908). The only difference is on the point in regard to mandibles. Some authors, Rang, Gould, Pease, Cooper, and Fewkes, do not touch on this point, and for that reason one cannot tell whether the particular specimens with which they dealt actually had such organs. With the exception of the mandibles, all the generic characteristics as set forth by the earliest writers on this type of the molluscs agree (Rang, 1829 ; Gould, 1852 ; Pease, 1860 ; Cooper, 1863 ; Alder and Hancock, 1864 ; de Filippi, 1867 ; Tapparone-Canefri, 1876 ; and Fewkes, 1889 ; as well as the numerous descriptions of Bergh, 1863-1908). The discovery of the genus *Melibe* by Rang (1829) seems to have been unknown to Gould (1852), who created a new genus (*Chioraera*) for this type. Cooper (1863) and Fewkes (1889) employed the nomenclature of Gould. The generic characteristics as enunciated by the original author for *Melibe*, Rang (1829), are practically identical with those set forth by Gould twenty-three years later for *Chioraera*. Tryon, Jr. (1883 : 328), without



stating a reason, classifies *Chioraera* as a synonym of *Melibe*. Owing to the fact that Gould and also Cooper were ignorant of the actual discovery of the genus *Melibe*, the name *Chioraera* was invented by Gould and subsequently used by Cooper. The name is, in fact, a mythical term that is related in meaning to the former. Bergh (1904), describing a species from the territory of Gould, Cooper, and Fewkes, does not hesitate to employ the nomenclature of Rang (1829), so similar is this form to the *Melibes* from other parts of the world. No other author, except Bergh, gives mandibles as a generic characteristic. That is, this feature is not observed by Rang (1829), Gould (1852), Pease (1860), Cooper (1863), de Filippi (1867), Tapparone-Canefri (1876), or Fewkes (1889). Although *Melibe* Rang (1829), and *Chioraera* Gould (1852), differ somewhat in shape, they are very similar in most other respects. Both have a series of papillae on each side dorsolaterally; a large hood, cowl, or veil; a pair of tentacles (the so-called rhinophoria) on the veil; the veil fringed with at least two rows of cirrhi; and a narrow grooved foot which is blunt in front and pointed behind; the head distinctly separated from the body, and in each case it is very large; the gizzard is lined with a 'keratinized' secretion which protects the delicate epithelium, the so-called stomach-plates of Alder and Hancock, or 'Magenzähne' of Bergh; these two types are carnivorous; both are pelagic; and both are distinctly cladohepatic. Therefore the species of the American west coast which falls within this description must be the same genus, i.e. *Melibe*. The effort, therefore, to build further on the nomenclature of Gould, as was done by Cooper (1863), Fewkes (1889), and more recently by Heath (1917), seems to me to be indefensible. And, owing to the fact that the genus *Melibe* may either possess mandibles (Bergh, 1875*b*) or not, (Alder and Hancock, 1864; de Filippi, 1867; Tapparone-Canefri, 1876; Eliot, 1902), the generic description may be modified to read, in part, *Bulbus pharyngeus aut cum mandibulis aut sine mandibulis; radula et lingua destitutus*. None of the authors (Gould, Cooper, Fewkes, Heath) who has not



employed the nomenclature of Rang for this type, has described mandibles, and O'Donoghue (1921) states: 'The radula and jaws or any representatives of such structures are entirely absent.' Although O'Donoghue (1921) also employed the nomenclature of Gould for the genus *Melibe*, in a subsequent letter to me he states: 'I have quite given up *Chioraera* as a name.' In recent publications by this author (1922: 125; 1922*a*: 165) and by O'Donoghue (1922: 134) it is suggested in a foot-note that *Melibe leonina* would be a 'better' name than *Chioraera leonina*. Neither Cooper, Fewkes, nor Heath made an intensive study of the type; this is evident from their descriptions. A careful study of Gould's *Chioraera* has brought out sufficient reason to merge it with *Melibe* as indicated by Tryon, Jr. (1883), Bergh (1908), and Agersborg (1921*a*). The structures and the general characteristics of *Chioraera leonina* Gould, correspond in many details with those of the *Melibes* of Rang, Bergh, et al. For this reason I have adopted the name as indicated by Tryon, Jr., and also suggested by my friend, Professor Trevor Kincaid, viz. *Melibe leonina* (Gould) as indicated in the title of this work. (Vide Agersborg, 1921*a*, 1922*a*, 1923.)

#### IV. MELIBE LEONINA (SYN. CHIORAERA LEONINA GOULD).

The type of the genus *Melibe* was discovered at the Cape of Good Hope and was described by Rang in 1829. Since that time a number of species (vide supra) have been added by various authors.<sup>1</sup> In 1852 Gould described *Melibe* (s. *Chioraera*) *leonina* from Puget Sound, founding for it the genus *Chioraera*, now merged with *Melibe*. In 1914 I observed this animal at the Puget Sound Biological Station (vide Agersborg, 1916, 1919, 1921, 1921*a*, 1922, 1922*a*, 1923).

<sup>1</sup> My designation of *Melibaea australis* Angas (1864), as *Melibe australis* (Agersborg, 1919, 1921) is not justified, as indicated by the description of Angas. His description seems to fit the genus *Doto* (vide Kjerschow Agersborg, 1921).



Since the descriptions of Gould and also of Cooper and Fewkes, each of whom described a species from the American west coast, are rather incomplete, and since the anatomy had not been worked out, I felt that there was sufficient reason to engage in such an investigation upon this very interesting animal. As a result of this work I have succeeded in bringing to light some points of considerable zoological interest.

The body-substance of *Melibe leonina* appears as a mass of brown jelly, when the animal is alive or freshly caught: in the aquarium it turns practically transparent; when it has been preserved in alcohol or formaldehyde it gradually loses its brown colour, and becomes almost white. O'Donoghue (1922: 125) says: 'Hundreds of individuals of this species have been seen, but there is practically no variation in colour. In some forms the yellowish or whitish-grey jelly-like body may be tinged with pale brown but hardly sufficient to notice.' However, while this is really the general colour of *Melibe leonina*, I have also seen it deep green in colour (vide Agersborg, 1922a: 439-42). Gould (1852), in his original description of this species, says: 'Body limaciform, smooth and of a pearly and whitish colour, finely reticulate with orange.' The colour of the animal is caused by an extensive ramification of the brownish-coloured liver in the body-wall (Pls. 1 and 30, figs. 1, 2, 4, 7, 18-23, 25); a ramification which extends to the hood, the tentacles, the papillae, and to the ectoderm of the rest of the body. The colour of nudibranchs has sometimes been attributed to their food, Hecht (1895), Eliot (1910); but Alder and Hancock (1845) ascribe the colour to the liver and the gonads. Bergh (1879a: 163, 165), describing *Melibe vexillifera*, says in fact: 'Durch die dünnen Körperwände schimmerten, besonders an den Seiten, die denselben angehörenden, dicht an einander liegenden, schmalen, weisslichen, parallellaufenden Längsfasern hindurch; ferner undeutlich die Eingeweide, besonders Theile der Leber und die vordere Genitalmasse; . . . Die Leber wie bei anderen Meliben eine lose, gelblichweisse Masse, welche vorne an den Magen reicht, hinten sich bis an das Ende der Eingeweidehöhle



erstreckt.' From this one might infer that the author was describing the species from preserved material; for the liver is brown in colour as a rule, and from it *Melibe* obtains most of its colour. The internal organs, however, may be partly seen through the body-wall in living specimens of *M. leonina* (Pl. 27, fig. 2). Gould describes the brownish ramifications of the papillae as vascular; these, however, are branches of the liver. He also says that the tentacles are 'destitute of venation', referring no doubt to the hepatic branches which are very abundant everywhere. The hepatic branches are less abundant in the tentacles but they are not wholly absent.

### 1. The Head or Veil.

The head of *M. leonina* is very prominent because of its exceedingly large veil or hood. This is modified by two rows of cirrhi (Pls. 27, 28, figs. 1, 3, 10, 17) which fringe its edge, and by a pair of ear-like tentacles (Pl. 27, figs. 1, 2, 3). The cirrhi of the outer row are much larger and far less in number than those of the inner row. The average, taken from a number of specimens, was 48 in the outer row, and 123 in the inner row, or 2.56 small cirrhi to 1 large. The outer row does not extend entirely around the rim of the hood, but, in an animal about 6 centimetres long, terminates about 1 centimetre from the mid-ventral line. The inner row extends all around the periphery of the hood, although the last three cirrhi, on each side of the mid-ventral, are rudimentary (Pl. 28, fig. 17, *Icr*, *Icr*<sup>1</sup>). A large veil or hood, except in *M. ocellata* Bergh (1890*b*), is a common thing for *Melibe* Gould (1852), Alder and Hancock (1865), Bergh (1875*b*, 1902, 1904), Eliot (1902). In *M. bucephala*, Bergh (1902), 'The edge of the head is rather thin above and almost smooth; its outer parts, however, are thick, inwardly somewhat refolded or convoluted, and provided with several, mostly perhaps about five, close-set series of cirrhi, which are displaced among each other; these cirrhi are conical, somewhat constricted at the base, the innermost ones are the larger, toward the outside they decrease



regularly in length.' Gould (1852), describing *M. leonina*, says: 'The mouth is inferior and surrounded by a series of long cirrhi, each of which has an independent motion.'

### (1) The Cirrhi.

The cirrhi (Pl. 27, figs. 1, *C*, 10, *Ic*, *Oc*, Pl. 28, 17, *Irc*, *Orc*) have an inner median axis (Pl. 28, figs. 11, 12, *Cg*, 13, *Cga*) from which radiating fibres pass to the periphery (*Rf*). The inner axis seems to consist of a series of nerve ganglia from which fibres radiate to the periphery of the cone-like cirrhus, ending in the basal layer of the epidermis (Pl. 28, fig. 11, *Oe*, *Ie*). In other words, a cirrhus is a conic structure having an epithelial wall resting upon a delicate connective-tissue framework, with an inner axis which passes from the apex to the base of the cirrhus, and from this axis fibres radiate to the epithelial walls of the cone. These fibres have the resemblance of nerve-fibres, particularly in their relation to the cells in the ganglionic axis and to the epithelium of the epidermis. In one of the angles, formed by the radiating fibres at the axis, is a large bladder-like structure around which the fibres pass, and at the periphery are placed large and small cells (Pl. 28, fig. 13, *Pc*) the inner part being reticular in structure (*Ir*) and containing apparently no cells, or a few only (Pl. 28, figs. 11, 12, 13, *Ir*). The cirrhi are probably tactile or gustatory in function. Something to that effect was demonstrated experimentally (Agersborg, 1922*a*: p. 441). Sedgwick (1898: p. 366) writing on the gasteropods in general and opisthobranchs in particular says: 'Tactile organs are represented by the tentacles, the edges of the lips, which are often folded (labial palps), the tentacular and lobe-like prolongations which are found here and there on the head, mouth, and foot.' It should be remembered that there are sometimes two pairs of tentacles in nudibranchs; the anterior pair being the one referred to here; the posterior is the so-called rhinophoria of many authors, which, however, do not seem to be olfactory in function (Agersborg, 1922*a*: 423-44).



## (2) The Dorsal Tentacles or 'Rhinophores'.

On the outside of the veil, in *M. leonina*, is a pair of tentacles, supposed to be equal to the posterior pair in, e.g., *Aeolidia* Cuvier (1798). According to the original description of the genus *Melibe* by Rang (1829) the tentacles are 'au nombre de deux, situés à la base du voile, très allongés, coniques, terminés par une petite capsule, de laquelle sort un organe conique et rétractile'; Gould (1852), in his description of *Chioraera leonina* (s. *Melibe leonina*), points out: '... tentaculæ cephalicæ foliatae, retractiles;'; and Pease (1860) for *M. pilosa* says: 'Tentacles on the posterior portion of the veil rather remote, small, ovate, closely and transversely lamellated and retractile into long trumpet-shaped sheaths, which are furnished with laciniated appendages.' Again, Tapparone-Canefri (1876) for *Jacunia* (s. *Melibe*) *papillosa* de Filippi, states: 'Tentacula (Rhynophoria) laminata, tenuia, apice obtusiuscula, retractilia, e vagina caliciformi angusta vix proeminentia.' Cooper (1863) and Fewkes (1889) are content with the description of Gould; neither of them mentions tentacles. Alder and Hancock (1864) refer to these organs as dorsal tentacles. The largest part of the tentacles in *Melibe* is the tentacular stalks; they are wedge-shaped bodies (Pl. 27, figs. 3, 8) somewhat rounded at their base. The wedge is like a broad axe, the edge of which is a little curved. They are arranged at right angles to each other, and this angle would intersect posterior to their base in the mid-dorsal line of the hood. Along the edge of the curved wedges are slits, in one of which, on the inner part of the curve, i.e. not on the apical part of the tentacle—except when it is expanded—is a small organ (Pl. 27, fig. 8, *Rh*), the real tentacle, that may be retracted below the surface of the wedge-shaped tentacular stalks (vide Agersborg, 1923, figs. 4, 5, *pa*). Gould, in describing these, says: 'On the top of the head are two foliate expansions destitute of venations, which answer to the true tentacles; on their anterior edge is an opaque whitish papilla, presenting something of a spiral or lamellar



structure; they are sometimes wholly retracted within a permanent sheath.' At the base of these tentacular organs, when they are retracted (Pl. 27, fig. 8 and Pl. 29, fig. 15, *K*), is a small knob. In sections (Pl. 29, fig. 15) the lamellar structure is indicated by certain lobations along the outer part (*S*). The knob (*K*) seems to be made up of a mass of large and small nerve-cells (Pl. 29, fig. 16), which fibres connect with similar cells distal in position to the former (*Nc*, *Nes*, *Nfb*, *Nfi*), and finally by innervation in the epithelium of the lamellar external parts of the organ (*Nfp*). From the distal border of the knob-like ganglion, fibres communicate with the base of the tentacle; these fibres are not made up of nerve-fibres only but also of muscle-fibres (*Nmf*). This is known from their staining reaction and also from the fact that some of these fibres communicate with fibres within the organ which are decidedly nervous, while the other fibres terminate on the organ. The muscle-fibres help to retract the organ below the surface of the tentacle, that is, to withdraw the tentacle within its stalk, which in that case serves as a sheath; the nerve-fibres to convey stimuli. There is no permanent sheath, as indicated by Gould, save that part of the tentacular stalk which surrounds the organ, and acts as a sheath when the tentacle is retracted.

The function of these tentacular organs in nudibranchs according to various authors is olfactory. Thus, Alder and Hancock (1845: 19) say: 'The dorsal tentacles are the organs of smell, and, judging from their development, this sense must be more acute in most of the nudibranchs than it is in many other molluscs, with the exception, perhaps, of *Nautilus*.' Hancock and Embleton (1852: 242), discussing a *Doris*, say: 'The dorsal tentacles, which have never been observed to be used as tactile organs, we believe to be the seat of the sense of smell; and this belief is strengthened when we reflect that these sense organs are most highly developed and minutely laminated; that they are plentifully supplied with nerves from the ganglia placed in front of all the rest of the cerebral masses; that they are externally covered with



vibratile cilia, and so placed on the head as easily to receive impression from any odorous particles that may be mingled with the circumambient water.' Likewise, Jeffreys (1869) claims olfaction for the dorsal tentacles, but he says: '... olfaction in these animals probably is not so much to assist in the discovery of alimentary matters, as to give warning of the unhealthy state of the surrounding medium, arising from putrescence or other causes. . . . and its outer surface, in all the nudibranchs, is provided with vibratile cilia.' The tentacles in *M. leonina*, however, are not ciliated. Bergh adopts the term 'rhinophoria' for the dorsal tentacles, not only indicating in that way the function, but he claims, in fact olfaction to be their function. Later writers, Lang (1896: 48, 103), Sedgwick (1898: 366), seem to agree on this point. Copeland (1918: 177-227) demonstrated experimentally that the monotocardiate prosobranchs *Alectrion obsoleta* and *Busycon canaliculatum* respond to stimulations by dilute food extracts and materials emanating from distant food; he thinks that the snails do not find food by coming upon it accidentally, but are directed to it by movements brought about through stimulations of the olfactory organs with odorous substances conducted to the receptor in varying concentrations by the moving siphon. By means of an olfactory apparatus consisting of a single organ of smell associated with a siphon terminating in a shifting 'nostril', for sampling the surrounding water and its contents, the snail is as successfully directed toward distant food as an animal which, like the dogfish, possesses paired olfactory organs and fixed nostrils. After the osphradium in *Busycon* was destroyed the snail failed to respond to dilute food materials, but a year later, when the lamellae of the organ were partly regenerated, the scenting responses returned. The osphradium, therefore, is an olfactory organ. This author claims further that taste in the snail (*Busycon*) is a diffused sense as compared with olfaction, and that a large portion of the surface of the snail possesses this sense. But Arey (1918: 531) distrusts the capability of snails to analyse chemical stimuli as discrete sensations, and thinks that it would be safer to avoid referring in their case



to a sense of taste and smell at all, or even to a common chemical sense, but rather to designate the particular senses in question a general chemical sense. Moreover, Arey working experimentally on several nudibranchs, *Chromodoris zebra*, *Facelina goslingi*, *Elysia crispa*, and *Fiona marina*, found that there was nothing in the tests which he applied to these animals that connected the rhinophores with olfaction, with the exception perhaps of *Facelina* whose non-retractile rhinophores react by a lashing withdrawal and more vigorously than the oral tentacles when stimulated by oil of pennyroyal, carbon bisulphide, and anilin oil. All these forms, however, responded to tactile stimuli. Like Copeland, he found that the general body-surface also responded to chemical stimuli. Crozier and Arey (1919 : 301) elaborated on this by stating that in *Chromodoris* the rhinophores and the oral tentacles are in a general way the parts most sensitive to chemical stimuli. Again, as regards the rhinophores, these authors (1919 : 278-81) found that while *Chromodoris zebra* may creep in an entirely normal fashion after the rhinophores have been removed, it loses its power of orientation to the water current. In other words, these authors claim that to currents of adequate velocity the nudibranchs are negatively rheotropic and that the rhinophores are the prime receptive organs for this kind of reaction. However, as I have pointed out elsewhere (Agersborg, 1922*a* : 432, 439), the dorsal tentacles (rhinophores) of *Hermisenda opalescens* (Cooper),<sup>1</sup> do not seem to have a rheotropic function, because specimens with one or both of the dorsal tentacles removed oriented as easily and moved against the current as did the normal individuals. It did not seem to make any difference whether the dorsal tentacles were present or not. At any rate, the rhinophores or dorsal tentacles do not seem to be 'rheotropic' in *Hermisenda*. Copeland, Arey, and Crozier found that the types with which they worked were more sensitive around the anterior than elsewhere on the body. Such a specialization of the integuments is also the case

<sup>1</sup> The correct name is *Hermisenda crassicornis* Eschscholtz. Vide C. H. O'Donoghue (1922), 'Nautilus', 35 : 74-7.



in *Hermisenda*, *Dendronotus*, and *Melibe* (Agersborg, 1922*a*: pp. 423-44). Indeed, as recently brought to light by Gross (1921), on *Nereis virens* Sars, the general integuments of this organism are sensitive to chemical stimulation with a localization or concentration of the chemical sense in the palps and tentacles, a circumstance correlated with the rich innervation of these appendages and the relation of their nerves to the brain. However, I have not yet found any specialized receptors either in the dorsal tentacles or in the cirrhi of nudibranchs. Their function, therefore, as far as the nudibranchs are concerned, may not be so definite as previously indicated. For this reason, and because of the facts brought to light by experimental evidence (Copeland, 1918; Arey, 1918; Arey and Crozier, 1919; Agersborg, 1922*a*), I have used the original name *tentacles*, as employed by Alder and Hancock (1845, 1864), Hancock and Embleton (1848), and Gould (1852), rather than the suggestive 'rhizophore' as adopted by Bergh and freely used by subsequent writers. For, although the tentacles of the hood are highly specialized as indicated by Alder and Hancock, Hancock and Embleton, and by my drawings (Pl. 27, fig. 8, Pl. 29, figs. 15 and 16), it is now very doubtful whether their function is olfactory *per se*, or even slightly so.

The remainder of the hood is apparently smooth, but upon close examination it is found to be covered with tubercles, a feature so common to the ectoderm all over the body of *Melibe leonina*; these tubercles are macroscopic in *M. fimbriata* Alder and Hancock (1864), Eliot (1902). The ventral side of the cowl (Pl. 27, fig. 1, Pl. 29, fig. 17) is concave in *M. leonina*; muscle-fibres, radiating from the muscles of the neck, support the veil. In the middle of the concave area between the bases of the tentacles (Pl. 29, fig. 17, *R*) is a marked depression (*Mdp*). The ventral side of the cowl (Pl. 27, fig. 6, *En*) is tuberculate like the external side, but it has no odoriferous glands (Pl. 27, fig. 4, *Oo*, Pl. 30, fig. 25, *Og*): to be discussed below. The head is set off distinctly from the body by a neck (Pl. 27, figs. 2, 3).



## 2. The Papillae or Epinotidia.

Among the Cladohepatica, where the papillae are mostly foliaceous or lobate structures, the denomination of papillae is preferable to the term cerata, branchiae, or gills. Many English authors have adopted this term: Hancock and Embleton (1848), Jeffrey (1869), Gamble (1892), et al. Others use a different nomenclature: Alder and Hancock (1845), branchial papillae; Parona (1891), Viguiier (1898), dorsal appendages; Parker and Haswell (1910), secondary branchiae; Lang (1898), dorsal respiratory appendages (cerata); and still others, Herman and Clubb (1892), Sedgwick (1898), Hertwig (1912), Arnold (1916), Pratt (1916), use the term cerata for the cladohepatic nudibranchs, and branchiae for the Holohepatica. The following authors, dealing with Melibe in each case, designate the papillae as follows: Rang (the founder for the genus) (1829), branchiae; Gould (1852) (*Chioraera* s. *Melibe*), foliaceous branchial expansions; Pease (1860), tuberculated lobes; Cooper (1863), branchiae; Tapparone-Canefri (1876), branchial lobes; Fewkes (1889) (*Chioraea leontina* s. *Chioraera leonina*, *Melibe*), branchial appendages; Bergh (1908), epinotidia; Heath (1917) (*Chioraera dalli* s. *Melibe leonina*), lappets; and O'Donoghue (1921) (*Chioraera* s. *Melibe*), branchial cerata. The last-named author employs the term cerata for the following cladohepatic genera: *Dendronotus*, *Aeolidia*, *Coryphella*, *Hermisenda*, and *Doto*; but he applies the word branchiae to the Holohepatica. This is in keeping with the usage of many authors (vide supra). Boas (1916, 1920) employs the term gills for both the Aeolidiidae and the Dorididae, while Bergh (1879c: 73) says that he uses the term papillae for the Aeolidiidae partly because it is a Linnean term, partly because the organs do not exclusively serve for respiration, which is partaken of by the whole surface of the skin, that over the papillae as well as elsewhere, among all the Nudibranchiata. This fact was pointed out earlier by



Hancock and Embleton (1848: 103), who wrote: 'The function of respiration we believe to be performed by the whole surface of the skin, including the papillae, the skin of the back and of the sides between the papillae, and the entire surface of the latter organs. . . .' It may, therefore, be quite incorrect to designate these 'branchial lobes' *cerata*; moreover, this term stands nearer *ctenidium* or true gill in meaning, and on that account, and for the reason stated by Bergh, and the facts recorded by Hancock and Embleton, papillae may be the most appropriate term. The Tethymelibidae being cladohepatic nudibranchs, of course, come under this terminology. Bergh also uses the term papillae for the Tethymelibidae, and is the most consistent writer in this as well as in other respects relative to the nomenclature he employs.

*Melibe leonina* has six pairs of papillae, alternating in position (Pl. 27, figs. 1, 3). They appear smooth to the naked eye, but fundamentally they are tufted or fimbriated as in *M. fimbriata* Alder and Hancock, *M. bucephala* Bergh, and *Tethys leporina* Linnaeus, although in *M. leonina* (Gould) the fimbriated condition of the papillae is hardly distinguishable. The first pair is located dorsad and a little posterior to the genital pores, and approximately in line with the hepatic junction to the stomach. The arrangement, the size, shape, and structure of the papillae may be seen in Pl. 27, figs. 1, 3, and Pl. 30, figs. 18-25 respectively. Microscopically, the papillae show two principal morphological constituents, viz. (1) terminating branches of the liver (the brownish vascular ramifications of Gould), and (2) smooth muscle-fibres; but also vascular spaces (Pl. 30, fig. 25, *Osp*), odoriferous glands (*Og*), and a tubercular surface (*Tbr*). But the papillae are, however, subject to variation in their structure, depending on the age and the position of the papilla. The two anterior pairs (Pl. 30, figs. 18-21) are far more profusely supplied with hepatic diverticula and muscle-fibres than are the remaining pairs (Pl. 30, figs. 22-4). The last pair does not seem to have any appreciable amount of muscle-fibres or liver-branches.



The muscles ramifying in the papillae form a sort of supporting wall; underlying this are the hepatic branches (Pl. , fig. 25, *Cshb*), with many transparent spaces between (*Osp*). On the outside of the muscle-wall, just beneath the ectoderm, are odoriferous glands (*Og*). The size of the papillae decreases gradually from the anterior to the posterior pair, the last pair being very small, and its hepatic as well as muscular contents are reduced accordingly. Regenerating pairs of the anterior papillae show a great number of hepatic branches and muscle-fibres; this is a striking contrast to old posterior papillae which apparently have no muscle-fibres and no hepatic diverticula. It has been observed quite frequently, by different authors, that the papillae of *Aeolidia* when cast off swim through the water like worms, propelled by the vibratile cilia, and occasionally by the spasmodic action of the muscles (Jeffrey, 1869). I have myself kept papillae of *Aeolidia*, at Woods Hole, and of *Hermisenda*, at Friday Harbour, alive in glass dishes for weeks at a time, the papillae being in constant motion, swimming in a circle owing to ciliary action on their curved surface. This phenomenon is not so extraordinary as it seems. It is found in other invertebrates (*Planaria*, *Echinoderms*, &c.). Gamble (1892) reports that the papillae of *Lomanotus* show remarkable co-ordinative movements when they are touched gently. Autotomy and regeneration of the dorsal appendices, according to Parona (1891), is a common occurrence among *Tethys* and *Aeolidia*. Pease (1860), referring to *M. pilosa*, says: 'When slightly disturbed they would cast off one or all of their lobes . . . : they may be consequently reproduced, after being cast off.' This is also true for *M. leonina*, for it frequently throws off some or all of its papillae, and yet I have kept specimens of this species for a number of days without autotomy taking place; I have also kept preserved specimens for years without the papillae having dropped off, even though they were subjected to considerable handling (see Pl. 27, figs. 1, 2, 3). Lang (1896) also records the fact that if the papillae fall off they are regenerated. It is believed that the papillae serve as organs



of respiration, that is, they are at least partly respiratory in function; for this purpose large intercellular sinuses are present which communicate with the heart through the efferent branchial veins (Pl. 30, figs. 25, *Osp*, 54, *Aur*). Such sinuses, however, are not present in the papillae only.

### 3. The Foot.

The foot (Pl. 27, fig. 1, Pl. 28, fig. 9) extends a little beyond the trunk both anteriorly and posteriorly. Its general form is like an inverted flat-bottom dory, with the anterior end wider than the posterior, curved, and extended forward about 1 cm. from its base, the so-called keel. The posterior end, also curved but narrower than the front, projects about 1.5 cm. from the base in an adult. The edges bend considerably outward, making the width from rim to rim about twice as wide as the base. Between the edges, on the ventral side, is a depression so deep that the comparison with a dory is quite fitting. This groove is highly tuberculate and ciliated (Pl. 30, figs. 26, 27, *Cil*, *Tbr*). The internal structure of the foot varies. The anterior end has a fine network of nerve-cells spread throughout its length, and at the posterior end is an aggregation of nerve-cells into a ganglionic centre (Pl. 30, figs. 26, 27, 28, 29). The anterior end of the foot has also a great number of small glands which open to the outside all along the foot by fine crypts through the ciliated ectoderm (Pl. 30, figs. 28, 29, *Mug*) and decrease in number and size toward the posterior end. The secretion of these glands is perhaps of use to the animal in helping it to move over fronds of marine vegetation and other solid objects. Very fine neural fibres extend from the pedal ganglion (Pl. 30, fig. 29, *Nt*) to the base of the ciliated columnar epithelial cells and to the glands. This suggests that the cilia of the ectoderm of the foot and the glands in the foot are under nerve control. And, as I have previously recorded (1919, 1921), *M. leonina* may move without any visible bodily contortions, the foot being then either in touch with the surface tension of the water, or with the fronds of marine vegetation or some other solid. In the



laboratory it moves along the side of the glass aquarium as other nudibranchs do, e.g. *Aeolidia*. Such movements seem to be caused by the ciliary action of the foot. In this respect my observations differ decidedly from those of Pease (1860) on *M. pilosa*, who writes: 'Their foot cannot be used for creeping on a flat surface, but it is well adapted for clasping sea-weed;' and O'Donoghue (1921: 194), who says in part: 'It does not creep about on the eel grass but only seems to adhere for the purpose of laying its eggs. In the laboratory, too, it does not creep on the sides of the aquaria and only partly clings to them. It has not been observed creeping on anything after the manner of other nudibranchs, and if not entirely a pelagic form like *Phyllirhoe* it is beyond doubt very nearly so and is a most interesting form.' Although O'Donoghue thinks *Melibe* is mainly pelagic, it is quite evident, judging from its habitat, that the pelagic habit is periodic at the most, i.e. its recurrence is spasmodic (Agersborg, 1916, 1919, 1921, 1921*a*, 1922, 1922*a*, 1923). *M. leonina* occurs not only as a pelagic form, but may be found at a considerable depth, which is perhaps its habitat the greater part of the year. Gould's specimen, 133 mm. long, 17 mm. high, and 32 mm. wide, was dredged at about  $5\frac{1}{2}$  metres depth; Cooper's, 70 mm. long and 17 mm. high, at a depth of 38 metres. Presumably, when it is at the bottom, it crawls on the bottom, for it has a well-developed foot not only for clinging to sea-weeds but also for actual creeping and, indeed, for 'galloping', to use a term employed by previous writers for other forms (Agersborg, 1923).

On one occasion, as I was trying to feed *M. leonina*, it dropped to the bottom of the aquarium and commenced gliding along the bottom. I continued the feeding experiment, when to my astonishment this nudibranch, *Melibe leonina*, suddenly elongated to nearly twice its normal length, showing a method of creeping similar to that described by Parker (1917) for the sea-hare, *Aplysia californica* Cooper (Pl. iv, fig. 9). When elongating the body, the anterior one-third of the foot was lifted above the substratum and



then let down; the posterior third then passed toward the middle of the body which became much wider at the base and along the sides, and then the forward stretching was repeated. This sort of creeping was accomplished by a large muscular wave which passed from the anterior to the posterior, i.e. by direct monotaxic waves. In ordinary locomotion (creeping) the cilia of the foot may play an important part because the locomotor waves are almost indiscernible (Agersborg, 1923: 93-6). *M. leonina* is, indeed, pelagic, but it is a poor swimmer as compared with *Dendronotus giganteus* O'Donoghue (Agersborg, 1922: 264); it is less pelagic than *Phyllirhoe*, which has lost its foot, and it is perfectly able to use its foot both for clinging to sea-weed and other solids and for creeping.

A ciliated foot is a common thing among the gasteropods and other molluscs. This was recorded by Flemming as early as 1869 for *Helic hortensis*; List (1887) for *Tethys fimbriata*; later by Stempell (1899) for the lamellibranch *Solemya tagota* Poli; and recently by Copeland (1918) for *Alectrion obsoleta*, et al. I have myself examined the foot of various cladohepatic nudibranchs (*Aeolidia olivacea*, *Ae. coronata*, *Ae. concinna*, *Ae. diversa*, *Doto coronata*, et al.) at Woods Hole, Massachusetts, and found a uniformly ciliated foot in each case. Pedal glands are recorded by various authors: Leydig (1876), List (1887), Lang (1896), Sedgwick (1898), Stempell (1899), Lankester (1906), Parker and Haswell (1910), Hertwig (1912), but no one has described the pedal gland in *Melibe*. Lankester (1906) comes the nearest to describing the condition as it exists in this species. That is, the pedal gland is not an aggregation of glands or a simple branched invagination of the integuments opening in the mid-ventral line of the foot as in *Triton nodiferus* in particular and other gasteropods in general according to the records of Parker and Haswell, and Hertwig, but consists of a number of unicellular glands, apparently equally distributed all over the foot, that open by small crypts through the ciliated columnar epithelial surface



of the ventral side. List finds three kinds of glands in the foot of *Tethys fimbriata* Linnaeus; two of these are unicellular and the third is multinuclear. The unicellular glands with one nucleus are located on the dorsal side of the foot; the multinuclear glands are found on the ventral side of the foot. Some of the mononucleate unicellular glands contain a fatty substance. The foot is covered by a layer of ciliated columnar epithelium with basally placed nuclei. Between these epithelial cells unicellular and multinucleated glands open to the outside through an individual pore or crypt. The structure of the foot of *M. leonina* conforms very nearly to that recorded by List for *Tethys*. It is not, however, my present intention to make a critical physiological or morphological comparison of the foot in these two types. The 'mehrkernige Drüsen' of List I am unable to recognize in this species. Pl. 30, figs. 26, 27, 28, and 29, show the relation of the unicellular mucous gland to the ectoderm. These glands are highly granular in structure with a central nucleus (Pl. 30, fig. 28, *Gmug*, *Nu*). They are basophil in their staining and there is a marked contrast between them and the nerve-cells which are scattered all through the foot as a net. The latter, however, is firmly aggregated into a pedal ganglion in the posterior end of the foot (Pl. 30, figs. 27, *Gl*, 29, *Pdgn*).

The function of the pedal glands seems to be that of secreting a mucus for the purpose of aiding the animal in its progressive movements when creeping on the surface of any object. This, in fact, is also practised among terrestrial gasteropods, some of which may use the pedal secretion to spin themselves from the limb of a tree or some other plant to the ground. In the *Aeolidia* the activity of the pedal glands is so great that a few specimens (circ.  $1\frac{1}{4}$  cm. long) confined in a finger-bowl for a few hours may produce a complete film of slime on the surface of the water, to which the organisms adhere.



#### 4. The Body-wall.

##### (1) The Odoriferous Glands.

The entire surface of the body of *M. leonina* is fimbriated or tufted, although it is not recognizable to the naked eye, but it is easily detectable with the aid of a lens (figs. 6, *Ex*, 25, *Tbr*, 26, 27, *Tbr*, 31, *Pec*). In this respect it resembles *M. rosea* Rang, *M. pilosa* Pease, *M. papillosa* de Filippi, *M. fimbriata* Alder and Hancock, *M. bucephala* Bergh, and also *Tethys fimbriata* Linnaeus (s. *fimbria*, Bohascht, Delle Chiais). Closely associated with the fimbriated ectoderm are several kinds of glands (Pl. 31, fig. 30, *Glo*, *Sm*, *Um*). There are at least three kinds of these glands: (1) odoriferous (*Glo*), (2) saccular mucous (*Sm*), and (3) unicellular mucous (*Um*). The former is the largest of the three and most numerous (Pl. 27, figs. 4, *Go*, 7). In structure, the odoriferous and saccular mucous glands are similar, but the latter react to Delafield's haematoxylin very much like that of the mucous glands of the foot, while the former seem to be like serous glands. The odoriferous glands, in addition to being larger than the mucous glands, are also a little more complex, i.e. compound saccular (Pl. 31, figs. 30, 31, *Glo*). One reason for assigning the odoriferous function to the largest and most numerous of the cutaneous glands is the fact that this species exudes a rather strong odour, which in a previous paper (1921) I have designated as a means of defence, when it is touched, and at the same time mucus secretion is not noticeable. The unicellular mucous glands are typical glands of its kind (Pl. 31, fig. 30, *Um*). The skin of *M. vexillifera* Bergh (1879a) is also noted for its numerous 'ähnliche Drüsenzellen'. And according to Hancock and Embleton (1848: 103), referring to *Aeolidia*, 'The outer or dermal layer of the skin appears to secrete the abundant tenacious matter that exudes from the animal, and to be the seat of an exquisite sensibility. This layer is thin but continuous with the next or muscular layer, which might be called the cellular for its structure.' But Flemming (1870) thinks the subepithelial connective tissue in *Helix pomatia* secretes slime.



## (2) The Muscular System.

The muscular system of *M. leonina* is one of the most striking features of the animal. When the skin and the caecal endings of the liver (Pl. 27, fig. 3) are removed, the main arrangement of the muscles may be seen to be like that of the interwoven fibres of a basket, the sides of the animal being supported by a network of muscular fibres. One set runs parallel to the median axis from the anterior to the posterior ends, terminating anteriorly in the periphery of the hood. Dorsally these fibres end by branching in the ridge of the back and in the papillae; posteriorly they end in the ridge and in the base of the papillae of that part of the body; ventrally they run parallel to the foot, ending anteriorly and posteriorly in the base of the foot; the last parallel fibres end in the groove of the foot. Another set runs diagonally, also parallel to each other, and ends in fine fibres anteriorly, posteriorly, dorsally, and ventrally. Hartmann (1880: 11) describes the muscles for *Tethys fimbriata* as follows: 'Die Oberseite des Kopfsegels und des Rückens zeigt auch öfters gedüpfelte, manchmal wieder weiss gesäumte Schräg- und Querbänder. Dies hat bereits G. Cuvier recht gut abgebildet (Mollusques, Tab. VII, Fig. 1).' It is then seen that *Tethys* and *Melibe* resemble each other in the arrangement of the muscles of the body. In *Melibe* the muscle-fibres are located midway between the ectoderm and the boundary of the visceral cavity (Pl. 31, fig. 30, *Mb*). Between the ectoderm and the muscles are a great many connective-tissue cells (*Ct*) and fibres (Pl. 31, fig. 34, *Pmc*), ends of the branching hepatic system (Pl. 27, figs. 4, 7, *Hep*), and plasma (Pl. 31, fig. 31, *Sp*). The finer structure of the muscles is of the type common to molluscs: a circular arrangement of finer fibrils in each individual muscle-cell (Pl. 31, fig. 33, *My*). The beautiful picture, however, presented by a transverse or longitudinal section through a muscle-bundle needs to be commented on a little further.

Schneider (1908), describing the muscle structure of *Chiton sicularis*, says: 'Ueber die feine Structur der Muskelzellen ist nicht viel auszusagen. Die langen Fasern



sind Bündel von Myofibrillen ohne innere Sarcaxe. Der längliche Kern liegt der Faser dicht angepresst.' Continuing on the same subject, but dealing with a different type, i.e. *Helix pomatia*, he says: 'Die Fasern sind von rundlichem Querschnitt, langgestreckt, glattfibrillär und zeigen den Kern seitlich in einem geringen Sarcrost (Zellkörper) anliegen.' His comment on the muscles of *Anodonta mutabilis* is much the same as for those already cited, i.e.: 'Die glatten Muskelfasern zeigen gewöhnlich nichts Auffallendes. Jede Faser besteht aus parallel verlaufenden Fibrillen. Der längliche Kern liegt der Faser einseitig an, innerhalb einer geringen Sarcmenge die als Zellkörper zu bezeichnen ist.'

Schneider's description of molluscan muscle is rather generalized and, in fact, fails to bring out the facts concerning the finer structure. The muscle-bundles of *M. leonina* are surrounded by a thin membranous sheath, the perimysium (Pl. 31, fig. 33, *Ms*), and each individual muscle-cell by an exceedingly thin membrane, the endomysium (*Mt*). Between the muscle-fibres, or muscle-cells, are primitive connective-tissue cells (*Inct*). The muscle-cell or -fibre (Pl. 31, fig. 33, Pl. 37, fig. 82,) is differentiated into two sarcoplasmic regions: an outer finely granular and an inner coarsely granular region with a transparent ground substance. At the periphery of each region, very coarse granules are arranged in such a way so as to give the appearance of a granular network enclosing each (figs. 33, *Sar*, 82, *Myf*). The outer of these may be in close relation with the sarcolemma if such a one is present; the inner granular network holds a similar relation to the finely granular region as the outer granular network holds to the periphery of the cell, each enclosing, as it were, two different cytoplasmic regions of the cell. There are thus four kinds of granules in the muscle-cell relative to their location and size. These granules may be designated as myofibrillae because of their linear arrangement. The nucleus is placed centrally within the ground substance of the inner region surrounded by the coarser myofibrillae, immediately, and ultimately by the outer and more finely granular substance. In staining capacity,



the ground substance (hyaloplasm or sarcoplasm) of the inner region shows less affinity for cytoplasmic stain than that of the outer region. The granules (macromeres) of the inner region are farther apart than those (micromeres) of the outer region of the muscle-fibre. This is perhaps also the reason why the muscle-cell of molluscs appears as being, according to Schneider, 'innerhalb einer geringen Sarcmenge'. Chromatin bodies are distributed throughout the nucleus, either in the meshes of the linin and around the nuclear periphery, or around the peripheral part only (figs. 33, *K*, 82, *Kar*). The peripheral granular net (sarcolemma?) may be seen, in the whole mounts of muscle-fibres stained by Congo red, as a fine granular structure around the periphery of the fibre (Pl. 31 fig. 32).

The structure of the inner body-wall as found beneath the basket formation (Pl. 27, fig. 3) of the muscle arrangement in the body-wall, shows apparently no regular arrangement of fibres as in the case of the muscles; the fibres here, which are of connective tissue, seem to extend in every conceivable direction (Pl. 27, fig. 5), and this layer is continuous until some visceral organ or the pericardial chamber is reached. In this plexus of irregularly arranged connective-tissue fibres and cells are the visceral bodies: the brain, the heart, the stomach, the intestine, the organs of reproduction with their adjuncts, and the renal organs. The amount of connective tissue in the body-wall does not render it opaque. This is partly due to the loose arrangement of the various kinds of tissues and to the presence of numerous sinuses (Pl. 31, fig. 31, *Sp*) containing a transparent fluid. This fluid contains characteristic, primitive connective tissue cells and strands (Pl. 31, fig. 34, *Pnc*).

### 5. The Visceral Cavity.

According to Lang (1896: 211) the Mollusca are said to have primary and secondary body-cavities. The former is the system of lacunae and sinuses, into which the arteries open, and out of which the veins, where these are present, draw their blood. It has no epithelial walls of its own. Its



boundaries are formed by connective, nerve, or muscle tissues, or by epithelia, which, however, belong to other organs, such as the intestine, the kidneys, or the body-wall. The latter, the so-called secondary body-cavity or coelom, is in most *Mollusca* very much reduced, usually consisting of only two small cavities, the pericardium and the cavity of the gonads. The coelom is always lined by an epithelium of its own, the coelomic epithelium, and corresponds with the true coelom of the *Annelida*, which also possesses such an epithelium.

The primary body-cavity of Lang corresponds with the perivisceral cavity of Sedgwick (1898: 375), who says: 'In *Gastropoda* there is usually a well-developed perivisceral cavity in relation with the alimentary canal or with the anterior part of it.' The secondary body-cavity of Lang corresponds to the pericardial cavity of Sedgwick. 'There is also another cavity, which has no connexion with the perivisceral, and is called the pericardial because it is related to the heart. By most anatomists the perivisceral is regarded as haemocoelic in nature. It is part of the vascular system, and therefore haemocoelic.'

In regard to the *Tethymelibidae* Bergh (1908: 97), writing on *M. rosea* Rang, says: 'The cavity of the body reaches to the region of the last of the papillae.' In *M. leonina* Gould, I find that the cavity extends anteriorly to the oesophagus, dorsally to the back, ventrally beyond the genital ducts, posteriorly as far as the anus, back of which the branching of the liver and the kidneys is so profuse, together with the crossing of connective-tissue fibres, as to render it very difficult to tell whether the perivisceral cavity extends beyond the anus. This cavity is not a true coelom. It corresponds with the primary body-cavity of Lang or the perivisceral cavity of Sedgwick. There is no definite termination of an inner body-wall, although the muscle-wall seems to represent one, but that is really superficial. Beyond the muscle-wall the connective-tissue fibres run in all directions, all through the cavity. It is, therefore, not a well-defined cavity. It is in this so-called cavity that all the visceral



bodies are located, hence the visceral, or perivisceral, cavity. The pericardial chamber, discussed below, is a true coelom.

## 6. The Alimentary Canal.

### (1) The Buccal Cavity.

As in other organisms the buccal cavity of *M. leonina* is the beginning of the alimentary canal. It corresponds very closely with Alder and Hancock's (1864) and Eliot's (1902) descriptions of *M. fimbriata*. The mouth is bounded by the two lateral, slightly furrowed lips (Pl. 27, fig. 1, *L*, Pl. 29, fig. 17, *M*, Pl. 32, fig. 35); the furrows are not seen in fig. 1 as they are smoothed out by the swelling of the lips, but they may be seen in fig. 35 which is a photograph of a transverse section through the buccal cavity. Within the mouth there is a uniform invagination of the ectoderm (fig. 35), and this invagination produces a number of folds or corrugations which increase in depth and finally merge with those of the oesophagus. The food, as it is engulfed, passes directly through the oesophagus into the proventriculus. No masticatory process is carried on in the mouth for the simple reason that this species is absolutely void of tongue, radula, or mandibles. The food is swallowed whole, as evidenced by the contents of the alimentary canal including the intestine, and is disintegrated by the digestive processes only. The jawless condition of this species is a character common with that of its relative, *Tethys* Linnaeus. Jeffreys says: '*Tethys* has neither jaw nor tongue.' And Vayssi re (1901) finds for *Tethys fimbriata* (*S. leporina*): 'Buccal bulb absent. Large anterior chamber; having exterior circular muscle-fibres probably used in mastication. (Cette r gion offre   sa surface ext rieure un anneau musculaire, auquel correspond int rieurement un anneau de plis longitudinaux presque tendineux, que l'on peut consid rer comme un organe masticateur.)' However, this jawless condition does not prevent *Tethys* or *Melibe* from being carnivorous, as is shown by the contents of their stomach (von Jhering, 1876: 37; Berg, 1882; Vayssi re, 1901: 84-5; Eliot, 1902: 69; Agersborg, 1919: 272; 1921: 228, 232).



### a. Mandibles and Radula.

Bergh (1902: 207) reports the presence of mandibles for the species *M. bucephala*, saying: 'The mandibles joining above are of a form like that of other *Melibes*. . . . The masticatory edge is finely dentate in the upper part, in the lower part provided with coarser, rounded teeth.' For the species *M. pellucida* (1904: 13) he reports: '... die gelblichgrauen Mandibel ganz zerbröckelt.' And for *M. rosea* (1908: 94-9) he writes: '... through the walls the outlines of the mandibles were very distinctly visible (fig. 3b). The clear yellow mandibles (fig. 5) resembling those of *f. ex.*, the *Tritoniadae* or *Pleurophyllidiae*; . . . very plump denticulated masticatory edge, the denticles reaching a height (fig. 5) up to 0.08 mm. (The *bulbus pharyngeus* with its mandibles agree very likely in other species of *Melibes*; in general with that of the typical species.)' It is thus seen that Bergh finds mandibles in many of his *Melibes*, in fact, in all species of *Melibe* which he described, or nearly so. He even took issue with Hancock's description. It really seems strange that Bergh should be so insistent on this point. I have my doubt as to the correctness of his description of one of the species (*M. pellucida*), collected from the mouth of Columbia River in the State of Washington, as no other authors (Gould, 1852; Cooper, 1863; Fewkes, 1889; Heath, 1917; Agersborg, 1916, 1919, 1921, 1921*a*, 1922, 1922*a*, 1923; and O'Donoghue, 1921, 1922, 1922*a*) who have collected the species from the same coast, i.e. off the coast of Santa Barbara, at Monterey, South-eastern Alaska, Puget Sound, and the Vancouver Island region, have recorded mandibles for the types with which they dealt. A number of other authors who have described several species from different parts of the world also, do not record mandibles for this genus: Rang (1829), *M. rosea*; Pease (1860), *M. pilosa*, 'mouth probosciform, and the orifice vertical'; de Filippi (1867), *Jacunia papillosa* (s. *Melibe papillosa* de Filippi); Tapparone-Canefri (1876), *M. papillosa* '... nel suo interno ha nè lingua, nè radula, nè mascelle.' On the



findings of Bergh, however, Lankester (1906: 175) characterizes *Melibe* as having mandibles; but Lang (1896: 180) says: 'Jaws are wanting or rudimentary in . . . many Nudi-branchia (*Tethys*, *Melibe*, *Doridopsis*, *Phyllidia*).' According to this, it would be best to state, at least in part, as a generic characteristic for *Melibe*: the pharyngeal bulb is either with or without mandibles; radula and tongue always absent.

The alimentary canal is remarkably straight (Pl. 28, fig. 9), in fact there is no coiling or looping whatever; only the intestine curves a little from the median position and to the anus, which opens on the right side, a little out of the median line. In this way, the alimentary tract extends somewhat diagonally through the body-cavity, and only the intestine curves. This corresponds with Lang's (1896: 33) statement for the Nudi-branchia: 'The anus lies either dorsally in the median line, or laterally to the right.' In *M. leonina*, the anus is on the right side of the body (Pl. 27, fig. 2), a little ventral to the base of the second papilla of that side. This is also its position in *M. bucephala* Bergh (1902), though in this case it is midway between the first two anterior pairs of the papillae. In *M. leonina* the ureteric pore is laterodorsal to the anus.

#### b. The Buccal and Salivary Glands.

The buccal cavity is highly corrugated (Pl. 32, figs. 35, 36, *Oe*), but it is without jaws or radula. Specialized organs for chewing are substituted by the folding and invagination of the ectoderm. The folds are non-glandular, but just beneath this ectodermal layer are numerous glands, even in the external parts of the mouth. These glands correspond to the buccal glands of various authors. Lang (1896: 185) distinguished clearly between these glands and the salivary glands and says, referring to the *Opisthobranchiata*: 'The salivary glands, of which only one pair is almost always found, here vary in size and shape still more than in the *Pulmonata*. Those glands which enter the pharynx must not be confounded with



other glands which in many *Opisthobranchiata* enter the buccal cavity, and are sometimes more strongly developed than the salivary glands.' Sedgwick (1898: 371), referring to the same organs, says: 'In addition to buccal glands, sometimes found round the buccal opening, there is always a pair of salivary glands opening into the buccal cavity. The buccal cavity leads into the oesophagus which is followed by a dilated stomach, and is usually provided with a caecal appendage.' In *M. leonina* the glands of the oesophagus consist of a series of small, simple, saccular glands (Pl. 32, fig. 41, *Sg*) arranged in rows along each side of the swallowing tube. They open directly into the oesophagus by small crypts (*V*). Heath (1917: 147) reports that the salivary glands are absent in *Chioraera dalli* (s. *Melibe leonina*), but, of course, he is mistaken about this. The activity of the salivary glands in gasteropods was beautifully demonstrated by Lange (1902: 85-153), who showed there is a close relation between the structure of the nucleus and cytoplasm and the physical condition of the organism relative to starving and feeding of the animals.

## (2) The Oesophagus.

The length of the oesophagus in an animal circ. 10 cm. long is 3 mm. (Pl. 32, fig. 36, *Oe*). The oesophagus itself is simply a narrow part of the alimentary canal between the mouth and the proventriculus. Corrugations, which begin at the lips and increase progressively in the mouth, deepen still more in the oesophagus. The lining is still non-glandular, but the glands in the underlying tissue increase until the anterior part of the proventriculus is reached, when they end quite abruptly. The corrugations of the oesophagus are largely longitudinal, which suggests that the oesophagus is capable of expansion in case the animal swallows some large food particle. In some nudibranchs, e.g. the *Tritoniadae*, according to Vayssi re (1877), the oesophagus is very long.



## (3) The Stomach.

*a. Proventriculus.*

Following the oesophagus, the alimentary canal enlarges into a chamber 3 mm. long, 1.51 mm. in diameter, and is constricted posteriorly by extensive evaginations of its epithelial lining. This chamber, the glandular stomach or proventriculus, constitutes the preliminary digestive cavity of the alimentary tract. Its epithelial lining is distinctly different from that of the oesophagus, by being highly glandular (Pl. 32, fig. 38, *Gl*). The food is probably kept here until acted on by secretions of the unicellular glands of its columnar epithelial lining.

*b. Gizzard.*

The remaining part of the stomach is the gizzard. Its length in an animal 12 cm. long was 10 mm., with a diameter of 4 mm. at its widest part. The structure of the gizzard is variable. Its walls consist of two coats (Pl. 32, figs. 37, 42, 43) or layers, each of which may be divided into two parts. The outer layer consists of a thin outer cover of connective tissue and occasional muscle-fibres, which run longitudinally with the organ (*Cc*), and of a thick median circular layer (*Mus*). The inner layer consists of a single layer of tall columnar epithelial cells of glandular nature (*Ept*) and a false epithelial cell border (*Stpl*), formed from the secretion of the underlying glandular epithelium. This secretion fuses into a homogeneous mass giving the appearance of a transitional epithelial layer of cornified type (Pl. 32, fig. 42, *Trs*, 43, *Trp.pl*). This cornified border is about as thick (Pl. 32, fig. 37) on the dorsal side of the middle part of the gizzard as the other two layers together, and gradually decreases until, on the ventral side, . . . it becomes very thin (*V*). It is far more marked in the anterior part of the gizzard than in the posterior. The glandular nature of the epithelial border is well marked in the anterior part of the gizzard but decreases in the ventral region of this part of the stomach, where the cornified border also entirely disappears.



In the extreme posterior part of the stomach the epithelial lining becomes ciliated, a feature which is continuous throughout the remainder of the alimentary canal. In this respect the alimentary canal of *M. leonina* differs greatly from that of *Neritina fluviatilis*, a prosobranch, which according to Lensen (1899) is ciliated from the oesophagus to the anus. The stratum corneum of the epithelial border of the gizzard represents in *M. leonina* the so-called stomach-plates of various authors, which are supposed to be a common characteristic of *Melibe* and related forms. Thus, Alder and Hancock (1864), in their description of *M. fimbriata*, say: 'The stomach is a rather large pyriform pouch, with its small extremity placed backwards. It lies diagonally across the anterior portion of the visceral cavity and is divided into an anterior and posterior chamber by a slight constriction near the centre. The anterior of the lower portion of the chamber is encircled transversely by an almost complete belt of horny, compressed, lancet-shaped process, similar to those in the gizzard of *Scyllaea*.' Bergh (1875*b*), referring to *Tethys* and *Melibe*, says: '... und das in der Tiefe des Kopftrichters hervorstehende Mundrohr leitet unmittelbar in die Speiseröhre und in den ersten Magen hinein, der, wie bei den Meliben, mit starken (Cuticular-) Falten bewaffnet ist,' p. 346. And again on p. 356: 'Die Innenseite der mittleren kleineren Abtheilung des Magens zeigt ... eine Masse von sehr kleinen und niedrigen Längsfalten (fig. 1 *c*) oder eine geringere Anzahl (15–20) von stärkeren; die Falten sind mit einer horngelblichen Cuticula überzogen, die im ersten Falle nur von geringer Dicke, im anderen vielstärker, mit Leisten sich zu einer Höhe von etwa 0.5–0.75 mm. erhebt; an den dickeren Cuticula-Falten tritt eine (Taf. XLV, fig. 22) deutliche Querstreifung oder mehr unregelmässige Theilung hervor. Die Unterseite des Cuticula-Ueberzuges zeigt ein fein körniges Aussehen, das auch an der Oberfläche der unterliegenden Schleimhaut hervortritt und von den zahlreichen, dicht gedrängten Papillen derselben hervorgebracht wird.' Again, on p. 366, referring to *M. capucina*, he says: 'Magenzähne ... 10 starken Kielen



gebildet.' Finally, referring to *M. rangii*, he finds: '... die Magenzähne viel zahlreicher als bei der vorigen Art, schmaler und im ganzen von einem Individuum 26, bei dem anderen 31.' Also von Jhering (1876), writing on *Tethys*, says: 'Der Magen trägt nach innen von der Faser- und Muskelschicht ein einfaches Epithel 0.02 bis 0.03 mm. grosser Zellen, und darauf folgt nach innen eine oft mehr als 0.3 mm. dicke Schicht, welche aus einfachen, schlauchförmigen 0.014 mm. dicken Drüsenschläuchen besteht, deren histologischer Bau... nicht sagen lässt ob es gestattet ist, sie mit der bekannten Cuticularschicht im Muskelmagen der Vögel zu vergleichen. Diese Schicht erinnert sowohl in ihrem Aussehen als in ihrer Consistenz an Knorpel, indem sie zwar weich und sehr elastisch ist, aber doch durch diese an Gummi erinnernde Elasticität dem Magen denselben Schutz gewährt, wie eine harte Kalk- oder Chitinauskleidung.' And Vayssière (1877: 300), in his description of a new genus of the family Tritoniadae, writes: 'L'œsophage, qui est très long, aboutit à une première dilatation qui est le gésier: c'est dans l'intérieur de cette cavité que se trouvent près de quarante dents cultriformes, placées côte à côte et formant un anneau complet. Ce caractère ne se montre parmi les Nudibranches que dans le genre *Scyllaea*.' And again (1911: 102), working on the species *Bornella digitata*, he records the following: 'Cette poche dans son tiers antérieur possède des parois musculaires assez épaisses, muscles transverses et longitudinaux; cette forte musculature est destinée à soutenir à l'intérieur une quinzaine de rangées longitudinales de longues épines un peu recourbées, de nature chitineuse. Cette partie de la poche constitue un véritable gésier dont l'armature sert à broyer les aliments qui y arrivent.' This is further considered by Bergh (1879a: 165) in his description of *M. vexillifera*: 'Der hintere Teil des Magens ist kürzer als der vorige und hat festere Wände; an seiner Innenseite (fig. 9 c) 14 starke Magenplatten und zwischen denselben meistens eine (seltener) kleinere und meistens kürzere (fig. 9 c); die Platten, die Falten darstellen, an denen die Cuticula stärker entwickelt ist,...



schwach harngelber Farbe eine Länge bis beiläufig 0·8 bei einer Höhe bis etwa 0·20, und einer Breite bis 0·25 mm. erreichend. Das hintere Ende des Magens (fig. 2) mit von etwa der Mitte eradiirenden Falten, neben dem Pylorus hier eine taschenförmige Erweiterung (fig. 2fg) (etwa wie in *Tethys*) mit starken Falten der Innenseite.' In 1888: 691, the same author, describing *M. ocellata*, writes: '... die Magenplatten schimmerten undeutlich durch; diese letzteren fast wie in der *M. papillosa*.' And for the last-named species (1884a): '... hinter der Mitte (des Magens) der Länge nach schimmert der Zahngürtel undeutlich hindurch.' And in 1902: 107, for *M. bucephala*: 'The belt of the stomach-plates shines through in about the first half of it, and immediately before the belt the foremost liver-branch is attached on either side somewhat upwardly. . . . The belt of plates consists of twenty-eight faint lemon-coloured firm plates partly alternating in height.' Eliot (1906), describing *Tritoniopsis*, says in regard to the stomach: '... into a rather small membranous and fragile stomach, almost entirely covered by the liver, and no trace of plates.' And in 1910: p. 40 he writes: 'The liver secretions harden in the stomach and form a protecting membrane which is found to cover the stomach.' On the previous page he stated: 'Into the posterior part open four or five liver-ducts and also a pear-shaped gastric pouch, whose orifice in the stomach-wall is closed with a more or less distinctly developed flap. This pouch is often called the gall-bladder, but nothing indicates that its functions correspond to this name. Its walls are glandular, and appear to secrete globules of a glistening material which is also found in the intestine. It is possible that this secretion subsequently dissolves and forms a membrane which is found to cover the walls of the stomach and intestine, and probably serves to protect these delicate surfaces against the spicules abounding in the sponges on which most Dorids feed.' Stomach-plates constitute a common feature among species of *Melibe* and other related forms; something similar to stomach-plates is present in other species (Eliot,



1910). The origin of the stomach-plates in *M. leonina*, which no one seems to have described, is not the same as indicated by Eliot (1910: 39-40) for the Dorids. This may be plainly seen in sections which are represented in my drawings (Pl. 32, figs. 42, *Trs*, 43, *Trp.pl*). In the case of *Melibe* the plates originate as a secretion-product of the epithelial lining of the gizzard. This secretion accumulates within the cell and is voided, little by little, by the cell into the cavity of the stomach. As these secreted droplets pass into the stomach they become attached to their predecessors, harden, and form into a continuous layer resembling the stratum corneum of the human epidermis but, of course, arises differently. The secretion droplets seem to originate around the nucleus of the epithelial cells; they then coalesce into larger droplets and finally break up into smaller ones that pass out of the cell and into the stomach and then form by a keratinization (?) process into the hard or protective lining of the stomach. This protective lining, the stomach-plates of *Melibe*, no doubt serves a double function: to protect the living cells against the spines of the crustaceous food; to help in masticating the food before it passes into the intestine. This latter use seems to be necessary, particularly in those cases in which the organism is void of mandibles or radula of any kind.

### c. The Pyloric Diverticulum.

The pyloric diverticulum (Pl. 27, fig. 9, *Pd.*) is described by Alder and Hancock (1845: p. 14) as pancreatic in function. Whatever function it may have, it seems logical to think that it plays a specific part in the process of digestion because of its internal structure. This part of the alimentary canal is situated at the constricted posterior part of the stomach. Externally it consists of an elaborate evagination into a number of folds, beginning laterally and continuing ventrally, until meeting on the opposite side. Internally (Pls. 32 & 33, figs. 39, 44) the pyloric diverticulum is considerably corrugated, being thrown into much larger folds than the remainder of the tract. Ciliation of the mucous layer begins here. The corrugations are formed,



as in other animals, by the connective tissue which intervenes between an outer muscular layer (although in this case the muscular layer is very thin) and an inner mucous layer. The latter consists of ciliated columnar epithelium, and, as in the stomach, is glandular in nature (Pl. 33, fig. 44), but the secretion of the intestine does not harden after it reaches the lumen of the tract. The epithelium contains large and small vacuoles which are formed in the neighbourhood of the nucleus but in the distal region of the cell. As in the stomach, these vacuoles or secretion droplets coalesce into larger ones which either break up into smaller droplets before leaving the cell, or pass directly into the lumen. But in no case does the epithelium form into regular goblet-cells, nor does the secretion form into protection-plates of the lining as in the stomach.

#### (4) The Intestine.

That the intestine is the principal digestive region of the alimentary canal is well shown by the different conditions of the food in the stomach and in the intestine. In the former, the food seems to have undergone little or no disintegration, while in the latter, only the skeletal parts of the food remain. As the food passes through the pyloric diverticulum, it is perhaps acted upon in such a way that the intestinal juices more easily complete the digestion that takes place in the posterior part of the alimentary canal. The slightly enlarged part of the anterior portion of the intestine has parallel corrugations externally, which may go to show that it is capable of considerable enlargement. In specimens 7 cm. long the corrugated enlargement was circ. 7mm. in diameter.

The absorptive surface of the intestine is increased very greatly by the presence of a typhlosole which extends from the pyloric diverticulum to the anus. The typhlosole is very large in the anterior portion of the intestine, where it protrudes into the intestinal cavity from the ventral side until there is little free space left between it and the rest of the intestinal walls. Posteriorly, the typhlosole gradually decreases in size, and just before reaching the anus it is obliterated in the ventral part of



the tract. Only the ordinary corrugated part of the intestinal lining remains. The extent of the typhlosole, however, varies, because one specimen, whose intestine was sectioned, had no typhlosole in the smaller part of the canal.

The structure of the intestine is similar throughout. There is an outer fibrous layer and an inner glandular one. Between these are fine connective-tissue fibres and small cells and colourless lymph. The glandular layer consists of tall ciliated columnar epithelium (Pl. 33, figs. 45-7). There is no difference in the glandular layer of the typhlosole and of the remainder of the intestine, or in these parts of the pyloric diverticulum. A close study of the internal layer of the intestine reveals some interesting morphological facts, viz. this layer consists of very tall columnar cells with the nucleus located, in most cases, in the middle (Pl. 33, figs. 45, 47) with vacuoles either around the nucleus, on either side, or on the distal side only. The vacuoles arise as a confluence of smaller vacuoles which arise in the neighbourhood of the nucleus, and again break up into smaller ones and then pass into the lumen of the intestine. The epithelial secretion does not keratinize here as it does in the gizzard. Eliot (1910) suggests that the hepatic secretion hardens in the intestine and the stomach of Dorids. The hard substance, however, which covers the endoderm of the alimentary tracts of Eliot's Dorids and of *M. leonina*, is at least in the case of the latter of an entirely different origin. Sometimes more than one nucleus may be present in the same cell (Pl. 33, fig. 46). The most striking feature of this epithelium is the regular fibrillar structure, and the linear arrangement of the cytoplasmic granules from border to base of the cell running parallel with the cilia; these do not converge on the nucleus but pass to the base of the cell. The cell rests on a distinctly granular basement membrane (Pl. 33, fig. 45, *Bm*). There are two distinct rows of basal granules, or terminal bars (desmochondria), the proximal being the larger of the two (*Bg*). The cilia (*Cil*) may be seen readily between the two terminal bars. Beneath the basement membrane (*Bm*) is a loose connective-tissue layer (*Lcc*) which is covered by a denser



fibrous coat with a few occasional muscle-fibres (*Cc*). This same cover, in the pyloric diverticulum, is very loose (Pl. 33, fig. 44, *Vas*), and suggests a possibility of interchange of body-intestinal fluids in this part of the alimentary canal. The outer coat of the remainder of the intestine, though much thicker, is, however, so loose that it may allow ready interchange of intra- and extra-intestinal fluids.

There are then, five distinct regions of the alimentary canal each differing from the other in structure and function. These are (1) the oesophagus with the non-glandular lining below which are the oesophageal or salivary glands (Pl. 33, figs. 36, *Oe*, 41, *Sg*); (2) the proventriculus with distinct glandular lining (Pl. 33, figs. 36, *G*, 38, *Gl*); (3) the gizzard with its stomach-plates (Pl. 33, figs. 37, 42-3, *Stpl*); (4) the pyloric diverticulum with its glandular and ciliated internal surface, which secretions, as in the glandular stomach, do not keratinize (Pl. 33, figs. 38, 39, 44); (5) the intestine with its large typhlosole and glandular ciliated epithelial surface (Pl. 33, figs. 40, 45, Pl. 34 figs. 56, 57).

#### (5) The Liver.

The gastro-hepatic apparatus, or hepatic caeca of *M. leonina*, does not arise as in *M. fimbriata*, '... a little in advance of the belt of horny processes' (Alder and Hancock, 1864), but it arises from the anterior portion of the gizzard and consists of a very extensive arborization which passes to all parts of the body (figs. 1, 2, *Hp*, 7, 9, *Hc*, 40, *Hep*). As in other members of this genus, the liver consists of three principal tubular trunks which start at the anterior end of the gizzard and pass to the various parts of the body. Two of these trunks, situated opposite each other, send out branches as follows: the one on the left side runs in the main to the gonads, branching very profusely in that region; it also sends out other but minor branches, some to the papillae, some to the body-wall, and one to the mucous gland. (The mucous gland = (1) albuminous gland, and (2) nidamental gland.) The right trunk sends out several major and minor branches. Of the



former, one goes to the mucous gland and the other to the gonads and prostata; of the latter, one goes to the veil and others to the papillae and the body-wall. Both of these trunks branch profusely in the posterior part of the body-cavity. A third trunk situated in front of the other two on the left anterior side of the stomach sends out two main branches, one to the hood and the other to the left papilla of the first pair. Besides these there are many minor branches which go to the body-wall. The extreme branches, and particularly those lying within the body proper and surrounding the gonads, are highly glandular. The contents of the gizzard are affected by the secretion of the liver, which is shown by the fact that particles in the stomach near the hepatic openings stain very similarly to the hepatic tracts through the stomach-plates. The arrangement of the hepatic system in the different species of this genus is considerably variable, and still in some of them it is very similar to that of *M. leonina*. Thus Bergh (1875*b*: 366) finds for *M. capucina*: 'Die Leber scheint eine lose, aus mehreren grossen, unregelmässigen, lose mit einander verbundenen Lappen gebildete, etwas gelbliche Masse zu sein, die sich durch die grösste Strecke der Eingeweidehöhle hinzieht, fast überall an den Lappen der Zwitterdrüse angeheftet ist und, wie es scheint, auswärts gegen die Körperwand (gegen die Papillae?) kurze dicke Aeste ausschickt. Aus dem vordersten Theile der Leber entspringt der ziemlich weite Gallengang (fig. 19*e*), der in die Rückenseite des (Cardeatheils des) Magens einmündet.' In 1879*a*: 165, for *M. vexillifera*: '...die Leber wie bei anderen Meliben eine lose, gelblich-weiße Masse, welche vorne an den Magen reicht, hinten sich bis an das Ende der Eingeweidehöhle erstreckt; sie ist eine sehr stark verästelte, mit gerundeten, dünnwandigen Endkolben und Ausbuchtungen versehene Drüse (fig. 10), von welcher sich aber zwei Lappen ganz abgelöst hatten, die sich im ersten Papillenpaare verbreiteten und in die vordere Abtheilung des Magens einmündeten. Diese Lebermasse ging vorn in einen ziemlich weiten, kurzen, dünnwandigen, gemeinschaftlichen Gallengang über.' The hepatic system in *M. papillosa* Bergh (1884)



is not so completely broken up as in *M. leonina*. Again (1890*b*: 283) he calls attention to the fact that the liver of *M. ocellata* opens into the stomach behind the stomach-plates, and in that way it is seen to differ from *M. leonina*. But the distribution of the hepatic branches is similar: 'Dicht hinter dem Gürtel der Magenplatten münden die dicken Leberstämme ein, rechts der besonders dicke aus der ersten rechten Papille, links der aus der entsprechenden linken, und dicht neben demselben der grosse Hauptleberstamm, längs der Rückenseite der Zwitterdrüse und über dieselbe hinaus verlaufend.' Finally, describing the species *M. rosea* Rang, he shows (1908: 98) that it is quite similar to *Chioraera* Gould, when he writes: 'The three principal liver-branches with their ramified hepatic ducts and the principal branchlets to the dorsal epinotidia as usual. . . . Network of liver-branches is interwoven with the much branched renal tubes (figs. 9, 10) the branches reaching the root of the epinotidia, but did not seem to ascend into them.'

Pease (1860: 34) refers to the liver in *M. pilosa*, only by stating: ' . . . body punctured with brown, which are most conspicuous along the flank.' And Alder and Hancock (1845: 13), writing on this subject, say in part: 'In the greater number of Eolididae (Aeolidiidae), however, the liver has entirely disappeared from the abdomen and is broken up into numerous minute portions or glands which are thrust into the branchial papillae. The delicate ducts from these glands pass onward and unite to form great hepatic ducts or trunk channels, which open into the stomach.' Hertwig (1912: 335) concurs in this by saying: 'In Aeolidae (Aeolidiidae) branches of the digestive tract enter the cerata, expand distally to small sacs filled with nettle-cells used for defence; they are derived from hydroids on which these animals feed.' So also Lang (1900: 300) writes: 'Bei zahlreichen Nudibranchiern löst sich die Verdauungsdrüse in sich verästelnde Darmdivertikel auf, die sich fast nach Art der Gastrokanäle oder Darmäste der Tubellarien in Körper ausbreiten und bis in die Rückenanhänge des Körpers emporsteigen (cladohepatische Nudibranchier), wo sie mit den



Nesselkapselsäcken communiciren können Diese Form der "Leber" macht wahrscheinlich, dass sie nicht etwa bloss verdauende Secrete absondert, sondern sich auch selbst bei der Verdauung und bei der Resorption der Producte der Verdauung theiligen wird. In der That weiss man schon lange, dass bei den Nudibranchiern Speisebrei in diese Verästelung des Darmes hineingelangt; aber auch für eine Form mit ganz compacter Leber, nämlich für *Helix pomatia*, wurde kürzlich der Beweis erbracht, dass in der That in der "Leber" Aufsaugung oder Resorption der verdauten Nahrung stattfindet.'

Quatrefages (1844, 1844*a*, 1848) maintained that the liver in Nudibranchs is of a threefold function; hence his term 'Plebenterism' to designate that species of gradation which consists in the union of different functions in one system of vessels. That is, he maintained the absence of anal opening, heart, and blood-vessels, adopting the term gastro-vascular system introduced by Milne H. Edward (1842, 1845) for the digestive organs in the family Aeolidiidae, the true significance of which has since been the subject of much controversy. It is now, however, a well-established fact that the group of molluscs with which de Quatrefages dealt (Aeolidiidae) has a well-established circulatory system, i. e. heart and blood-vessels, and alimentary tract with anal opening. The liver branching off from the digestive tract forms into many parts and ramifies to various parts of the body. One unquestionable function of the liver, as far as Aeolidia is concerned, is an exit for harmful and indigestible parts taken in with food (Alder and Hancock, 1845; Glaser, 1903; Hertwig, 1912). Glaser describes the hepatic caeca as secondary exits in nudibranchs which feed on hydroids whose nematocysts produce indigestible formic acid; the mollusc rids itself of its useless stomach contents through these secondary openings of the liver-branches which end in the dorsal papillae. *M. leonina* does not feed on hydroids, but on crustaceans (Agersborg, 1916, 1919, 1921, 1921*a*, 1922*a*, 1923); and, although the hepatic system is tubular (Pl. 30, figs. 25, *Cshb*, 31, *Ch*; Pl. 33, figs. 51, 53), it does not end with openings



through the ectoderm (Pl. 27, figs. 1, 2, 4, 7; Pl. 31, fig. 30), but caecally between it and the muscle-wall (Pl. 27, figs. 2, 3).

Frenzel (1886 : 273) believed with other authors that the liver of molluscs performs a double function : (1) as in Crustacea it is a digestive gland, 'd. h., dass sie ein Secret bildet und ausscheidet, welches zur Verdauung der in den Darmkanal aufgenommen Speisen verwendet wird.' (2) In addition, this gland is according to Max Weber (1880) for the Crustacea, and according to Barfurth (1883) for the Gasteropoda, of 'excretorische Function'. They think that the liver of these forms is analogous to that of vertebrates. They describe cells that have special functions, such as secretory and excretory. Frenzel points out three kinds of epithelial cells of the liver of Tethys: (1) 'Kornzellen', (2) 'Keulenzellen', (3) 'Kalkzellen'. To these different cells he ascribes the various functions of the organ. These cells are further described by Hecht (1895 : 675), as follows: 'La présence de trois types bien définis de cellules : (1) Cellules vacuolaires excrétrices caractérisées par leurs grandes dimensions et leurs grandes vacuoles (Frenzel: Fermentzellen, Keulenzellen) contenant chacune une granulation. . . ; (2) Cellules excrétrices à grosses sphères brunes (Leberzellen, Kornzellen); (3) Cellules à ferments. Leur coloration en gris par les réactifs osmiques; on y joindra; (4) Cellules indifférentes qui, je le suppose, peuvent évoluer dans un sens ou dans l'autre.' The structure and function of the liver in a Doridiform cladohepatic nudibranch, is still further commented on by Eliot and Evans (1908) as follows: 'The cells which line the hepatic lobules are columnar or cuboidal and highly granular. Some are in a distended condition, others are attached to the wall of the lobule only by a strand or are free in its cavity. It would seem, therefore, that some of the liver cells are excretory in function, and are dropped into the follicle as they become extended with excreted material.' Eliot (1910 : 39) attributes to the liver the function which, in the case of *M. leonina*, I have shown to be the function of the epithelium of the posterior chamber of the stomach, i.e. the gizzard, viz.:



'Into the posterior part open four or five liver-ducts and also a pear-shaped gastric pouch, whose orifice in the stomach-wall is closed with a more or less distinctly developed flap. This pouch is often called the gall-bladder, but nothing indicates that its functions correspond to this name. Its walls are glandular, and appear to secrete globules of a glistening material which is also found in the intestine. It is possible that this secretion subsequently dissolves and forms a membrane which is found to cover the walls of the stomach and intestine, and probably serves to protect these delicate surfaces against the spicules abounding in the sponges on which most Dorids feed.' Finally, Arnold (1916: 353-4), referring to the *Cladohepatica*, thinks that the liver, which in most nudibranchs is extremely large and completely surrounds the stomach, in *Dendronotus* also extends into the dorsal cerata (papillae), so that they may have some digestive function.

The hepatic diverticula of *M. leonina* consist structurally of two main layers: an outer fibrous coat and an inner columnar epithelial membrane. The fibrous layer, consisting of connective tissue, is thrown into corrugations—inwardly—so that the surface of the lumen of the hepatic appendages is greatly increased (Pl. 33, figs. 51, 53). The cytoplasm of the epithelium is highly glandular and one may notice considerable variation in the contents of the cells. Some of the cells show a similarity to the 'Keulenzellen' of Frenzel, or 'Cellules vacuolaires excrétrices' of Hecht. In fact, as is shown in Pl. 33, figs. 48, 49, 50, some of the cells have large vacuoles containing granules of different sizes (Pl. 33, figs. 48-9), and some are vacuolated and contain no granules, while others have no vacuoles but their cytoplasm is highly granular. Others, again, show a remarkable linear arrangement of the granules, basal to the nucleus (Pl. 33, fig. 49). The greatest activity of the cell seems to take place around or near the nucleus with a progressive differentiation toward the border, where the cell in many cases is more homogeneous than in the remaining part. Sometimes a large secretion vacuole may contain threads of darkly stained substances with a darkly



staining cap toward the periphery. Such threads may be present in the cell without the cell being vacuolated. The secretion product, at other times, aggregates from a number of small vacuoles at the border of the cell and passes out en masse, when it seems to be basic in staining reaction. That is, the basophil reaction is shown in material which has been fixed in an osmic acid mixture and stained with Heidenhain's haematoxylin. The nucleus, as a rule, is basal in position and contains one or two nucleoli (Pl. 33, fig. 48). The morphological aspect of an actively functioning liver of *Physa gyrina* Say, and *Planorbis trivolvis* Say, does not differ much from that of *Melibe leonina* (Gould) (vide Agersborg, 1923*a*, figs. 35, 36, 38, 41, 42). It is not my purpose at this time to discuss the function of the hepatic system of *M. leonina*; but it is evident from the facts observed, and as pointed out above, that at least some of its products passes into the stomach, and for this reason it is secretory in function. Perhaps, owing to the peculiar granular nature of the cytoplasm of the epithelial layer, it may be absorptive in function also. In that connexion it is interesting to note the extensive distribution of the liver to the various organs of the body, the significance of which at the present time may only be conjectured. The peculiar granular nature of the cytoplasm of the epithelium shows that its function is different from that of the epithelium of the alimentary tube proper.

#### 7. The Circulatory System.

The work of Milne Edwards (1842) on *Aeolidiidae*; Alder and Hancock (1845) on the *Aeolidiidae* and *Tritoniidae*; Hancock and Embleton (1848) on *Aeolidia*, (1881) and (1882) on *Doris*; Hancock (1865) on *Doris tuberculata*, *D. reponda*, *D. bilamellata*, *Tritonia hombergii*, *Bornella*, and *Scyllaea*; Bergh (1875) on *Melibe* and *Tethys*, (1884*a*) on *M. papillosa*; Lansberg (1882) on *Neritina*; Boas (1886) on *Pteropodes* (*Limacina*, and *Cleodora acicula*); Sedgwick (1888) on *Peripatus*, (1898) on gasteropods; Bouvier (1891) on



Opisthobranchiata; Lankester (1893) on gasteropods and other molluscs; Goodrich (1895) on nematodes, chitons, *Peripatus*, &c.; Hecht (1895) on nudibranchs; Lang (1896) on the Mollusca, (1900) nudibranchs; Shipley and Macbride (1915) on the molluscs; and others, have thrown a great deal of light on the nature of the organs of circulation in Invertebrata, particularly the works of Sedgwick (1888), Lankester (1893), Goodrich (1895), and Lang (1900).

#### (1) The Pericardium.

According to Hancock (1864: 513) the so-called pericardium in Dorids lies immediately above the renal chamber and directly below the dorsal skin in front of the branchial circle. It is, with the exception of the opening leading into the pyriform vesicle, a closed membranous sac, formed apparently by what has been designated the peritoneum, and is just sufficiently large for the accommodation of the dilated auricle and ventricle. It is lined with its own proper membrane which is closely adherent to and intimately confounded with the peritoneal membrane, but can be observed reflected upon the heart at the root of the aorta. It has just been stated that this cavity is closed—previous communications to the contrary were erroneous owing to defective material used.

Goodrich (1895: 484-6) maintains that the vascular system or blood system is simply a liquefaction, as it were, of the mesoblast (Lankester's view). This corresponds with facts as found in *Diploblastica*, e.g. (adult) *Coelenterata*, where blood-spaces are entirely absent, '... while as to the nematodes, ... it seems probable the body-cavity is a blood-space, corresponding in relation to the parenchyma of the planarians.' He shows, following Erlanger, how the pericardium in *Paludina* arises as two coelomic sacs on either side—a hollowing out of the mesoblast. These coelomic cavities then fuse, and later by processes of special growth form a peritoneal funnel that opens to the outside on either side. 'The gonad develops from the wall of the coelom; then together with the rudimentary left peritoneal funnel, it



becomes constricted off from the main division of the coelom (the pericardium), forming a small genital sac. From the wall of this sac the genital duct grows out, and joins an epidermal invagination like the peritoneal funnel of the right side.' In *Melibe* the gonads are situated ventrally with openings on the right side; the single kidney (nephrocoel) is situated dorsally and communicates internally with the pericardium through the renal syrx and externally through the ureter on the left side of the anal pore. The perigonadal coelom (perigonadium) and pericardium are completely separated by the visceral cavity or vascular (haemocoels) cavities. These cavities are blood-spaces into which the blood percolates from the atrial vessels bathing the visceral organs. According to Goodrich (1895), in *Chitons*, a separation has taken place in the genital region of the coelom from the renal; the gonads then require special ducts which may not be homologous with the peritoneal funnels. In *Peripatus*, soon after the metameric somites have been hollowed out from the coelomic follicles, the upper half of each coelomic cavity becomes nipped off from the lower half. From the wall of each of these lower coelomic sacs a peritoneal funnel is formed as an outgrowth which fuses with the epidermis. While these organs have developed in this way, the dorsal or genital halves of the somites in the posterior segments have become fused, forming two genital tubes communicating posteriorly with the undivided coelomic follicles of the last segment. The peritoneal funnels of this segment retain their primitive function and develop into the genital duct; Sedgwick (1898: 375) finds that the coelom of the *Gasteropoda* is in three sections. (1) The pericardium; (2) the nephridia; (3) the gonads. The pericardium is in relation with the heart; it normally communicates with the nephridial system, and part of its lining is generally glandular and forms the pericardial gland. It has no connexion with the blood system. Finally, Lankester (1893: 428) points out the following: the perigonadic spaces and the pericardial space are, then, the coelom of the *Mollusca*. It is quite distinct from the haemocoel. In cephalopods, and



in the archaic gasteropod *Neomenia*, the pericardial and perigonadial coelomic remnants are continuous, and form one cavity. There is strong reason to believe that in ancestral molluscs the haemocoel was more completely tubular and truly vasiform than it is in living molluscs. In the later molluscs the walls of the vessels have swollen out in many regions (especially in the veins) and have obliterated the coelom, which have shrunk to the small dimensions of the pericardium and perigonadium. There are, however, many molluscs with complete capillaries, arteries, and veins, in certain regions of the body.

## (2) The Heart and Arteries.

While the intestine in *M. leonina*, by its diagonal course through the visceral cavity, disturbs the apparent bilateral symmetry, the heart is situated in the median line, just anterior to the anus (Pl. 31, fig. 33), and to the left of the intestine. The heart consists of two chambers, a dorsal and a ventral (Pl. 34, fig. 55, *Au*, *Vent*). The dorsal chamber is the smaller of the two; it is partitioned off into small spaces through which the blood is returned by the efferent branchial veins (*Au*). These chambers may be called auricular chambers; they are perforated (*Av*), and the partitions (*Ar*) which may serve as valves may also close the perforations. The partitions or valves with their apertures are so arranged that the openings do not coincide with each other, and are therefore easily closed. The ventricle or the larger of the two cardiac chambers has a regular valve at its lower and constricted portion (Pl. 34, fig. 59, *Valve*). The heart, therefore, may be completely closed upon the contraction by the valves of the two chambers. The heart is enclosed within the pericardium which also encloses the efferent branchial veins (Pl. 27, figs. 9, *Au*, *V*; Pl. 34, fig. 54, *Au*, *Per*, *Vent*). The aorta passes from the floor of the ventricle (figs. 9, 54,  *Ao*) to the ventral region of the visceral cavity where it divides into two anterior and posterior trunks (fig. 54, *Aa*). Just ventral to the ventricular valve is an enlargement of the wall, the structure of which



is like that of a lymph-node (Pl. 34, fig. 59, *Bgl*). Within this gland (node) are a number of free cells (Pl. 34, fig. 56), which vary considerably in size and structure (Pl. 34, fig. 58, *a, b, c*). Some of the cells of the inside of the gland are pseudopodic (*a*), which is also perhaps the condition of the cells free in the lumen (Pl. 34, figs. 56, *L*, 58, *c*). The structure of these cells may also be the same, but the cells within the gland remain in a more stable environment during the time of death, and on that account may be less subjected to physical shock than the cells within the lumen of the blood-vessels at the time of the killing. In fact, the cells from the lumen (Pl. 34, fig. 58, *c*) show a considerable morphological difference in that they are highly vacuolated. It is known from the study of invertebrate blood that the cells contained in the blood-fluid are exceedingly unstable (Tait and Gunn, 1918). In fact, these men were able to destroy the blood-cells of the circulation of the fresh-water crayfish, *Astacus fluviatilis*, by injecting india ink into the circulation of the living animal; the cells explode very easily upon contact with foreign solids. The cells of the circulation of *Melibe* may not be as easily destroyed or as sensitive as the blood-cells of *Astacus*. Whether the difference in environment relative to that of the blood-plasma and the node is sufficient to produce this difference in post-mortem structure by the same killing method cannot be determined here.

Boas (1886) finds for *Cleodora acicula* that the ventricle is constructed of a few, large, short, flattened, perhaps muscle-cells, which touch each other by their edges. Each cell has a nucleus which lies on the outside of the contractile substance, surrounded by a small protoplasmic mass. The contractile substance consists of fine fibrillae, which are visibly transversely striped. In *M. leonina* the cardiac wall does not consist of muscle-cells exclusively, but of large nucleated fibrillated epithelioid cells (Pl. 34, fig. 57, *Cfm*), but I cannot at this time tell definitely whether the fibrillae are striped transversely; it is quite evident, however, that these cells are different from the muscle-cells of other organs and of the body-wall of this animal.



### (3) The Venous System.

The venous system seems to consist of a number of very thin-walled sinuses so that the blood easily exudes through them, bathing the surrounding organs. The efferent branchial veins collect the blood from the sinuses of the papillae, and perhaps also from the larger sinuses of the body-cavity. The so-called pericardium lies closely below the mid-dorsum, and in front of the intestine and the ureter, and above the anterior branches of the kidney. I have not at this time determined the exact nature of the pericardium and its relation to the blood, whether it is a completely closed chamber or not; whether it is invested with its own peritoneal membrane, or whether it is fenestrated, allowing blood to enter it from the surrounding sinuses. It is, in fact, usually thought that the pericardial space in the molluscs contains blood, and is in free communication with veins; but Lankester (1893) has succeeded in showing by observations on the red-blooded *Solen legumen*, and by more recent careful investigation on *Anodonta cygnea*, *Patella vulgata*, and *Helix aspersa*, that the pericardium has no communication with the vascular system and does not contain blood.

## 8. The Organs of Excretion.

### (1) The Kidney.

According to Pelseneer (Lankester, 1896: 111) the kidney is a compact mass, as a rule, without external projections, but it is divided into lobes in *Stenoglossa* in general, and in some *Taemoglossa*, viz. *Paludina* and *Cypraea*. In a fairly large number of nudibranchs (*Doridomorpha*, *Janus*, &c.) the kidney is divided into ramifications which extend between the visceral organs of the greater part of the body. Shipley and MacBride (1915) say the kidney is a vesicle, into the cavity of which numerous folds project covered by the peculiar cells which have the power of extracting waste product from the blood, which flows in spaces in the kidney wall. The kidney in *Mollusca* varies a good deal in structure, but



is always built on the same fundamental plan as that of the snail. The excretory system of *M. leonina* consists of a bilateral structure with two main renal trunks, ureter, and renal syrx. The trunks extend anteriorly and posteriorly, dividing into two sub-trunks, each of which pass into primary and secondary branches. The anterior trunk divides much earlier than the posterior, and the spread of the anterior bifurcation is much larger than that of the posterior (Pl. 35, fig. 60, *Ab*, *Pb*).

### (2) The Ureter.

The ureter (Pl. 35, fig. 60, *U*) follows the intestine very closely and empties a little to the anterior and left side of the anal opening. This corresponds to Pelseneer's description (vide Lankester, 1906), where it is recorded that the external opening of the kidney is situated near the anus and sometimes the two open together into a sort of common cloaca, as may be seen in *Gymnosomata* and in certain *Pulmonata*, such as *Limax*. In rare cases, he says, such as in the nudibranch *Janus*, the excretory aperture is distant from the anus. The anterior bifurcations of the renal organ (*Ab*) extend just beneath the pericardium with one sub-trunk on each side of the aorta. The posterior renal trunk sends its branches among the hepatic arborizations and connective tissues in the posterior region of the animal, caudal to the ureter and the intestine.

### (3) The Renal Syrx.

On the side of the ureter, midway between the junction of the ureter to the renal trunks and the ureteric pore, is a bilobed and somewhat convoluted whitish body which empties into the ureter (Pl. 35, fig. 60, *Rs*). This body is described by Hancock (1865) as the pyriform vesicle; von Jhering (1876) as the 'Pericardialtrichter'; Bergh (1884*a*) as renal syrx that drains the pericardial chamber. The renal syrx is quite peculiar in structure (Pl. 35, figs. 61, 64, 67). In sections, it is shown to be extensively plicated, but its walls are not muscular as observed by Hancock (1865) on *Tritonia hombergii*. The plicae are strongly ciliated. The cilia of the individual cells are kept



together in such a way that under a low magnification they appear to form tufts which give to the lining the appearance of flask-shaped cells (Pl. 35, figs. 61, 64). Higher magnification brings out their true nature, that they are moderately columnar cells with large cilia nearly four times longer than the cell (Pl. 36, figs. 67, 68, 69). The renal syrinx communicates with the pericardium by a cyncital plate with the nuclei scattered, but as a rule nearer the base, i.e. toward the syringeal side (figs. 66, 67, *Sypl*). It communicates with the ureter, however, by a rather wide opening (fig. 61). There is then no reno-pericardial pore between the kidney and pericardium, through the renal syrinx. This I have determined by the study of serial sections of the organ. *Elysia*, according to Lankester (1906: 110), is exceptional in that the kidney is placed below and partly surrounds the pericardium, and the reno-pericardial orifices are multiple, some ten being present. And, according to Shipley and MacBride (1915) there is a reno-pericardial canal, a narrow ciliated passage, between the kidney and pericardium in the molluscs. In *Melibe leonina* on the pericardial side, the renal syrinx narrows into a neck (Pl. 35, fig. 60, *P*), which internally is formed into two channels by a plica or villus which extends from the cyncital plate and into the organ (Pl. 35, figs. 64, 65, Pl. 36, fig. 67, *Pl*). Only about one-third of this villus is ciliated, that is, its tip, or the part farthest away from the cyncital plate. The sides of the syrinx opposite the non-ciliated portion of the villus are also non-ciliated. The non-ciliated part of the walls has a large number of nuclei situated near the surface. The structure of the ciliated columnar cells of the renal syrinx, or pyriform organ, in *M. leonina*, shows the same remarkable feature as in the intestine, viz. the individuality of the cilia as they pass into the cell. In the renal syrinx there is first the plainly visible terminal bars, but unlike the condition found in the intestine, the terminal bars (basal granules) are shown only as one row, or one for each cilium. From the terminal bar the cilium continues to the base of the cell as a distinctly granular fibrillar structure. As in the intestine (Pl. 33, fig. 45, *Bm*), the basement



membrane is prominent, but unlike the condition here, where it seems to be granular, the appearance of the basement membrane in the ciliated cells of the renal syrx is a continuous, non-granular line, or the granules if present are fused. However, this may also be the condition in the intestinal cells (Pl. 33, figs. 46, 47), reflecting, perhaps, the fact that the bringing out of certain cytological features depends, at least, on two things: (1) the physical condition of the organism at the time of killing, (2) the method and kind of chemicals employed in the killing. Another differential feature of the ciliated cells of this organ, is, as pointed out above, the independent arrangement of the cilia. That is, the cilia are not mingled with the cilia of neighbouring cells, as in the case of the intestine. Still another feature is the size of the cilia both in length and diameter. This specialization of the cilia may point toward a special function of the organ. For example, it may be that of creating a suction within the organ in order to draw the pericardial fluid toward and through the cyncital plate. The cyncital plate, then, with the action of the specialized cilia of the plicae may function as an extracting organ, and one may expect this process to be that of ridding the pericardial fluid of waste. This is also the opinion of Hancock (1864: 520) for Dorids.

Von Jhering (1876: p. 49) applies the name 'Pericardialtrichter' to the renal syrx. By this name its function is indicated also. The case in question is that of *Tethys*, for which the author finds that the syrx communicates with the lumen of the ureter: '... in weiter Communication steht, andererseits durch eine kleinere runde Oeffnung mit der Pericardialhöhle zusammenhängt. Die letztgenannte liegt in einer Membran, welche quer zur Axe des Pericardialtrichters steht und sein Lumen von dem des Pericardium trennt. In dieser Membran liegen um die Oeffnung herum zahlreiche ringförmig angeordnete Muskelfasern, die also einen Sphincter bilden durch welchen die Communication zwischen Niere und Pericardium nach Belieben aufgehoben werden kann.'

Bergh (1884a: 76) does not describe the exact relationship



of the renal syrinx to the ureter and pericardium. Dealing with a number of types: *Phylliroe*, *Acura*, *Rizzolia australis*, *Bornella*, *Tritonia challengeriana*, and *Marionia* (pp. 3, 8, 30, 41, 47, and 51, respectively), he only describes the shape and size and a few of its finer structures, and also that it opens into the pericardium on the one hand and the ureter on the other. For the holohepatic form, *Chromodoris striastella*, he says: the renal syrinx is bulb-shaped of 0.75 mm. greatest diameter; the folds of the interior can easily be seen from the outside; the ciliated cells are as usual. The duct of the renal syrinx is about 1.5 mm. long, opening into the chamber; in the anterior are the usual villi and papillary outgrowths.

Pelseneer (1893: 458): 'Je crois que c'est le plus antérieur ou ventral qu'on doit considérer comme tel: les Nudibranches les plus voisins de *Elysia* (*Hermaea*, *Cyerce*) m'ont en effet montré l'orifice réno-péricardique à la même place, ventralement et à gauche. Les autres conduits seraient secondaires ou cénogénétiques et résulteraient vraisemblablement de la multiplicité des points de contact entre le péricarde et le rein, celui-ci entourant plus ou moins le premier.'

Stempell (1899: 142) finds for *Solemya togata*, Poli: 'Von histologischem Interesse ist zunächst die Beschaffenheit der Nierenspitzen. Dieselben besitzen nämlich nicht wie diejenigen der Nuculiden ein flaches, mit langen Geisseln besetztes Epithel, sondern ein gewöhnliches mittelhohes Cylinderepithel, welches nur mässig lange Cilien trägt.'

And MacFarland (1912: 527), for *Dirona picta*, writes: 'The reno-pericardial opening is found in the renal syrinx, a conspicuous pyriform body situated midway of the animal's length, upon the right dorsal surface of the visceral complex. It communicates below with the pericardial cavity, opening through the floor of the right side. Its lumen is divided by numerous folds of the wall, many of which in turn bear secondary folds. The complicated opening thus formed is lined in its upper portion by high columnar cells, bearing very long cilia, which are directed downward.'



Thus it is seen that, while the communication between the kidney and the pericardium differ, the internal structure of the renal syrinx seems to be similar as far as being lined with ciliated columnar epithelium.

The cilia of the renal syrinx of *M. leonina* discontinue in the region of junction with the ureter (Pl. 35, figs. 61, *A*, 62, *A*). The cells are indistinct in this region (Pl. 35, figs. 61, *B*, 63). The structure of the ureter is unique in itself. The epithelium shows a syncytium (Pl. 36, figs. 71, 72), some parts being conspicuous by the presence of large vacuoles which seem to have formed by the confluence of smaller ones that arise around the nucleus. These larger ones, then, as in the case of the intestine, pass into the lumen of the organ. The ureter is covered by an exceedingly fine fibrous cover (Pl. 36, figs. 71, 72, *Ex*). This cover as well as the epithelium vary according to their position. That is, nearer the renal syrinx it is more glandular in its feature (Pl. 36, fig. 72) than near the end of the ureter (Pl. 36, fig. 71). The renal chamber proper consists of a corrugated glandular lining with a small amount of fibrous tissue covering it (Pl. 36, fig. 70, *Pr. neph, Ct*). The structure of the epithelium suggests that the organ is one of periodic function. According to Stempel (1899 : 142), 'Das Epithel der Nierenschläuche selbst hat eine ziemlich typische Form. In den distalen Abschnitten der vergleichsweise hohen Zellen finden sich helle Vacuolen, welche . . . regelmässig kleine Concrement - Klumpen enthalten. Nach Conservirung mit Flemming'scher Flüssigkeit gelang es mir auch, deutliche Cilien auf den Zellen nachzuweisen.' The kidney of *M. leonina*, as far as I have seen up to the present time, is not ciliated. But the epithelium is highly glandular in structure, which also is the nature of the lining of the ureter, but there is considerable difference in structure, nevertheless.

The function of the kidney is supposed to be that of extracting waste from the blood (Shipley and MacBride, 1915). Ward (1900 : 152) finds that among the variable types of excretory cells two appear to be constant : the first absorbs indigo-carmin and refuses ammonium-carminate, while the second



precisely reverses this action. Rarely excretory cells do both, but even then an excretory cell absorbs the one substance more freely than the other, or vice versa. These two types are associated with voluminous organs. The indigo kidneys produce urea, uric acid, and urates, while in carminate kidneys, thus far known, none of these substances are formed, though some non-indigo excretory cells contain urates. Referring to special cases he states: 'In two groups of molluscs the nephridia instead of being lined throughout their entire extent by a single type of excretory cells present noteworthy differences: in *Amphineura* the reno-pericardial ducts of acid reaction eliminate actively carminate and litmus; while the rest of the nephridium, formed of different cells, and with alkaline reaction, eliminate indigo. Both nephridia of *Patella* eliminate equally indigo. The most numerous non-ciliate eliminate indigo; the others, ciliated, eliminate only carminate—the single nephridium being thus a physiological equivalent of two nephridia in the *Diotocardia* (*Trochus*, &c.).'

#### 9. The Organs of Reproduction.

It was pointed out by Lankester (1881, 1893), Sedgwick (1888, 1898), Goodrich (1895), and Lang (1896), that the true coelom in molluscs is much reduced, being divided into three parts: (1) the pericardium, (2) the perigonadium, and (3) the nephrocoel; the remaining body-cavities being haemocoels which are derived in part from a system of spaces which arise between the ectoderm and the entoderm (Sedgwick, 1888: 383). It is not my purpose to discuss here the homology of these cavities in *M. leonina*, but only to call attention to their relation to one another and their relative duct systems. As stated above the pericardium is a closed cavity which communicates with the nephrocoel by the renal syrx which seems to be closed at its point of communication by what I have called a cyncitial plate. The perigonadial coelom lies directly below the nephrocoel. It was shown by Erlanger, 1891–2, for *Paludina* that the pericardium arises as two coelomic sacs on either side by a hollowing out of the mesoblast.



These coelomic cavities then fuse and later by a process of special growth form a peritoneal funnel that opens to the outside on either side. The gonad develops from the wall of the coelom ; then, together with the rudimentary left peritoneal funnel, it becomes constricted off from the main division of the coelom (the pericardium), forming a small genital sac. From the wall of this sac, the genital duct grows out, and joins an epidermal invagination like the peritoneal funnel of the right side.

In *M. leonina* the perigonadium is situated caudoventrally in the perivisceral cavity. It has a complex duct-system which opens on the right side near the anterior end of the trunk of the body (Pl. 27, figs. 2, 3, *P*; Pl. 37, fig. 81). The single kidney (nephrocoel) is situated dorsally and communicates internally with the pericardium through the renal syrinx and externally through the ureter which opens on the left side of, and close to, the anal pore. The perigonadial coelom (perigonadium) and pericardium are completely separated by the visceral cavity or vascular (haemocoels) cavities. These cavities are blood-spaces into which the blood percolates from the arterial vessels, bathing the visceral organs. In Chitons, 'A separation has taken place in the genital region of the coelom from the renal ; the gonad then acquires special ducts which may not be homologous with the peritoneal funnels' (Goodrich, 1895 : p. 486).

#### (1) The Hermaphrodite Gland.

It is a well-known fact that the gonads among nudibranchs and many other molluscs are hermaphroditic, but the duct system of the two different functional regions varies relative to their complete development. Some authors who have worked on the Elysia diidae (Allmann, Hancock, Souleyet, Gegenbaur, &c.) maintained that the male and female parts of the hermaphrodite gland are separate as are the ducts (vide Pelseneer, 1891). It has been shown by Pelseneer (1891), who worked on several genera of the group in question, that the same part of the gland is both male and female ; some of the follicles of the hermaphrodite gland among certain



Doridiidae and Aeolidiidae, he found, were distinctly male or female; among the Elysiidae all the follicles, in fact, contained two genital products. Mazzarelli (1891 *a*) found that, while the hermaphrodite gland is divided into lobes with subdivisions somewhat deeply placed, each lobe presents a great number of acini contrary to that which up to that time had been observed in tectibranchs—referring in particular to the works of Lucaze-Duthier on *Pleurobranchus*, of Moquin-Tandon on *Umbrella*, of Vayssière on *Aphalaspidea*, and by himself on the *Aplysiidae*—each acinus produces at the same time and contains ova and spermatozoa. In *Pleurobranchiaea*, however, there are both male acini and female acini.

Lang (1896) characterizes three types of genital ducts in the molluscs as follows :

Type I.—‘The hermaphrodite gland has a single undivided efferent duct opening through a single aperture—*Gastropoda*, *Pteropoda*, *Cephalospedae* (*Bulla*, *Dorium*).’

Type II.—‘The hermaphrodite gland gives rise to a hermaphrodite duct which soon divides into two parts, the vas deferens or seminal duct, and the oviduct. The former runs to the male copulatory apparatus, the latter to the female genital aperture. The male aperture and the penis lie in front of the female . . . both lie on the right. This second type may be deduced from the first, if we assume that the common duct of the hermaphrodite gland divided into a male and female duct, but also that the seminal furrow closed to form a canal in continuation of the male duct. To this type belong :

- |  |                              |
|--|------------------------------|
| 1. A few species of <i>Dendebardia</i> | } of the <i>Pulmonata</i> .’ |
| 2. <i>Basommatophora</i> ,             |                              |
| 3. <i>Oncida</i> , and                 |                              |
| 4. <i>Vaginulidae</i>                  |                              |

Type III.—‘In all *Nudibranchia* and a few *Tectibranchia* (e.g. *Pleurobranchiaea*), the hermaphrodite gland gives rise to a hermaphrodite duct, which, as in the



second type, sooner or later divides into a male and female duct. These, however, do not open through distinct apertures, but again unite to form a common atrium genitale or genital cloaca.'

The first type is also demonstrated by Bonnevie (1916) for the pteropod *Cuvierina columnella* Rang, where the hermaphrodite duct arises first as a groove (Rinne) and later forms into a thin duct (Rohr) which makes its exit from the left dorsal edge of the hermaphrodite gland.

Type IV.—This is a new type. It is represented by the reproductive system of *Melibe leonina* (Gould) and is equivalent to types ii and iii plus a more complete duct system. The organs of reproduction in this species (Pls. 28 and 37, figs. 9, 81) consist of a well-defined pair of gonads, each consisting of many lobes or acini; an oviduct, a 'prostate gland' (convoluted portion of the female duct), a uterus (enlarged distal portion of the oviduct), a spermatheca, and a vagina; a vas deferens with its ampulla, a penis, and a mucous gland. The male duct is further modified into vasa efferentia. Each of these parts is peculiarly modified, and together furnish a unique system of reproduction. The relative position of these organs in the body-cavity is shown in Pl. 28, fig. 9.

The male and female ducts in *M. leonina* do not unite to form a common genital atrium as set forth by Lang for 'all Nudibranchia and a few Tectibranchia', but open close together through separate apertures (Pl. 37, fig. 77, *Mgp*); that is, the penis lies in front of the vagina (Pl. 28, fig. 9, *P*); in that way, it resembles the second type of Lang. Both branch, i.e. a vas efferens and an oviduct pass to the same acinus, which is to say: the hermaphrodite gland gives rise to a double genital duct system which passes from the respective male and female germ-cell area of the various acini. In this respect the reproductive system of *M. leonina* differs from all the three types of Lang, and for this reason I have designated the genital duct system of this mollusc as constituting a fourth type. However, since the oviduct is still connected to the ampulla of the vas deferens by a duct,



it is evident that this type is derived from the third type of Lang.

The hermaphrodite gland lies in the caudo-ventral region of the perivisceral cavity and consists of a great number of bilobed acini (Pl. 37, fig. 81, *Ot*). The eggs and the spermatozoa are situated in different regions of the same acinus, which is easily demonstrable in the neutral phase, that is when the male or female germ-cells are in a regressive or progressive stage of growth ; as soon as the one has gained the ascendancy either a male or a female phase appears which seems to take over the entire acinus. At such a time the small duct system which leads from the indifferent or resting region of the acinus is nearly crowded out by the actively employed ducts, and then the acinus may give the appearance as having only a single duct arising from it. That is, during the ripe male phase, the female germ-area with the ducts of any acinus may be crowded to the periphery or to one side in such a way so as to give the appearance of only one duct system leading out from that acinus. However, in any stage of either male or female phases, the two duct systems may be discerned in some of the acini. I cannot determine with any certainty whether this species is protandrous or not, as I have not studied sufficiently young individuals on this point. All the individuals, whose glands I have sectioned, have shown ripe spermatozoa in the acini and also ova.

Pelseneer (1895 : 31) states that protandry ought to be regarded as a general phenomenon in Euthyneurous gasteropods. That this is notoriously the case in pulmonates, and that it has been recognized in various opisthobranchs which have been studied from this point of view, viz. Lohiga, the Thecosomatous pteropods, e.g. *Cliostricola*, &c.; nudibranchs, among which he observed it in *Aeolidia* and *Elysia*; and lastly *Clione limacina* (*Gymnosomata*), in which he noticed that individuals of a length of 15 mm. (or less) do not as yet show any ova in their genital glands, but stages in the development of spermatozoa only. He also found that the ovogenous and spermatogenous



regions of the acini in *Onchidiopsis* are not demarcated with any regularity, that in the middle portion male and female acini can be seen in sections lying side by side. Also, that the products of the two sexes either do not arise in the same caecum or they do not arise in the same region of a caecum.

Bonnevie (1916) finds that *Cuvierina columnella* is protandric; the spermatozoa pass into the 'Zwittergang' and then the eggs develop; there being only one ripening of the germ-cells in the life of the individual. If this be also the case among individuals of *Aeolidia (Coryphella) landsburgii*, as reported by Pelseneer (1895: 23), that the acini of the hermaphrodite gland produce ova in their distal portion and spermatozoa in their proximal portion, it is not so difficult to understand how the product of the peripheral region of the acinus with only one duct system may gain access to the duct, the ripe spermatozoa simply passing out of the way, giving its former position to the oncoming mass of the ripening ova. Pelseneer reports that the same condition as noticed in *Aeolidia landsburgii* has been recognized as general in all the Elysioidea (*Cyerce*, *Hermea*, *Elysia*, and *Limapontia*). Mazzarelli (1891*a*) found male and female germ-products present at the same time in the acini of *Aplysiidae*, and in *Pleurobranchaea* separate male and female acini. 'In the former there are only spermatozoa and spermatids in varying stages of development, and spermatozoa with sheaths (fascetti) seem joined together by cytophors. In the latter (female acini) there occur only ova. The tiny ova in diverse grades of development lie distributed all around the internal aspect of the wall of the acinus as an epithelium. Of the original germinative epithelium there remains slight traces. The ova which are larger and nearly being expelled are found more or less in the centre of the lumen. This fact, that of the formation of spermatozoa and of ova in separate acini in the male-female gland which is abnormal in the Tectibranchs, is seen to be true or ordinary in effect in many Nudibranchs.'



## (2) The Hermaphrodite Duct.

Mazzarelli (1891 *a*) found that the hermaphrodite duct which leaves the male-female gland is very minute in diameter at its beginning, but later, after a certain descent, dilates abruptly to a greater lumen. From this point it gradually narrows again only to bifurcate, giving origin to two minute ductuli. From this point one passes straight to the penis (oedagus), in which it constitutes the deferent channel. The other ductule which is the oviduct enlarges rapidly after its origin and here presents a tiny caecum, then the oviduct contracting gradually, only again abruptly to dilate, develops the first ampulla. In *M. leonina*, however, I find that the hermaphrodite duct has separated into two distinct male-female ducts, i. e. from the time an exit is formed in the acinus it is double. It should be pointed out, however, that the male duct caudad of the ampulla is larger than the corresponding female duct.

## (3) The Oviduct.

The oviduct, after it leaves the last acinus (Pl. 37, fig. 81, *Od*), passes into the prostata (*Pr*), which, in fact, is a part of the female duct. It stands in relation with the ampulla of the vas deferens by a biluminate duct (*Bil.dpr*) (Pl. 37, figs. 73, 79, *Pro*); the so called prostate gland is a much-coiled portion of the oviduct, consisting of two kinds of coils, a large and a small coil system coiled upon itself. The ampulla-prostate duct shows that the female-duct system formerly was in functional relation with the male-duct system at the ampulla; the genital-duct system from the ampulla and to the gonads constituted the hermaphrodite duct. At the point of exit from the prostata the oviduct dilates into a much saccular portion (Pl. 37, figs. 79, *Ut*, 80, *F*, 81, *Ut*), which after some distance passes into a narrow portion. From the distal part of this (Pl. 37, fig. 81, *Osp*) there is a large sac, the spermatheca, and from this point to the orifice the duct dilates a little (*Va*) forming into what I have called the vagina. The most distal portion of the duct lies in communication with the mucous gland (*Mgl*).



The prostate portion of the oviduct is not very glandular. The wall of the uterus consists mainly of fibrous and of some muscular tissue. Its lining consists of glandular epithelium (Pl. 37, fig. 80, *Ms*, *Gl*).

#### (4) Ovispermatotheca.

The ovispermatotheca has a most unique internal structure (Pl. 37, fig. 82). Its outer part consists of a loose vascular connective tissue (*L*) and a muscular layer of circa two cells in depth. Its middle part is a connective-tissue layer (*Sm*) upon which rests a papillated epithelial layer. The muscle-cells of the muscle-layer show the interesting structure already described. The epithelium retains Delafield's haematoxylin stain very well. The papillated epithelium consists of cells that are free (*Ept*) at their two-thirds distal portion, abutting (Pl. 37, fig. 74, *Spt*) into the cavity as finger-like processes (Pl. 37, fig. 82, *Spt*). The larger of these seem to be supported by the underlying basement layer (*Sm*, *Bm*). In the cytoplasm there is a distinct micromeric network (*Mic*). The nucleus is situated at the base in the smaller cells, and midway between the base and the free end in the larger cells. The cells of the larger papillae are wider at their free or distal portion, so that they actually approach each other. The spermatheca contains both semen and ova, and, since in some cases this organ is filled with eggs, I have called it ovispermatotheca.

Mazzarelli (1891 *a*) found that the structure of the spermatheca was plical. He says: 'Indeed the entire aspect of the wall of this presents a great number of longitudinal folds (or plicae) highly developed and disposed in such a manner as to constitute a series of correlated passages or channels (rooms) ('concameragioni'), on the periphery of the lumen of the ampulla which are commonly engorged with the sperm.'

Eliot and Evans (1908: 287) write: 'The walls of the spermatheca in *Doridoides gardineri* are thick and produce a secretion. In some specimens small clumps of spermatozoa are imbedded in this secretion. In others all the spermatozoa form a central mass in the main cavity of the



spermatotheca. It is possible that the secretion serves to form small pockets of spermatozoa or spermatophores.'

MacFarland (1912) found, in the Dironidae, that the spermatotheca was almost rudimentary, and that the dilated oviduct seemed to have assumed in part the function of a spermatotheca, 'for it is frequently crowded with spermatozoa, while the spermatotheca itself contains relatively few.' On the contrary, 'in *Diron albobineata* the oviduct is short and slender: spermatotheca very large, reaching a diameter of 1.3 mm., total length being 4 mm. in a large specimen'. In this connexion it is well to note that, in *M. leonina*, which has a large spermatotheca, the male germinal product also frequently passes into the distal regions of the female genital duct system even as far as and including the prostata.

#### (5) The Male Genital Duct.

The male genital duct starts in the hermaphrodite gland as small tubules (Pl. 37, fig. 81, *Ve*), which join into a common median duct that enlarges into a round bulb-like part (*Amp*) at the anterior region of the ovitestes (gonads). This enlargement I have called ampulla. From the ampulla the male duct passes anteriorly as a large organ of fibrous tissue (Pl. 28, fig. 9, *Vd*). It is surrounded by a sheath of its own (Pl. 37, figs. 78, *Iglp*, 74, 76, 77, 79, 83, *Oc*). Intervening between the penial sheath and the penis itself, is lymph or mucus, a colourless, structureless substance (*M*). The penis is covered with cells of epithelial structure, perhaps both of these, and the cells of the lining of the penial chamber just described, secrete the mucous substance also mentioned. The organ itself is made up mainly of fibrous connective tissue (Pl. 37, figs. 75, 78, 83, *Int*, *MI*). In fig. 75 the biluminate effect as shown here is due to the coiled condition of the organ at the point of section. The main bulk of the organ consists of this fibrous tissue (Pl. 37, fig. 76, *P*). The lumen of the organ is lined with ciliated cuboidal epithelium (Pl. 37, fig. 83, *Iepl*, *cil*). The ampulla of the penis seems to be quadroluminate; anteriorly these lumina converge into three, then two, and finally into one, which becomes the seminal tube



of the penis. The structure of the seminal vesicle and of the ampulla is alike; it consists of a heterogeneously arranged cell-mass, so well welded together that the whole structure is quite compact. The penis is, indeed, so large that when it is withdrawn it fills a large part of the body-cavity. The penis is simply an extension of the seminal vesicle. The sheath of its anterior portion is firmly lodged on the mucous gland (Pl. 37, fig. 81, *Cl.p*) with the penis in its pore. The penal pore merges with the body-wall, adjacent to the vaginal orifice (Pl. 37, fig. 77, *Mga, Fv*). The penis is sometimes extended to the outside, and is then curved like a screw (Pl. 27, fig. 3, *P*). In copulation the penis, which is long, twisted like a screw and of tough musculature, is inserted into the posterior (female) genital pore of the mate, and so firm is the union that separation may not occur even though the couple be dipped from their natural abode and placed in a vessel (Agersborg, 1921 : 238). I have not found mutual coitus effected at the same time in this species, although it is supposed to be a common practice among nudibranchs, according to different authors: Alder and Hancock (1845 : 25), Mazzarelli (1891 *a* : 237), Crozier (1919) et al.

#### (6) The Mucous Gland.

The mucous gland constitutes the albuminous and nidamental glands (Pl. 37, figs. 74, 76, 79, *Mg*, 81, *Mgl*, and 84, *A, B, C, D*). It consists of laminations so arranged that sections through the side of it have a six-layered aspect; continuous sections soon bring out the true conditions. The gland is made up of simple, tall, ciliated columnar epithelium, highly glandular in nature, and which rests on thin connective-tissue fibres with cells which connect the gland to the body-wall. The gland extends almost to the outside of the vaginal orifice (Pl. 37, figs. 74, 76, 77). It functions when the animal spawns; the mucus and the capsulated eggs pass out together.

Mazzarelli (1891), in *Pleurobranchaea*, finds that the vagina at the back of the oviduct's terminal point prolongs itself remarkably dorsad becoming sacculated, its walls being



formed of robust folds and studded with glands which are the glands of the nidamento; near the opening of the oviduct into the vagina but still more dorsad opens the gland of the albume. This is contrary to that noted in other tectobranchs in which the albume gland terminates in a vast number of minute ductuli with blind origins arranged in such a way as to constitute un fitto gomitolo. The albume gland of *Pleurobranchaea* resembles much in structure the albume gland of some nudibranchs, e. g. *Ercolania* (? *Hercolania*) as described by Trinchese.

The albuminous gland of *M. leonina* seems to be more uniform in its physiological condition relative to that of the mucous gland. Unfortunately, I have not at the present time worked out its exact relation to the oviduct, but in general it is somewhat like that described by Mazzarelli for *Oscanius* and *Acera*, i.e. the nidamental gland is nearer the orifice of the vagina than is the albuminous gland. The epithelium of the nidamental gland which secretes a great deal of mucus at the time of oviposition shows some very interesting things relative to its activity during such a time (Pl. 37, fig. 84, A-C):

1. The nucleus (*B*) presents no visible membrane, the nucleoplasm being filled with almost uniformly sized granules which seem to be formed by the nucleolus and then pass as a liquid into the cytoplasm of the cell where from small, minute micromeres the cell becomes entirely filled with darkly staining macromeres which seem to have grown from these smaller ones so that the ordinary and less stainable cytoplasm is practically obliterated, i.e. obscured by these granules. These granules are very strongly basophil in their staining reaction. The macromeres then liquefy and pass out of the cell and into the lumen of the gland.

2. This leaves the cell in a condition strongly contrasting to the one before the liquefying of the mucus. The cell is now very vacuolated, containing a non-stainable, or rather oxyphil, substance (*A*, *Rs*) with relatively few granules. These granules are micromeric, and are aggregated in the meshes of the reticular net-work of the cytoplasm.



3. In the proximal region of the cell may be seen the nucleus, small and shrunken, containing a small nucleolus, and lodged at the base of the cell.

4. A state of refilling now ensues (C). The nucleus begins to enlarge and then a homogeneous cytoplasmic substance is accumulated around it, which then spreads throughout the cell. At the same time the micromeres of the vacuolated cytoplasm of the cell increase in size.

That the nucleus takes a very active part in the formation of the mucinous substance is clearly evident, but the micromeres of the cytoplasm seem also to take an active part in the refilling of the cell as indicated by the growth of the micromeres formed in the meshes of the reticular network of the cytoplasm before the nucleus has assumed its normal condition. In semi-vacuolated cells, i.e. cells which are in the state of refilling, the nucleus is intermediate in size and granulation to those described under (B). It is of interest to note some of the findings of Lange (1902) from his studies of the structure and function of the 'Speicheldrüsen' of gastropods. This author found that the cells of the glands showed great differences during feeding as compared with periods of starvation. Some of these phases of activity of the cell are quite similar to those recorded above for the mucous gland of *M. leonina*. Lange says:

In allen Stadien der Fütterung und auch des Hungerzustandes finden sich nie sämtliche Sekretionszellen auf derselben Sekretionsstufe. Es kommen in jedem Stadium der Fütterung und des Hungers alle Stadien vor, doch in verschiedener Häufigkeit. Der Kern nimmt innigen Anteil an der sekretorischen Thätigkeit, indem im Anfang seine Membran sich auflöst und sein Inhalt sich mit dem Protoplasma vermischt, sodass der erste sekretorische Vorgang sich am Kern bemerkbar macht. Die von Barfurth als 'Speichelkugeln' bezeichneten Gebilde sind Sekretvakuolen, welche angefüllt sind mit muciginer Substanz. Man kann deutlich verfolgen, wie sich das Mucigen in diesen Sekretvakuolen zu Mucin umwandelt. Ist das Mucin gebildet, so verliert der Kern seinen Turgor wohl durch Austritt von Kernflüssigkeit. Dabei steht das Kerninnere stets im offenen Zusammenhang mit dem



Protoplasma. Es lassen sich zwei Teile an dem Zellich unterscheiden: der den Kern umgebende protoplastische Teil und der periphere parablastische mit den Sekretvakuolen; dieser letztere wird mitsamt dem in ihnen gereiften Mucin bei der Sekretion ausgetossen. Es bleibt in der Bindegewebskapsel allein der protoplastische kernhaltige Teil übrig, von dem aus die Neuproduction des Zelleibis vor sich geht, sodass die Sekretion zunächst in der Bildung von Sekretionsvakuolen, sodann aber in der Ausstossung des ganzen peripheren Teils der Zelle mit dem gebildeten Sekret aus der bindegewebigen Kapsel besteht.

In the epithelium of the mucous gland of *M. leonina*, as in the epithelium of the intestine and of the renal syrinx, basal granules or desmochondria are demonstrable; but in the mucous gland the linear fibrillar arrangement of the micro-macromeres of the cytoplasm is absent. The reason for this is obvious; the cilia also seem to end on the distal basal granular border (Pl. 37, fig. 84, *Bg*, *Fcb*).

#### V. SUMMARY.

1. It is evidenced by the work of various authors that Gould's *Chioraera* (1852) is identical with Rang's *Melibe* (1829); *Chioraera*, therefore, is a synonym of *Melibe*; Gould, at the time of his description, did not know of the genus discovered by Rang. For these reasons I have consistently named it throughout all my works on this species *Melibe leonina* (Gould) in spite of the attempt of certain authors to build on the nomenclature of Gould.

2. *Melibe leonina* is absolutely void of masticatory organs; the generic description of Gould may be augmented, therefore, to read in part, *Bulbus pharyngeus aut cum mandibulis aut sine mandibulis; radula et lingua destitutus*.

3. The anterior end of *M. leonina* is formed into a large cowl; this has a pair of stalked foliaceous tentacles which may be retracted below the edge of the stalk which then acts as a sheath. The tentacles are very complex in structure, being innervated with nervous tissue. The tentacles are not ciliated, as claimed by Jeffreys (1869) for all nudibranchs. The cowl



is fringed with two rows of cirrhi which also are highly complex in structure. From an inner ganglionic axis, nerve-fibres radiate to the peripheral ectoderm of the cirrhus. The exact function of the tentacles, as well as of the cirrhi, is not known. The tentacles are commonly called rhinophoria but, since the exact function is not known, I have employed the original term tentacles (dorsal tentacles) instead of the commonly used term 'rhinophoria'. The cirrhi are more sensitive to tactile stimulus than are the dorsal tentacles (Agersborg, 1922a: 441-3).

4. The body-surface of *M. leonina* appears smooth, but upon close examination it is found to be everywhere tuberculate, including the sole of the foot and the ventral side of the hood; in that way this species corresponds to other members of this genus.

5. The dorsal appendages, which in *M. leonina* consist of six pairs of foliaceous lobate structures, I have called by the Linnean term papillae, instead of cerata, or branchial papillae for the reason as stated by Bergh (1879c): 'Respiration takes place all over the surface in Nudibranchs,' &c. The papillae alternate in position; they are subject to variation in structure relative to position and age (Pl. 27, figs. 1, 2, 3, and Pl. 30, figs. 18-25).

6. The foot projects in front of, and behind, the main body. It is highly tuberculate and ciliated. Internally, a fine nerve network is seen spread throughout its length and breadth, and at the posterior end it aggregates into a ganglionic centre. Fine nerve fibrils are seen to pass to the ciliated ectoderm. A great many mucous glands are present all through the foot, which open independently through small crypts between the ectoderm cells. These glands are the pedal glands which are scattered all through the foot (figs. 1, 2, 3, 9, 26, 27, 28, 29).

7. There are three kinds of glands in the body-wall: (1) the largest and most numerous are the odoriferous glands; (2) the next in size and number are the saccular mucous glands; and (3) the unicellular mucous glands (Pl. 31, figs. 30, 31).

8. The muscle system lies below the glandular fimbriated



ectoderm ; the muscle-fibres are arranged in a fashion like the fibres in a basket (Pl. 27, fig. 3).

9. The muscle-cell consists of two sarcoplasmic regions each containing an abundance of micromeres : those in the inner region are larger (Pl. 31, fig. 33, *Ca*) than those in the outer region. The larger are called in the text macromeres. Each of these micro-macromeric sarcoplasmic regions is invested by a coarsely granular net-work (*My*, *Sar*). The nucleus is placed centrally within the cell. Its chromomeres (*K*) are scattered differently, i. e. sometimes around the periphery of the nucleus (Pl. 31, figs. 32, 33, Pl. 37, fig. 82) and sometimes less so.

10. There is no definite body-cavity. The body-cavity as it exists corresponds to the primary body-cavity of Lang (1896) or the perivisceral cavity of Sedgwick (1898).

11. The alimentary canal consists of five regions :

- (1) The oesophagus with the non-glandular lining, and back of it the oesophageal glands or salivary glands (Pl. 32, figs. 36, *Oe*, 41, *Sg*).
- (2) The proventriculus with distinct glandular lining (Pl. 32, figs. 36, *G*, 38, *Gl*).
- (3) The gizzard with its stomach-plates which are formed by the secretion of the epithelial lining (vide supra), (Pl. 32, figs. 37, 42, 43, *Stpl*).
- (4) The pyloric diverticulum with its glandular and ciliated and much corrugated surface, which secretion does not keratinize as that of the gizzard (Pl. 32, figs. 35, 39, 44).
- (5) The intestine with its large typhlosome protruding into the cavity from the ventral side, and glandular ciliated surface (Pls. 32 and 33, figs. 40, 45, 46, 47). The structure of the intestinal lining is unique as concerns the fibrillar nature of the cytoplasm, the clearly visible terminal bars, and the basement membrane ; also, the non-convergence of the cytoplasmic portion of the cilia on the nucleus.

12. The liver ramifies all the parts of the body. Its secretion



into the gizzard does not harden in the alimentary canal. The glandular structure of the epithelium of the liver exhibits that it has an active function in vivo, owing to the presence of a variable series of granules and vacuoles in the adjacent cells fixed at the same time in the same way (Pl. 27, figs. 1, 2, 4, 7, Pl. 33, 48-53).

13. The heart consists of two chambers enclosed within the pericardium. These chambers are separated by valves from the efferent branchial veins and the afferent aortic trunk-vessel. In the aorta, just below the valve of the ventricle, is a blood-gland or node which contains pseudopodic cells. The cells found on the outside of this node, i.e. within the lumen of the aorta, are different in structure from those found within the node (Pl. 34, figs. 54-9).

14. The wall of the heart consists of epithelioid and some semi-musculofibrilloid cells (Pl. 34, fig. 59).

15. The kidney is much branched, and is situated between the pericardium and the gonadium. It communicates with the pericardium through the renal syrinx which is closed at the point of junction with the pericardium by what I have called a cyncitial plate. The lining of the kidney is glandular; so is also that of the ureter, but neither is ciliated. The renal syrinx, however, is ciliated. The cells of the renal syrinx are peculiar in that the cilia are very large and independent in position, i.e. they do not mingle with those of adjacent cells. The renal syrinx is plicated, and from the cyncitial plate a ciliated villus protrudes into the organ (Pls. 35 and 36, figs. 64, 65, 67, Pl).

16. The organs of reproduction represent an additional type to the three types enumerated and described by Lang (1896). The male and female ducts in *M. leonina* do not unite to form a common atrium genitale as set forth by Lang for all nudibranchs and a few tectibranchs, but open close together through separate apertures (Pl. 37, fig. 77, *Mgp*); the penis lies in front of the vagina (Pl. 28, fig. 9, *P*); in that way it resembles the second type of Lang. Both genital ducts pass independently to the same acinus; in this respect it differs from all three types of Lang, and, for this reason, I have



designated the genital duct system in this mollusc as constituting a Fourth Type. During any ripe phase of the gonads the duct leading from the inactive area of an acinus may be quite obscured by the ripening mass of germ-cells. The organs of reproduction are represented in Pl. 37, fig. 81.

17. The spermatheca I have called ovispermatheca because it is frequently filled with eggs from the oviduct. The structure of the ovispermatheca is quite peculiar owing to the plicated nature of its lining. The cells lining this organ are flask-shaped, the neck being longer than the body and abutting into the cavity (Pl. 37, fig. 82).

18. The mucous gland is relatively rather large. A great deal of mucus is formed by this gland at the time of oviposition (Agersborg, 1919, 1921, 1923*a*). Sections of the gland which I have studied show that during the act of mucus-formation the nucleus takes an active part. The nuclear membrane is then very obscure or apparently absent, the nucleus goes through fragmentation, the smallest cytoplasmic granules of basophil nature are the nearest to the nucleus; after the mucous granules have liquefied and passed into the lumen or cavity of the gland, the nucleus of the gland-cells is small, shrunken, and non-granular, with a small nucleolus, and basal in position within the cell. The cell then passes through a period of refilling during which time the nucleus first grows in size, and at the same time the micromeres of the cytoplasm, which are lodged in the meshes of the reticular structure of the cell, also grow.

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## VII. NOTE TO EXPLANATION OF FIGURES.

Figs. 11, 12, 13, 14, 15, 16, 46, 47, 48, 49, 50, 52, 53, 56, 57, 59, 61, 62, 63, 64, 65, 66, 67, 69, 72, and 74 were drawn by the aid of Spencer's compound microscope, tube length 16 mm., and camera lucida, angle of mirror 35. The others are either free-hand drawings, microphotographs, or photographs from preparations.

n.p.r. = low power with front lens removed. l.p. = low power.  
 h.p. = high power. o.i. = oil immersion. c.l. = camera lucida.

## VIII. EXPLANATION OF PLATES 27-37.

Fig. 1.—Photograph of *Melibe leonina* (Gould) from the ventral side. Specimen preserved in 70 per cent. alcohol. *C*, cirrhi; *F*, foot; *Hp*, hepatic diverticula; *L*, lips; *M*, mouth; *Ml*, marginal edge of hood.  $\times 1$ .

Fig. 2.—Photograph of a preserved specimen from the right side showing



the profuse arborescence of the liver. *Ao*, anal pore; *Ap*, anterior right papilla; *F*, foot; *P*, penis; *R*, tentacle.  $\times 1$ .

Fig. 3.—Photograph of a preserved specimen from which the ectoderm and hepatic arborizations of the body-wall have been removed to show the arrangement of the muscles of the body-wall. *P*, penis.  $\times 1$ .

Fig. 4.—Microphotograph of the skin to show the odoriferous glands (*Go*); *Hep*, hepatic branches; *M*, muscle-fibres.

Fig. 5.—Photograph of a whole-mount of the skin with the underlying fibrous tissue to show the heterogeneous arrangement of the connective tissues.

Fig. 6.—Photograph of a trans-section of the hood to show the tufted or tuberculate surface of both the external side (*Ex*) and ventral side (*En*) of the hood. In the ectoderm of the external side of the hood are also shown the odoriferous (...) glands, which are absent from the ventral side.  $\times 24$ .

Fig. 7.—Microphotograph of the body-wall seen from the inside. It shows the caecal endings of the hepatic diverticula. Contrast with fig. 4, which is of the skin, photograph taken from without; note the relative position of the odoriferous glands in the body-wall.

Fig. 8.—Photograph of dorsal tentacle with the sense organ (papilla of Gould) (*Rh*) retracted. *C*, lamellated part; *K*, neural knob. See also *K* in fig. 15. (Vide Agersborg, 1923, figs. 4, 5, *pa.*)

Fig. 9.—Schematic drawing of a dissected adult to show the general arrangement of the visceral organs. *A*, anus; *Au*, efferent branchial veins; *Br*, brain; *hc*, hepatic trunks; *Ft*, foot; *G*, proventriculus; *Li*, larger part of the intestine; *M*, mouth; *Mg*, mucous gland; *Oe*, oesophagus; *Od*, oviduct; *Ospt*, ovispermatheca; *Ot*, ovitests; *P*, penis; *Pc*, pericardium; *Prg*, prostate gland; *Si*, smaller part of the intestine; *Vd*, vas deferens; *V*, ventricle; *Vg*, vagina; *Sto*, gizzard; *Pd*, pyloric diverticulum.

Fig. 10.—Part of the rim of the hood to show the arrangement of the cirrhi. *Ic*, inner row; *Oc*, outer row; *M*, muscle-fibres.

Fig. 11.—Cross-section of a large cirrus, showing the axis at *Lcm* from which fibres radiate (*Rf*) to the sub-epithelial (*Ie*) layer of the periphery. *Oe*, outer epidermal layer. (l.p., c.l.)

Fig. 12.—The axis of the cirrus shown in fig. 11. *Ccm*, smaller central cell-masses with a reticular structure; *Cg*, central ganglion; *Lcm*, large central cell-mass with a few cells scattered; *Rf*, radiating fibres. (h.p. c.l.)

Fig. 13.—Same as fig. 12. *Ir*, inner reticular network of the large central cell-mass (*Lcm*); *Pc*, peripheral cells; *Cga*, central ganglion.  $\times 1,013.4$ ; (o.i., c.l.).

Fig. 14.—Part of the periphery of cirrus as shown in fig. 13. *Ie*, sub-epithelial layer with which the radiating nerve-fibres (*Rf*) communicate; *Oe*, super-epithelial layer.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 15.—Longitudinal section through the sense organ of the dorsal



tentacle (lamellar papilla of Gould). *Nfb*, nerve-fibres of a highly ganglionic knob; *Nfl*, the same fibres in the lamellated part; *Nfp*, nerve-fibres which communicate with the peripheral ganglion below (*S*); *Nc*, small nerve-cells surrounding central fibres; *Ncs*, ganglionic knob, consisting of nerve-cells only; *Nmf*, neuro-muscular fibres which inter-communicate between the sense organ and the base of the tentacle; *Owr*, the outer wall of the tentacle which serves as a sheath to the organ; *S*, lamellae.  $\times 75$ .

Fig. 16.—Nerve-cells from 'K' in figs. 8 and 15. *Nc*, larger nerve-cells; *Ncs*, smaller nerve-cells. Notice the large granular nucleus.  $\times 1,013.4$ .

Fig. 17.—Front view of *Melibe leonina*. *Fh*, rim of hood; *Fr*, front; *Ft*, foot; *Irc*, inner row of cirrhi; *Irc*<sup>1</sup>, mid-ventral rudimentary cirrhi; *L*, lip; *M*, mouth; *Mf*, muscle-fibres; *Mdp*, mid-dorsal depression; *Orc*, outer row of cirrhi; *R*, base of tentacle.  $\times 1\frac{1}{2}$ .

Figs. 18–24.—Papillae. Figs. 18, 19, first pair; 20, one of the second pair; 21, one of the third pair; 22, one of the fourth pair; 23, one of the fifth pair; 24, the sixth pair. *Hep*, caecal terminal branches of the liver. The parallel lines represent muscle-fibres.  $\times 1$ .

Fig. 25.—Longitudinal section of an anterior papilla. *Cshb*, cross-section of a hepatic branch; *Mf*, muscle-fibres; *Og*, odoriferous gland; *Osp*, vascular space or sinus; *Tbr*, tubercles.  $\times 2$ .

Fig. 26.—Cross-section through the anterior region of the foot. *Cil*, cilia; *Lv*, liver; *Mc*, muscle-bundle; *Og*, odoriferous gland; *Tbr*, tubercles.  $\times 8$ .

Fig. 27.—Cross-section through the posterior region of the foot. *Bc*, connective tissue; *Gl*, pedal ganglion. The other labelling as the preceding.  $\times 8$ .

Fig. 28. Section of a single tubercle from the anterior end of the foot. *Cec*, ciliated columnar ectoderm; *Cil*, cilia; *Gmug*, granules of mucous glands; *Grc*, granular border; *Mf*, muscle-fibres; *Nf*, nerve-fibres; *Ng*, nerve-cells; *Nu*, nucleus.

Fig. 29.—Section through the pedal ganglion of the foot (vide fig. 27). *Cec*, ciliated columnar ectoderm; *Cil*, cilia; *Gl*, ganglionic cells; *Mf*, muscle-fibres; *Mug*, mucous glands with crypts passing through ectoderm; *Nf*, nerve-fibres; *Ng*, nerve-cells; *Nt*, neural fibrillae ending on to ciliated ectoderm; *Pdng*, pedal ganglion.

Fig. 30.—Section through the body-wall. *Bv*, body-wall; *Cr*, crypt; *Ct*, connective tissue; *Ec*, ectoderm; *Sm*, saccular mucous gland; *Mb*, muscle-bundle; *Mf*, muscle-fibres; *Glo*, odoriferous glands; *Um*, unicellular gland.

Fig. 31.—Section from part of the wall of a large papilla (see fig. 25). *Cc*, connective-tissue cells; *Ch*, cross-section of hepatic branches; *Ct*, connective-tissue fibres; *Glo*, odoriferous gland; *Pec*, ectoderm of fimbriated surface.



Fig. 32.—From a whole mount of muscle-cells taken from the body-wall. The fine granular appearance along the periphery of the cells is represented in the next figure by 'Sar'; Nu, nucleus.

Fig. 33.—Cross-section of muscle-bundle showing section of a few fibres only. Ca, axial sarcoplasm; Intc, inter-fibre connective-tissue cell; K, chromatin granules; Lin, linin; Mc, muscle-cell cut through the centre; MCP, peripheral micromeric region of cell; Mfe, muscle-cell cut near its tapering end; Ms, perimysium; Mt, endomysium; My, myofibrillae; Nuco, nucleolus; Nu, nucleus; Nus, nuclear sap; Sar, sarcolemma.

Fig. 34.—A few connective-tissue cells and muscle-fibres from the body-wall. Mf, muscle-fibres; Pnc, granular connective-tissue cells.

Fig. 35.—Photograph of a cross-section of the pharynx near the mouth to show the corrugations (Cor) of the lining.

Fig. 36.—Microphotograph of a median sagittal section of the oesophagus. Oe, oesophagus; G, proventriculus; S, gizzard; Br, brain.  $\times 8$ .

Fig. 37.—Microphotograph of a cross-section through the gizzard. Hep, hepatic canals into the gizzard; V, ventral side.  $\times 14$ .

Fig. 38.—Microphotograph of a cross-section of the posterior part of the proventriculus showing the end of the glandular lining. F, remnants of food; Cm, circular muscle-layer; Gl, glandular mucous lining; M, stomach-contents (mucus?).  $\times 22$ .

Fig. 39. Microphotograph of a cross-section through the anterior part of the pyloric diverticulum. Mu, mucous coat; Mus, muscle-layer; Ty, typhlosole.  $\times 18$ .

Fig. 40. Microphotograph of a cross-section of the larger portion of the intestine. Ex, mucosa; Ty, typhlosole; Veb, ventral blood-vessel.  $\times 37$ .

Fig. 41. Drawing of a longitudinal section of the oesophagus. Bc, connective-tissue cells; Ept, epithelial lining; Mst, muscle-fibres; Nu, nucleus; Sg, salivary glands; V, crypts of salivary glands.

Fig. 42.—Drawing of a cross-section of the gizzard. Bm, basement membrane of the endoderm lining of the gizzard; Cc, external cover; Ept, epithelium of the gizzard; Mus, circular muscle-layer; Stpl, stomach-plates; Trs, transitional parts of the stomach-plates, a product of the epithelial lining.

Fig. 43.—Longitudinal section of the gizzard. Ct, connective tissue, and a few muscle-fibres; Cs, circular muscle-layer cut transversely; Ept, epithelial lining showing several secretion vacuoles in the cytoplasm and nuclei in various conditions of the so-called resting stage; Kar, chromatin granules; Lin, linin; Nuco, nucleolus; Nu, nucleus; Ol, external cover; St.pl, stomach-plates; Sv, secretion vacuoles; Trp.pl, transitional part of stomach-plates.

Fig. 44.—Drawing of one of the corrugations from the pyloric diverticulum (vide fig. 39). Bg, basal granules (terminal bars); Bm, basal



membrane; *Cil*, cilia; *Sb*, sub mucosa; *Vas*, highly vascular cover of the organ; that is, the tissue is very loose and seems to contain many spaces or sinuses; *Vac*, mucus vacuoles.

Fig. 45.—Cross-section of the wall of the smaller intestine. *Bg*, terminal bars; *Bm*, basement membrane; *Cc*, connective-tissue cover; *Cil*, cilia; *Kar*, chromatin granules; *Lcc*, loose connective-tissue layer or sub mucosa with many vascular sinuses; *Nuco*, nucleolus; *Nu*, nucleus; *Nus*, nuclear sap; *Sv*, secretion vacuoles.

Figs. 46, 47.—The same as fig. 45. The secretion vacuoles are not so large. *Bg*, terminal bars; *Cil*, cilia; *Sv*, secretion vacuoles.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 48.—Longitudinal section of one of the main branches of the hepatic caeca. *Nu*, nucleus; *Sc*, secretion cap (product).  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 49.—Longitudinal section of hepatic branch, showing the very variable condition in adjacent cells. (h.p., c.l.)

Fig. 50.—Cross-section of hepatic branch in the body-wall of the hood. *Sg*, secretion product.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 51.—Cross-section of hepatic branch from the body-wall. *Dsc*, darkly staining cells; *Gc*, vacuoles; *L*, lumen; *Nu*, nucleus.

Fig. 52. From 'x' in fig. 53. (h.p., c.l.)

Fig. 53.—Cross-section of a branch of the liver in the tentacle.  $\times 107$ . (l.p., c.l.)

Fig. 54.—Schematic drawing of the heart and part of the pericardium. *Aa*, anterior arteries; *Ao*, descending aorta; *Aosh*, very fine transparent sheath of the aorta; *Au*, efferent branchial veins; *Per*, pericardium; *Vent*, ventricle.

Fig. 55.—Longitudinal section through the auricular part of the heart. *Au*, efferent branchial veins; *Av*, auricular apertures in the auriculo-ventricular valves (*Ar*); *Bc*, blood-cells; *End*, epicardium; *Vent*, cardiac wall of the ventricle.

Fig. 56.—Blood-gland from the wall of the aorta just below the ventricular valve (vide fig. 59). *Aosh*, sheath of aorta; *L*, lumen.  $\times 107$ . (l.p., c.l.)

Fig. 57.—Longitudinal section of the aortic wall opposite the blood-gland seen in figs. 56 and 59. *Cmf*, cardiac muscle-fibres. Section 15 micra thick.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 58.—Blood-cells from the lumen of the aorta. *a*, *b*, from the inside of the blood-gland (node), fig. 56; *c*, from the lumen close to the gland.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 59.—Longitudinal section of the lower part of the ventricle of the heart. *Bgl*, blood-gland (node); *Pc*, pericardium; *Valve*, valves between the aorta and the ventricle; *Vw*, ventricular wall; *Wda*, wall of the aorta. (h.p., c.l.)



Fig. 60.—Schematic drawing of the kidney. *Ab*, anterior branches; *Pb*, posterior branches; *P*, point of communication with the pericardium; *Rs*, renal syrinx; *U*, ureter; *Up*, uretero-connexion with the renal syrinx.

Fig. 61.—Section through the renal syrinx showing its connexion with the ureter (*Ur*) and pericardium (*Rs*). Note the arrangement of the cilia of the renal syrinx; *Pw*, pericardium. (n.p.r., c.l.)

Fig. 62.—From *A*, in fig. 61, showing the transition of the epithelium from ciliated to non-ciliated. (h.p., c.l.)

Fig. 63.—From *B*, in fig. 61, showing the cyncitial relation of the cells. (h.p., c.l.)

Fig. 64.—Section through the renal syrinx showing complete connexion with the pericardium, *A-A*. *Crs*, cavity of renal syrinx; *Pl*, plica or villus of the cyncitial plate; *Ur*, ureter. (n.p.r., c.l.)

Fig. 65.—*A-A* in fig. 64. *Pl*, villus of the cyncitial plate.  $\times 107$ . (l.p., c.l.)

Fig. 66.—From *B* in fig. 64. *Pl*, plica or villus. (h.p., c.l.)

Fig. 67.—The cyncitial plate with villus (*Pl*). (h.p., c.l.)

Fig. 68.—From the wall of the renal syrinx. *Cil*, ciliated columnar cells lining the organ; *Sw*, syringeal wall covering the epithelium. (h.p., c.l.)

Fig. 69.—A single cell from the wall of the renal syrinx showing its remarkable structure. *Bg*, basal granules; *Bm*, basement membrane.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 70.—Cross-section of a renal branch. *Ct*, connective-tissue capsule; *Pr.neph*, periodically functioning cells.  $\times 267$ .

Fig. 71.—Section from the wall of the ureter. *Ent*, internal border; *Ex*, external cover; *Nu*, nucleus; *Nuco*, nucleolus.

Fig. 72.—Longitudinal section of the ureter nearer to the kidney than that part shown in fig. 71. Note the glandular condition.  $\times 1,013.4$ ; (o.i., c.l.)

Fig. 73.—Microphotograph of a cross-section of the body in the region of the prostate coils of the female genital tube. *Hep*, hepatic branch; *Int*, intestine; *Pro*, large coils of the prostata; *St*, stomach; *Vd*, vas deferens.  $\times 14$ .

Fig. 74.—Microphotograph of a cross-section through the region of the mucous gland. *Fd*, food in the stomach; *Hep*, section of the liver; *Mg*, mucous gland; *P*, penis; *Sept*, ovispermatheca; *Vg*, uterus.  $\times 14$ .

Fig. 75.—Microphotograph of a cross-section of the posterior part of the penis. *Lm*, lumen. Two lumina are shown owing to the coiling of the organ in this region.  $\times 15$ .

Fig. 76.—Microphotograph of a trans-section of the body in the region of the brain. *Cg*, cerebral ganglia; *P*, penis; *Mg*, mucous gland.  $\times 14$ .

Fig. 77.—Microphotograph of a trans-section of the body in the region



of the genital pores. *Fv*, female genital vestibule; *Mga*, male genital aperture; *St*, stomach. This section is of particular interest since it shows the two separate openings.  $\times 15$ .

Fig. 78.—Microphotograph of a cross-section of the penis. *Ig.lp*, glandular lining of the penal cavity; *Lm*, lumen; *Og.lp*, glandular cover of the penis; *Ms*, musculo-fibrous part of the penis.

Fig. 79.—Microphotograph of a cross-section of the body in the region of the female genital duct, showing the many corrugations of the uterus (*Ut*). *Mg*, mucous gland; *Pro*, prostata; *St*, stomach.  $\times 14$ .

Fig. 80.—Microphotograph of a cross-section of the uterus, showing semen in its lumen (*Sem*). *F*, uterine pocket; *Gl*, glandular lining; *Ms*, muscular wall.  $\times 42$ .

Fig. 81.—The organs of reproduction in *Melibe leonina*. *Bil.dpr*, biluminate ampullo-prostate duct; *Amp*, ampulla; *Cl.p*, penal cleft in the mucous gland; *Mgl*, mucous gland; *Od*, oviduct; *O.sp*, ovispermatheca; *Ot*, ovitestis; *P*, penis; *Pr*, prostata; *Sv*, seminal vesicle of the penis; *Ut*, uterus; *Va*, vagina; *Ve*, vasa efferentia.  $\times 2$ .

Fig. 82.—Drawing of portion of a cross-section of the ovispermatheca. *Bm*, basement membrane; *Ept*, tall columnar epithelium lining the organ; *Mf*, muscle-cell cut longitudinally; *Nu*, nucleus; *Nuco*, nucleolus; *Kar*, chromatin granules; *Lin*, linin; *Mic*, micromeres; *Myf*, myofibrillae; *Ret*, reticular structure or axial myofibrillae; *L*, loose connective-tissue cover.

Fig. 83.—Drawing of part of a cross-section of the penis. *Cil*, cilia; *Cc*, connective-tissue cells; *Exepl*, external epithelial cover of the penis; *Iepl*, internal epithelial lining of the organ; *Int.ml*, internal fibrous layer; *M*, mucous substance; *Oc*, lining of the penal cavity.  $\times 36$ .

Fig. 84.—Drawing of a few cells from the mucous gland, showing the gland to be composed of tall columnar epithelium with a short ciliated border. *Bg*, basal granules; *Bm*, basement membrane; *Ctc*, connective-tissue capsule; *Fcb*, free ciliated border of the internal surface of the gland; *Mic*, micromeres; *Nu*, nucleus, small and shrunken; *Pcnu*, nucleus of actively filling cells; *Rs*, reticular structure of cells in the state of refilling. The cells in *A* are in a state of exhaustion. They stained poorly with Delafield's haematoxylin. *B* represents a condition prior to liquefaction of the granula. Note the nuclear membrane seems to be wanting and there are a number of small chromatic granules near the nucleus. The nucleus (*Pcnu*) is filled with uniformly sized chromatic bodies. The nucleolus being in some cases irregular in shape. *C* represents cells like *A* and *B*, but in *C* the micromeres (*mic*) are larger than in *A*, and the nucleus not quite so shrunken. That is, these cells are in a state of refilling. *D*, cuboidal epithelium from a loop of a non-glandular part of the organ.





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