

NUDIBRANCHIA DENDRONOTACEA

A Revision of the System

BY

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The present revision of the system of the Dendronotacea is based not only on studies of the literature of this group but also on thorough investigations of material belonging in the first place to the Swedish State Museum (Riksmuseum) and brought together by several collectors during many years. These results have been completed by study of material from other museums kindly placed at my disposal. For loan or gift of material I am indebted to and beg to express my thanks to the following institutions and persons: Uppsala Zoolog. Mus., Dr. I. ARWIDSSON; Copenhagen Zoolog. Mus., Dr. TH. MORTENSEN and Dr. R. SPÄRCK; Berlin Zool. Mus., Prof. C. ZIMMER, Prof. J. THIELE and Dr. B. RENSCH; Senckenbergisches Museum, Francfort-on-the-Main, Dr. F. HAAS; British Museum of Natural History, London, Dr. W. T. CALMAN and Mr. G. C. ROBSON; Messrs G. P. FARRAN and A. W. STELFOX, Dublin, and Mr. MELBOURNE WARD, Sydney.

In order to avoid a too extensive list of Literature I have referred to the list compiled by HOFFMANN in Bronn's Klassen u. Ordnungen (1932), the reference years being in a few cases followed by a corresponding letter. Only for a few works some slight difference as to year may be present; in some cases such works have been quoted in my List together with the literature later than HOFFMANN's very complete and useful index.

PRINCIPLES OF CLASSIFICATION OF THE DENDRONOTACEA

To Professor PAUL PELSENER we are indebted for a lot of important works on the Opisthobranchiate Mollusca, and his exact investigations in this group have, as known, afforded a solid base for its modern classification. Having

been occupied for several years with systematical investigations of these mollusca, especially the nudibranchs, I use this opportunity for giving an exposé, as complete as possible in a systematical respect, of one of the subdivisions of the nudibranchs, which is rather apt to illustrate the importance of the liver system for classification in these animals, a question to which valuable contributions have been given by PELSENEER. Already ALDER & HANCOCK, however, in their classic work on British Nudibranchiata, and afterwards BERGH, have employed the liver system as a classificatory principle. BERGH did that in a radical manner when establishing his Cladohepatica and Holohepatica as the chief subdivisions of the Nudibranchia. Subsequent experience, however, learns that we cannot attribute to this organ the importance as the foremost principle for subdividing the nudibranchs, and that a holohepatic and a cladohepatic organization represent, in the Opisthobranchia, merely degrees or consecutive stages of development rather than distinct types of nudibranchiate morphology. If we consider the essential shapes in which the liver organization may appear in the Opisthobranchia, we shall find the following three cases of modification to be fundamental :

1. Right and left liver keep their individuality and relative size from larval to adult stage, that is the right liver remains smaller than the left one and separated from it (ex. Dorids, Eolids, *Marionia*, Arminids).
2. Right liver is separated from left one but developed to a similar size rendering the liver system a symmetrical aspect (*Elysia* and next allies).
3. Right and left liver indistinguishable, the right one either obliterated or fused with the left one into one entire mass (most primitive opisthobranchs).

This latter type, whether arisen by means of coalescence of left and right liver portions or obliteration of right one, is the original stage since general in the primitive opisthobranchia with remaining torsion, whereas the other types may be due, in first line, to secondary detorsion or to suppressed torsion of the larval hepatic region.

That a cladohepatic stage of liver formation may be developed quite independently in several cases and in different groups is obvious and was exemplified by me in 1934 in referring to the genera *Armina*, *Aeolidia* and *Hancockia* as typical cladohepatic nudibranchs. A still more significant example of the limited value of the liver shape for classification is furnished by the fam. Hedyliidae. When BERGH established this family in 1895, he included it into the cladohepatic nudibranchia, as mentioned one of his principal subdivisions. THIELE has followed BERGH, when, in his « Handbuch » of 1931, he referred Hedyliidae to the same subordinate group. And certainly, the liver of *Hedyle weberi*, BERGH's type, represents a cladohepatic morphology. But other species undoubtedly belonging to the same family though with right made the types of distinct genera (*Hedylopsis* and *Parhedyle* of THIELE 1931, the latter syn. of *Microhedyle* HERTLING 1930) have an unbranched liver, thus representing the holohepatic

organization. It therefore seems inconsequent to keep them together in the cladohepatic nudibranchia, and a closer investigation based also on the recent reexamination by BÜCKING (1933) ⁽¹⁾ shows that this is, in reality, even impossible. There are namely a few characters common to these genera of Hedyliidae which separate them from the true nudibranchs, above all that the liver is single and not divided into a right and left portion, a division which, as remarked above, is characteristic of the Eolids, and other representatives of cladohepatic nudibranchs, as well as *Elysia* ⁽²⁾. On the other hand, in the primitive, shell-bearing, opisthobranchs, a single and entire liver, with right and left portions not differentiated, is the rule. Thus we conclude that the Hedyliidae, in spite of their want of both shell and ctenidium, are closer related to shell-bearing opisthobranchs, and that they are to be classified among them and separated from the cladohepatic nudibranchs.

A further characteristic of Hedyliidae corroborating this conclusion is the position of the nervous ring in front of the pharynx, as in several Bullariacea like *Philine*, whereas all nudibranchs in a proper sense have the nerve ring placed behind the pharynx. These two extremes cannot be overbridged and must be considered as the final result of a development into different lines. These points of view, together with a respect to the whole organization of the Hedyliidae necessitates to establish, for this family, an order of its own, *Hedylacea*, coordinated with the Nudibranchiata. Whereas the latter have a close relation to the Notaspidea from which they probably originated, as was supposed first by PELSENEER, the Hedylacea have a quite different appearance and certainly a separate origin. They seem to be by far more widely separated from the Nudibranchia and from the Notaspidea, too, than these groups from each other. In wanting a ctenidium and a mantle cavity they agree with the Nudibranchia, it is true, and from shell-bearing opisthobranchs as well. Therefore, it would be justified to keep them in the Ordo Acoela established by THIELE (1931), unless this order might be, with better advantage, given up and the contained subordinate, strictly characterized, groups made to orders. Likewise the

⁽¹⁾ According to BÜCKING, the species investigated by him was described briefly in 1892 by STRUBELL. His description, reprinted by BÜCKING, is, however, so incomplete that it cannot be considered as a diagnosis sufficient to recognize the animal. BÜCKING (p. 573) therefore drops STRUBELL's genus name *Acochlidium* in favour of *Hedyle* BERGH 1895, preserves, however, his specific name and designates the species *Hedyle amboinensis* (STRUBELL). This choice of names is in good concordance with the rules of nomenclature and the more authoritative since BÜCKING has all rights as first reviser, except that the specific name should be *Hedyle amboinensis* BÜCKING 1933.

⁽²⁾ BERGH's figure of the liver of *Hedyle weberi* reproduced in 1895, pl. II, fig. 1, is quite peculiar and different from that of every cladohepatic nudibranch: there is no gall duct entering the right side of the stomach and consequently no distinct right liver, and this state of affairs, puzzling as it may seem, is verified by BÜCKING and consistent with the view here presented.

Ordo Pleurocoela of THIELE is superfluous if we elevate its constituting groups Bullariacea (= Cephalaspidea) and Aplysiacea (= Anaspidea) to orders. There is no doubt that the Aplysiacea have arisen from the Bullariacea, and I pointed out in 1926 that *Newnesia*, in several anatomical respects, may be considered as the ancestral of the Aplysiidae. The Bullariacea, furthermore, are certainly the origin also of Pteropoda and Sacoglossa and thus are more practically kept apart as a unity of its own than united with the Aplysiacea.

Though a discussion of the classification of the Opisthobranchia as a whole is not the purpose of the present paper, the above remarks may be of interest as showing the second hand importance of the liver formation for the classification of the naked opisthobranchs. It is PELSENEER's merit to have first seen the disadvantage of BERGH's division into Cladohepatica and Holohepatica, and already in 1892 he gave, therefore, a new arrangement of the Nudibranchia (as well as the Opisthobranchia in general), denominating the subordinate groups after typical genera, thus accepting for the nudibranchs the tribes Doridoidea, Tritonoidea, Aeolidoidea and Elysoidea⁽¹⁾. This classification, indeed, has turned out to be a decided progress. Nevertheless, ELIOT (1910) still used the older classification of BERGH in which, however, he tried to adopt PELSENEER's groups as subdivisions. For this purpose he thought it suitable to divide the Tritonoidea by placing the fam. Tritoniidae into the Holohepatica and retaining the remaining families as a coordinate division, Dendronotoidea. The splitting up of the Tritonoidea, however, did not imply any advance of the classification, since the close affinity of *Tritonia* (now *Duvaucelia*) and *Dendronotus* is an undeniable fact. Other circumstances, too, prove that a classification of nudibranchs according to their holohepatic or cladohepatic organization, as mentioned above, can be performed only in a secondary place, and that the first order categories are characterized by other marks; a special liver structure is mostly significant of each family, it is true, but similar stages of development may appear independently in different families. Under such circumstances, I found it necessary to restore (1934) PELSENEER's Tritonoidea though using for this group the name Dendronotacea. Since a closer argument of this theme and the adducing of new facts seemed desirable, I have chosen this occasion for giving a revised classification of whole this group of nudibranchs thinking this to be of value for continued work.

As I pointed out in 1934, the essential characteristic of the Dendronotacea is an external one: the presence of rhinophore sheaths within which the clubs can be retracted. These sheaths may be a remnant of the foremost parts of the back margin and persist even when the regressive development which dominates in the nudibranchs has proceeded so far that all trace of the lateral back margin has disappeared (e. g. *Dendronotus*, *Doto*; in *D. indica* a crest still remains on the sheaths). In the Eolidacea and Arminacea, on the other hand, we find, as I

(¹) Cf. LANG, *Lehrb. d. vergl. Anatomie*, 1900, p. 15.

pointed out in 1934, simple rhinophores without sheaths even in genera where a lateral back margin still persists (e. g. *Notaeolidia*, *Armina*); traces of rhinophore sheaths, however, may be seen in Antiopellidae and Arminidae (« caruncula »). As no reversibility is likely, the groups which have already reduced their rhinophore sheaths cannot be expected to bring them forth anew, and, besides, in the Dendronotacea, no transitions are known to combine typical forms with sheath-less ones. Thus these two types of nudibranchs can always be held apart from each other. In both, however, the development is characterized in a disintegration of the liver from a compact mass to a more or less extensively branched organ: either *ramose* (with central liver stem and finer distal branches) or completely *diffuse*: either of a *flocculent* structure (whole organ dissolved into tubes more or less beset with tubulose tufts, as in *Melibe*) or of *racemose* formation (as in *Hancockia* and *Doto*).

A similar disintegration of the liver is to be observed in two other chief divisions of the Nudibranchia, viz. Eolidacea and Arminacea, in each group passing on quite independently of the other. In all these parallel cases the primitive forms keep still a compact or else little divided liver mass, whereas the diffused liver, the former representing the right liver *and* the foremost part of the left cessive disintegration of the liver organ thus must be the leading idea in the task of their classification. In the Dendronotacea the primitive stage is that of Duvauceliidae in which the liver is concentrated into a single mass having, however, a distinct duct also from the right liver portion. A complete separation of the right liver from the common mass has been performed in the Duvauceliidae solely in *Marionia*. This is the first step towards a liver disintegration, and it coincides with the original plane of symmetry. But a tendency of establishing symmetry between left and right side makes itself marked also on an earlier stage, before the right liver separates; cf. *Lomanotus*, below. This tendency may take its expression in a bipartition into an anterior and a posterior liver, the former representing the right liver *and* the foremost part of the left one. Each part of this anterior liver (thus right and left half) has its own duct debouching into the stomach, even when it is fused to an entire mass. This state of affairs is represented by Scyllaeidae and the new genus *Aranucus*. In Scyllaeidae the anterior liver may be split up into its elementar halves, and so we find also in *Pseudobornella* (Fam. Bornellidae). The division of the liver organ in this way is, of course, accompanied by a complete bipartition of the original single duct from the left liver, which parts into a left-sided and a posterior duct. In this way a symmetry is attained by a liver which divides up into a few parts but still keeps a holohepatic appearance in being completely unbranched.

If the organization is cladohepatic, that is the liver branching in elongate stems and rami, the symmetry tendency brings about a branching which corresponds reciprocally in both sides of the body. Above all, the left liver attains a shape, the symmetry of which is completed by the right liver. The left-sided

correspondent or moiety to the right liver may still be united to the main part of the left liver by its duct, so that this debouches in common with the posterior liver duct and a separation of the left anterior liver part from the posterior one is not perfect. This latter state, represented by *Fimbria* and *Doto*, is evidently more primitive than a complete separation with quite distinct ducts as in *Hancockia*. Often these ducts debouch so closely that it is impossible to state whether they are separated or not, as in *Bornella*. BERGH states these facts in *B. arborescens* (1890, p. 888, pl. 89, fig. 1) :

« In den hintersten Theil dieses Magens mündete von jeder Seite und einander genähert (Fig. 1 fg) der glandulöse vordere Gallengang der Nebenleber; mit dem linken Gange verbindet sich, dicht vor seinem Eintreten in den Magen, der auch glandulöse gemeinschaftliche Gallengang aus der Hauptlebermasse. » In a foot-note BERGH remarks : « Bei den früher von mir untersuchten Individuen der *Born. arborescens* mündete der gemeinschaftliche Gallengang gesondert in den hintersten Theil des ersten Magens, während die zwei vorderen in den vordersten Theil sich öffneten; dasselbe Verhältnis fand sich in der *Born. digitata* und in der *Born. calcarata*, in der *Born. excepta* dagegen habe ich das Verhältnis wie oben gesehen. » Since *B. excepta* proves to be primitive in lacking all liver projections, it may be inferred that the common duct is also a primitive condition.

The liver may, consequently, show the same stages of disintegration in different families, as well as different stages within the same family; therefore it is

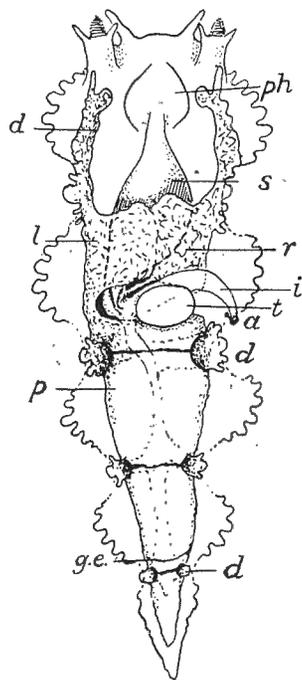


FIG. 1. — *Lomanotus genei*.
Liver extension

COMMON DESIGNATIONS IN TEXT-FIGURES.

- | | |
|---------------------------------|----------------------------------|
| a = anus | p.v. = pleurovisceral connective |
| a.s. = accessory sac | r = right liver |
| b.c. = bursa copulatrix | rh = rhinophore |
| b.g. = buccal ganglia | r.s. = renal syrinx |
| c = cerebral ganglia | s = stomach |
| d = liver diverticulum | s.g. = salivary glands |
| e = eye | t = heart |
| f = ampulla | u = urinary sac |
| g = gonad | v = vagina |
| g.e. = gonad end | v.d. = vas deferens |
| h = hermaphrodite duct | v.s. = vesicula seminalis |
| i = intestine | ♂ = male organ or aperture |
| l = left anterior liver part | ♀ = female aperture |
| l.d. = left anterior liver duct | nerves = 1 buccal nerve |
| m = mucus gland | 2 frontal nerve |
| n = nephroproct | 3 lateral nerve |
| o = oesophagus | 4 rhinophorial nerve |
| p = posterior liver part | 5 anterior pallial nerve |
| p.g. = pedal ganglia | 7 median pallial nerve |
| ph = pharynx | 8 anterior pedal nerve |
| pl = pleural ganglia | 9, 10 posterior pedal nerves |
| pr = prostata | 11 posterior pallial nerve |

not apt as a direct indicator of relationship. We can only say that *Bornella* represents a more primitive stage of division (like that of *Fimbria*) than *Scyllaea*, which, on the contrary, is more primitive (like *Pseudobornella*) in its lack of branchment.

A high degree of disintegration, of course, excludes all coalescence between right and left liver masses like that one occurring in *Duvauceliidae* and other genera where the liver mass is still concentrated round the stomach, as we have seen in *Aranucus* and *Scyllaea* and will find in *Lomanotus* and *Dendronotus*.

No particulars have been known about the liver of *Lomanotus* except those illustrated by ALDER & HANCOCK in their figure of *Eumenis marmoratus* (Fam. 2, pl. 5, fig. 8) ⁽¹⁾. Thanks to the kindness of Messrs. FARRAN and STELFOX, Dublin, who sent me a specimen of *L. portlandicus* (= *genei*), I could unravel the conditions in this species (Fig. 1). They prove to differ essentially from those of *L. marmoratus*. Right and left liver parts are namely fused quite as in *Duvaucelia* and cover the upper side of the stomach, left anterior liver part has its own duct (Fig. 2) but is not separated from the posterior one; their ducts debouch very closely, but their masses are continuous on the left side of the stomach. The posterior liver is surrounded by the gonad (not covered by it on the dorsal side only, as in *L. marmoratus*) and branches to each of the inward undulations of the back margin. These branches are short and little ramified, and their short ends do not penetrate into the papillae in sharp contrast to *L. marmoratus* as stated by ALDER and HANCOCK; a variation in this respect is probable (cf. ELIOT, 1910). From the anterior parts of the liver, lobes are sent forwards even to the outer sides of the rhinophore sheaths, into which they enter shortly, but no ones entered the papillae of the back margin.

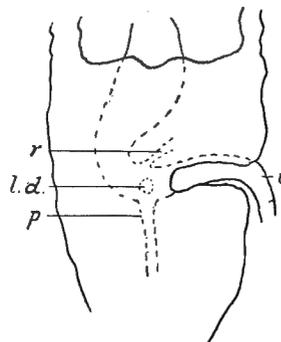


FIG. 2. — *Lomanotus genei*.
Liver openings into stomach.

These differences between the two species are very remarkable and prove that the inner anatomy may be very different in undoubtedly closely related species, when the type is primitive in its systematic position.

In the next vicinity of *Lomanotus* we find *Dendronotus*. Here the right and left liver (cf. ALDER & HANCOCK's fig., Fam. 3, pl. 2) are of a uniform appearance, but both are completely separated from the posterior liver part (Figs. 3, 4). The ramifications of all the liver portions recall those of *Lomanotus* and represent the same ramose type; no doubt *Dendronotus* took its origin in *Lomanotus*-like ancestors. A reexamination of the liver of *Dendronotus frondosus* from the Swedish west coast gave the following result somewhat differing from that of ALDER & HANCOCK as to liver extension (cf. fig. 4). The right liver (*r*) and the

⁽¹⁾ Here the central parts of the liver are not stated with certainty, as the authors admit.

anterior part of the left one (*l*) are fused together on the upper side of the stomach into a flattened mass, somewhat excavated in its upper side where the intestine is lodged, which forms a reflected curve forwards before running to the right side. The left anterior liver is narrower than its right moiety and more extended in a vertical direction. A slight asymmetry thus arises which appears in the branchment, the right liver branches emanating from a narrow lobe, the anterior ramus is much elongated and narrow.

An extreme stage of this cladohepatic disintegration is realized by *Hancockia*, in which all liver tissue has disappeared from the liver ducts and been included

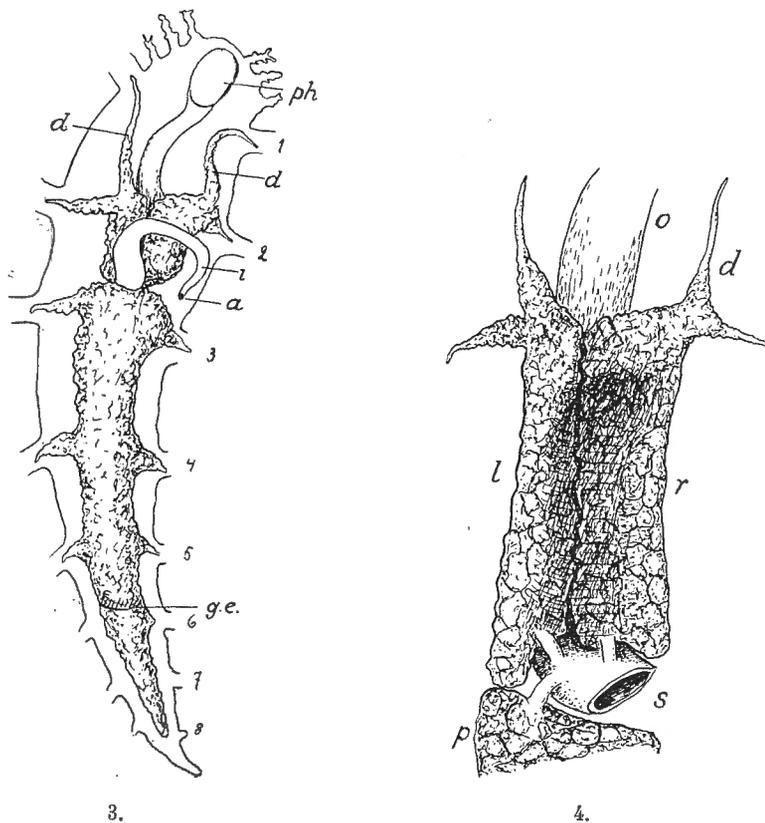


FIG. 3. — *Dendronotus frondosus*. Liver extension.
 FIG. 4. — *Dendronotus frondosus*. The liver portions and their ducts into stomach.

in the papillae : the racemose type. The liver of *Hancockia* might be derived, however, quite as well from a type like that of *Bornella*, but other organs than the liver disprove this assumption. *Bornella*, in its turn, seems to be, as mentioned, a descendant from the *Fimbria* stage. The latter liver type we may derive from a form like that of *Marionia*, thus with the right liver separated from the left one, which was originally in one single and compact mass. When the right liver began to attenuate and direct itself to the papillae, the anterior part of the left liver mass detached itself from the main body of the left liver, though it still

adhered to the original duct, and, by the tendency of attaining symmetry, was differentiated in a similar way as the right liver. So we find the conditions in *Fimbria*: the posterior liver is here still a compact mass, though with fine rami to the papillae, as a whole held together by the superficial gonad. BERGH (1875) described the anatomy of *Tethys leporina* (= *Fimbria fimbria*), but misinterpreted the liver conditions; the right and left anterior liver stems he thought to be the salivary glands and speaks of only one gall duct (cf. his figs. 1 and 2, pl. XLVII). It is the merit of v. IHERING (1876) that we know the real organization in this respect; he found the true salivary glands as a pair of short threads and recognized the anterior parts of the liver (cf. his pl. II, fig. 1), but even in 1917 MISURU describes and figures in *Tethys* (= *Fimbria*) these parts as salivary glands, though he doubts their nature as such because of their distance from the buccal cavity. BERGH (1892), however, described the liver in his fam. Tethymelibidae as consisting of two anterior portions and one posterior one. For details I refer to fig. 5.

The same mistake was made by BERGH (1875) in *Melibe*; in 1880, however, he describes the liver of *M. vexillifera* correctly. In this genus, indeed, the liver is normally built, inasmuch as it shows the right portion distinct. The whole liver is flocculent or else diffuse, not compact. The combination of the left liver ducts may vary: in *M. leonina* the left anterior portion is still in connection with the posterior duct, but in other forms of *Melibe* the ducts are completely separated. Thus we state in this genus a condition like that of *Bornella*.

The liver of *Doto* (cf. ALDER & HANCOCK, Fam. 3, pl. 4, fig. 2) shares with that of *Fimbria* and *Melibe leonina* the common duct of the left portion but otherwise represents a complete cladohepatic or racemose scheme, inasmuch as all the hepatic tissue has been concentrated within the papillae.

In *Phylliroe* the liver is tubular and unbranched; the dorsal anterior liver coecum is the right liver, the inferior coeca are the homologon of the anterior left liver portion.

Thus we establish in the Dendronotacea two ways of liver evolution towards a complete disintegration, the one marked by a series represented by *Duvaucelia*, *Aranucus*, *Lomanotus*, *Dendronotus*, *Hancockia* as well as *Scyllaea*, *Phylliroe*, the second by the series *Marionia*, *Fimbria*, *Melibe*, *Bornella* and *Doto*.

That *Melibe* is to be derived from *Fimbria*-like forms cannot be doubted on account of its great concordance in many morphological points, and yet the liver organ of the two genera is very different: in *Fimbria* a compact posterior liver, in *Melibe* one which has become diffused into a loose mass of tubes with or without flocculent tufts (cf. figs. 5 and 6). This difference may be due to the various formation of the gonad, which stands in an intimate correlation to the liver. In *Duvauceliidae* and *Aranucus* the gonad is spread over the whole surface of the posterior liver, and this is the case in *Fimbria*, too. But here the fore-

most left branch from the posterior liver duct is free from the gonad and runs on the upper side of the liver-gonad mass backwards to the second papilla on the left body side (fig. 5). On the right side, the foremost lateral branch comes from the interior of this mass, and so does the third pair of branches; like the preceding ones they fork within the body musculature and one of the rami sends a fine diverticle into the papilla. Whether this happens also in the hindmost pairs of papillae could not be stated in my material.

In *Melibe* both liver and gonad have been dissolved in the way mentioned :

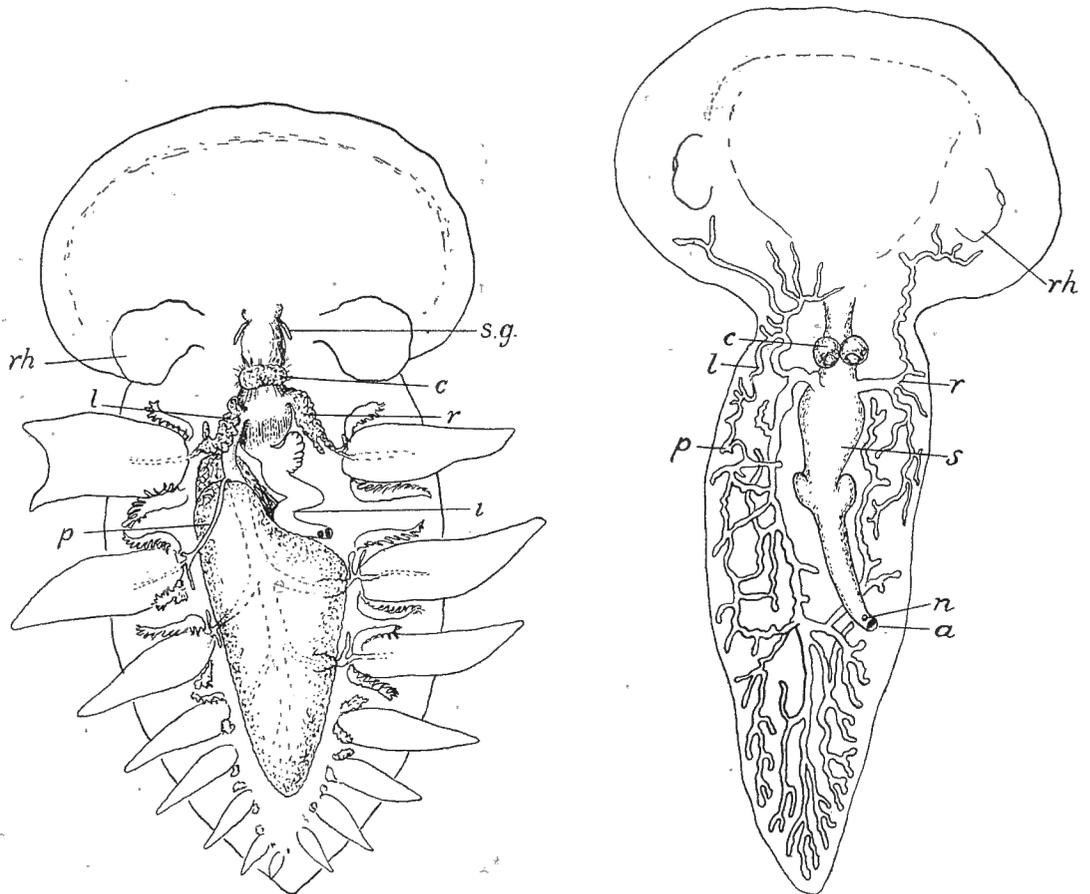


FIG. 5. — *Fimbria fimbria*. Liver organization.

FIG. 6. — *Melibe leonina*. Liver organization.

both are intimately woven together into each other with their diverticles. The gonad, consequently, does not any longer hinder the liver differentiation.

In *Lomanotus genei* the gonad has broken up into a lot of separate masses, and in *L. marmoratus* and *Dendronotus* (judging from the figures and statements of ALDER & HANCOCK) these cover only the upper side of the liver organ, which therefore is still less hindered to branch. The same we find in *Doto*; in *Bornella* and *Scyllaea*, on the contrary, the ovary is dissolved into a few globules,

which, in *Bornella*, lie dorsally of the posterior liver, symmetrically arranged inter se, whereas, in *Scyllaea*, the few (2-4) large ovarial masses are mixed up with the liver lumps in such a way that they form a bisymmetrical system together.

These 2 or 3 (4) liver lobes of *Scyllaea* (fig. 7) are of a globular shape and completely without branches. ALDER & HANCOCK (1855) and BERGH (1875), however, describe canals running from the liver lobes to the dorsal processes. The canals, however, are simply the renal tubes, which lie loosely on the surface of the liver globes and are separated from them by a thin tunica, so that no communication between the liver and the ends of the canal exists. Quite as ALDER & HANCOCK draw them in their figures (Fam. 2, pl. 5, fig. 1 or more distinctly in fig. 5) they are thinning out in their ends on the liver lobes but grow thicker in the opposite direction, a fact which proves that they do not lead from the liver. On the contrary, if we follow the kidney and its ramifications, we shall find the distal tubes to be identical with the canals in question (cf. Fig. 36). BERGH (1875, pl. XLIII, fig. 6, and pl. XLIV, fig. 13) draws some large branches from the posterior liver which make the impression

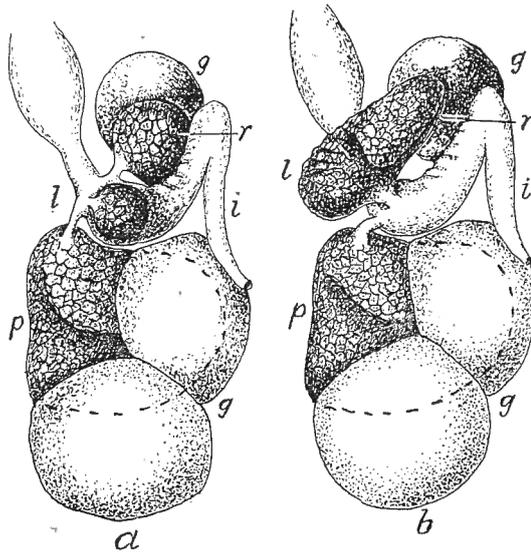


FIG. 7. — *Scyllaea pelagica*.
Two modifications of liver shape.

of real liver canals, but these may be nothing but the connective bands which attach the liver and the gonad portions firmly to each other. In all specimens of *Scyllaea* which I dissected, the liver masses proved to be more or less regularly rounded with a completely even surface without diverticula. As to *Crosslandia*, ELIOT says (1902, p. 67) that the liver masses « send forth very slender light green diverticula, which until carefully examined have rather the appearance of veins, to the base of the wings and rhinophores », but it may be doubted if these are really liver canals and not renal tubes. In 1908 (p. 92) ELIOT says that he could not find any hepatic diverticula extending into the cerata; so the liver globes even in *Crosslandia* seem entire and unbranched.

A recapitulation of the combination between liver and gonad gives the following facts. The gonad is a single superficial mass surrounding the posterior liver in *Duvauceliidae*, *Aranucus*, *Lomanotus genei* and *Fimbria* (the two latter less perfectly). The gonad lies to the right of the unbranched posterior liver in *Pseudobornella*. It appears as a single mass with signs of a beginning partition

and lies above the posterior liver in *Dendronotus* and *Lomanotus marmoreus* (both having a ramose liver) and in *Doto* (with a racemose liver). The gonad is dissolved into a flocculent mass in *Melibe*, where the liver is disintegrated in a similar way, or as a tubular net-work (*M. leonina*). In the remaining families of the Dendronotacea the gonad is divided in more or less numerous globular masses which either lie at the side of the liver in Scyllaeidae (liver masses globular) and Phylliroidae (liver masses tubular); in both cases the liver is unbranched; or lie dorsal of the posterior liver in Bornellidae (liver ramose) and Hancockiidae (liver racemose).

This scheme gives a brief survey of the evolution of liver and gonad in the Dendronotacea from the simple massiv complex to the completely disintegrated one but it separates not only forms widely different, but, on the other hand, types which have an undoubted close relationship, such as *Fimbria* and *Melibe*, *Pseudobornella* and *Bornella*, *Lomanotus genei* and *marmoratus*. In order to judge the affinity between all these forms we have to consider not only the organs mentioned but other characters of systematical importance, above all the genitalia, the radula and the external habitus.

A comparison of the genital system of the different genera of the Dendronotacea gives the impression that these organs are rather diverse in details. This holds true not only with the gonad, as we have just seen, but also with the distal parts. In the female duct we find in all the genera a vaginal bursa copulatrix, except in *Phylliroe* and *Hancockia californica*, where, instead, a vesicula seminalis is attached to the oviduct. The bursa copulatrix is, as a rule, situated close to the female aperture (in Duvaceliidae even separated from it, as in the pleurobranchid genera *Berthella* and *Bowyeria*, cf. ØDHNER 1934), but in a few cases a vesicula seminalis is said to exist in the inner end of the vagina or the oviduct (*Hancockia californica*, *Dendronotus*). It is very interesting that in *Dendronotus* a true but seemingly dwarfed bursa copulatrix is to be found in its general place near the distal end of the vagina (cf. figs. 38-41); it has a distinct internal cavity but is too small to fulfil any function. An analogous state of affairs is found by me also in *Scyllaea* (cf. fig. 30). The upper vesicula seminalis of *Hancockia californica* has different combinations than *Dendronotus*, inasmuch as its distal outlet leads to the simple female duct which is not split up into oviduct and vagina, but retains the primitive diaulic condition, whereas *Dendronotus* realizes a special differentiation. The latter genus has a typically triaulic genital apparatus, a most perfect one and singular in the Dendronotacea; it recalls that of the Doridacea. A bipartition like that of *Dendronotus* does not exist in any other genus of this group. In *Melibe leonina* KJERSCHOW AGERSBERG (1923) describes a prostata as part of the female duct and a split hermaphrodite canal, but these statements have proved to be incorrect (fig. 8) and the prostata belongs quite regularly to the male part, though it is situated so close to the bipartition point that it may easily mislead.

In order to verify the conditions described by MAC FARLAND (1923) in *Hancockia californica*, I examined two specimens of the Mediterranean *H. eudactylota* (Riksmuseum collections). Unexpectedly, they showed a normal type of the genital organs with a well-developed bursa copulatrix and no uterine vesicula seminis (fig. 9). In the genus *Hancockia* the genital organs thus seem to be quite as unsettled as the liver in *Lomanotus*, so that they offer specific characteristics instead of generic, as in other familiae.

In *Phylliroe lichtensteini* (= *atlantica*) I have found (fig. 9) the female duct aberrant from that of other Dendronotacea in totally lacking a bursa copulatrix. BERGH (1873) describes the genital organs of this species correctly and says that the oviduct, after its issue, has a « rötlichbraune Fortsetzung... (deren Innenseite starke, der Länge nach laufende Falten darbietet) », a formation which, in my

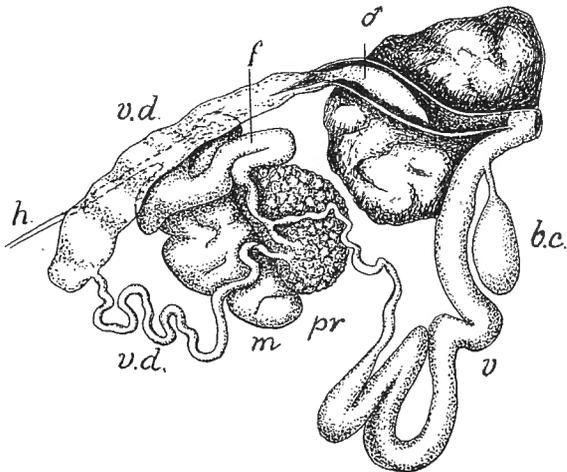


FIG. 8. — *Melibe leonina*. Genital organs.

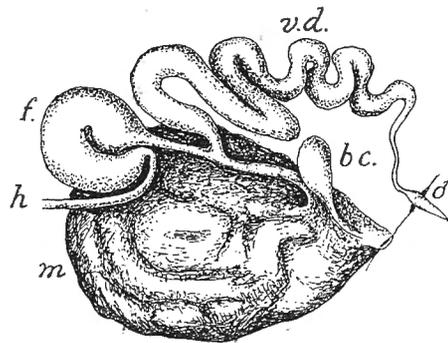


FIG. 9. — *Hancockia eudactylota*. Genital organs.

material, had the shape of a vesicula, because its fundus had at least the same length as its stalk, though this is a varying character. Its muscular walls indicate a contractory function, and I infer that this vesicula may act as a receptaculum seminis and that it and the interior of the mucus gland may fulfil the same function as the muscular vagina and the thin-walled bursa copulatrix of *Dendronotus*. The genital organs of *Ph. bucephala*, which are quite similar, were well described by VESSICHELLI (1908), but the figure of these reproduced in LANG (1900, p. 385, fig. 343) refer to SOULEYET's *bucephala* (1852) which is synonymous with *Ph. lichtensteini* (= *atlantica*).

Concerning the male portion of the genital organs the most prominent feature is not only the existence or absence of a prostata gland, but also the mode of separation of the ducts. In Duvauceliidae and Aranucidae the male canal is completely devoid of a prostata or a prostatic portion, but it emerges from the main glandular portion of the genitalia, which evidently serves as prostata and

female glands simultaneously. This state of affairs may be a primitive condition; hermaphrodite duct leads to the gland, and from this both female and male distal ducts emanate. The next step is the separation of a prostata gland from the main glandular mass (*Fimbria*, *Melibe*, *Doto*, *Dendronotus*, partly). Later on, the prostata obliterates again, first to a glandular portion of the vas deferens (*Lomanotus*, *Scyllaea*, *Bornella*, *Hancockia*). A reduction of the prostata takes place, gradually, in *Dendronotus*, the different species being characterized by a specific shape of the prostata. In *Fimbria* (fig. 11) the prostata has the shape of a thick discoid mass with numerous radiating vesiculae in a radiating arrangement, and in *Doto* it is a special gland debouching into the vas deferens.

Below, a survey is given of the duct differentiation; it shows, at the same

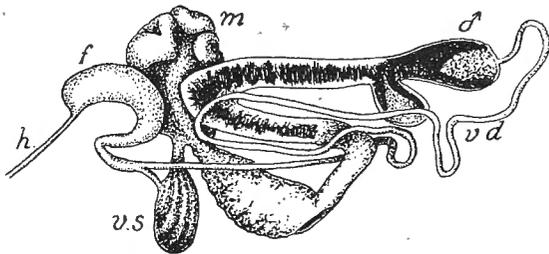


FIG. 10. — *Phylliroe lichtensteini* (= *atlantica*).
Genital organs.

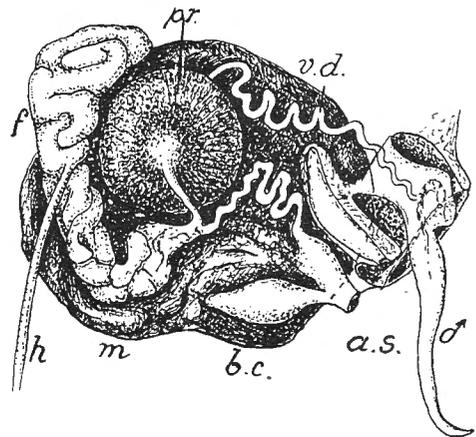


FIG. 11. — *Fimbria fimbria*.
Genital organs.

time, the main stages of evolution. Each stage, except the last one, has its analogon in fam. Pleurobranchidae, and the analogous genus is stated besides :

- I. The bipartition of a male and female duct takes place not earlier than in the albumen gland (here thus the hermaphrodite duct debouches and the vas deferens emerges).
Fam. *Duvauceliidae*, *Aranucidae*; analogous *Euselenops*.
- II. The bipartition takes place already in the hermaphrodite duct.
 - A. Female duct entire, not split longitudinally, thus *diautic* in the sense of ELIOT 1910.
 1. Male duct without own glandular part, thus with no prostata.
Fam. *Lomanotidae*, *Scyllaeidae*, *Bornellidae*, *Hancockiidae*, *Phylliroidae*; analogous *Bowvieria*.
 2. Male duct with own glandular part, probably separated from the main glandular mass, thus with prostata.
Fam. *Fimbriidae*, *Dotonidae*; analogous *Pleurobranchaea*.

B. Female part split longitudinally in an uterine and a vaginal portion which communicate proximally and distally, thus *triaulic* in the sense of ELIÖT.

Fam. *Dendronotidae*; no analogous pleurobranchid, but among nudibranchs *Doridacea*, *Eolidacea*.

We have still an important inner organ to consider, viz. the radula. In the Nudibranchia, as in general in the Gastropoda, the primitive type of radula is the broad one with numerous laterals of about the same shape of simple hooks. Starting from this type reductions and modifications are usual. A reduction of the number of laterals has taken place in *Aranucus* and attained its culmination in *Hancockia* with the radula formula 1.1.1 and *Doto* with 0.1.0, not to speak of the total reduction of radula and pharynx in *Fimbria*. A differentiation of the teeth is to be observed in *Duvauceliidae*, where both median tooth and inner lateral have been modified, and in *Crosslandia* and *Notobryon*, where the inner laterals have a shape differing from that of the remaining ones. All these manifestations are of secondary origin. In the jaws a progressive evolution may be indicated by their shape (primarily without, secondarily with a processus masticatorius) or their extension, whether still covering only the foremost part of the pharynx or the whole of it. Other internal characteristics which are to be considered for the classification but which are difficult to place in a series indicating their evolution are the optic nerve (elongate in *Duvauceliidae*, *Bornellidae*, *Dendronotidae* and *Dotonidae*, short or almost imperceptible in *Aranucus*, *Phylliroe*, *Fimbria*), and the presence of stomachal plates in certain *Duvauceliidae*, *Scyllaeidae* and in *Melibe*.

Whereas in shell-bearing mollusca the anatomy is the fundamental base of all classification, quite natural, because external differentiation is prevented by the shell and thus plays a subordinate role, a contrary state of affairs must be admitted in the nudibranchs. This is the case, above all, in the Dendronotacea and only to some extent in the Doridacea, in which all the Dorididae are characterized by a rather uniform external morphology. That, in the Dendronotacea, the external habitus offers very good systematical fundamentals, is due to the fact that this is an excellent indicator of the evolution in contrary to the shell of the gastropoda in general. We find this fact already from an examination of the body parts which are most significative of the group, viz. the rhinophores. The sheaths of these may be derived from the back margin of forms like the *Heterodorididae*; the back margin has been, as a rule, obliterated in all the Dendronotacea (except in the most primitive families: *Duvauceliidae*, *Aranucidae*), but it remains as the rhinophore sheaths, and their derivation from the back margin is often proved by a crest running up their external side (*Duvaucelia*, *Lomanotus*, *Scyllaea*, *Doto indica*), or in the papillae replacing this crest in *Dendronotus* and *Bornella*; and it may be supposed that a further sign of this origin is the entering of a liver diverticulum into the rhinophores (*Lomanotus*, *Hancockia*, *Bornella*) or to their base (*Dendronotus*). It may be supposed that the margin of the rhinophore sheaths is homologous with the ends of the furrow-shaped

rhinophores of the Notaspidea, and that the clubs have developed from the sensory epithelium and folds within them or their homologues (organ of HANCOCK). The rhinophore clubs are, likewise, in the Dendronotacea, of a good systematic value, inasmuch as they have a peculiar brush-like structure in Duvauceliidae and *Aranucus*, evidently a secondary acquisition, and a longitudinal folding in *Hancockia*, probably a modification of the former; in most cases they are laminated transversally, and only in Dotonidae and Phylliroidae they are smooth.

Whereas a trace of notum margin persists in the above-mentioned forms which are primitive also in their liver organization, this margin disappears in more advanced forms and is only marked by the processes or papillae (cerata) which, in their turn, undergo a differentiation in several directions thus offering good marks for distinguishing and classification. They are still simple, dendriform, in Duvauceliidae (where they may be totally reduced in some cases, e. g. *Tritonidoxa*) and they are much more simplified in branching, though differentiated in general shape, in *Aranucus*; they consist of simple papillae set in a single series in *Lomanotus* and in pedunculate lobes in *Hancockia*. Most of the remaining genera have the papillae differentiated into two directions, inasmuch as each process consists of a single or composed papilla together with gill-shaped plumes, the latter either at the base on each side of the papillae (*Fimbria*), or along the papilla itself (*Bornella*). In Scyllaeidae gills are spread over the surface of the marginal lobes. The gills are nothing but modified rami of the original processes, a fact obvious in *Doto*, where, generally, the papillae bear simple tubercles arranged in several rings; sometimes, however, as in *D. coronata*, some of the tubercles are modified into branched processes, that is gills. This phenomenon is most distinct in the new *D. japonica* described below and is located to the base of the inside of the papillae. It has given rise to the establishment of a distinct genus, *Bornellopsis* O'DONOGHUE (1929), which must, however, be considered synonymous with *Doto* (*vide infra*). It seems possible that a further reduction of the branches of the papillae may lead to the large simple lobes of *Melibe*; and even a complete reduction of the papillae may take place, as in *Phylliroe*, an evolution which probably set in from forms like *Scyllaea* having still an unbranched, but divided, liver.

As a consequence of the persistent back margin in Duvauceliidae and Aranucidae the anus is lateral in those genera, which is also a sign of primitivity; in other genera of the Dendronotacea the anus is displaced more or less dorsally. In the aberrant Phylliroidae it keeps an original lateral site in *Phylliroe* but is dorsal in *Cephalopyge*. The position of the nephroproct is an important characteristic: generally, it lies close in front of or inside the anus, and in Phylliroidae it lies about in the middle of the right side notwithstanding the position of the anus⁽¹⁾. The displacement of the anus is always located to the interhepatic space

(¹) The statement of BERTOLINI (1935) that no renal pore exists in *Ph. atlantica* is against BERGH'S clear establishment (1873, p. 213) and is easily disproved by observation.

between right and left posterior liver, so that it is always situated behind the first papilla following the rhinophores; in *Lomanotus* it is placed in the second inward curve of the papillated margin which corresponds just to that place.

A further external character of systematical value is the velum significative of the Arminacea in contradistinction to the Eolidacea, but in the Dendronotacea variously developed: well-marked in the primitive Duvauceiidae (and in *Hancockia*), which thus show agreement with the Arminacea, as well as in Tethyidae, where the velum attains an enormous size. This primitive velum differentiates into two directions: it simply diminishes in size in Dotonidae, or it becomes wholly dissolved into isolated papillae (Dendronotidae, Bornelliidae), till even these disappear (Scyllaeidae, Phylliroidae).

Taking into consideration all these points of view we may arrange systematically the families of the Dendronotacea as follows:

SYNOPSIS OF THE FAMILIAE OF DENDRONOTACEA

Vas deferens emerges from albumen gland:

I. Back margin continuous, though low, even running up the rhinophores, with or without branching tufts. Anus lateral. Velum well developed, as a rule with marginal processes and lateral furrow-shaped tentacles.

A. Cerata separate, in discontinuous series. Rhinophore club brush-like. Median tooth of radula well developed. Posterior liver mass compact and surrounded by the gonad.

1. Left liver in one mass; no liver diverticula. Rhinophore sheaths with more or less even (not lobate) margin. Velum with 4 to several papillae (or smooth). Cerata branched (rarely absent). Jaws covering only anterior part of pharynx. Radula with numerous laterals, median tooth smooth or with a few coarse denticles (never finely serrated). Nephroproct close in front of (or above or below) anus. Optical nerves elongate Fam. *Duvauceiidae*.

2. Left liver divided into an anterior and a posterior portion, the former fused to right liver and sending diverticula to the foremost pair of cerata. Rhinophore sheaths with smooth margins prolonged into an anterior lobe. Velum with one pair of papillae beside furrow-shaped tentacles. Cerata bifid. Radula with a few laterals and serrated median tooth. Nephroproct close above anus. Eyes almost sessile on brain. Jaws covering almost whole pharynx. Fam. *Aranucidae*.

Vas deferens emerges from hermaphrodite duct:

B. Cerata in a continuous series, simple, spoon-shaped. Rhinophore club perfoliated; sheaths with papillate margin. Median tooth of radula absent or obscure, laterals numerous. Liver branching more or less to cerata and to rhinophores. Gonad encircling or dorsal to posterior liver. No stomachal plates. Nephroproct close above anus ... Fam. *Lomanotidae*.

II. Back margin produced into large lobes (continuous or separated, with a trace on the rhinophore sheaths) covered more or less with branchial tufts. Anus lateral

or latero-dorsal. Velum indistinct; no frontal papillae. Rhinophore club perfoliate. Liver divided into 2-4 compact, not branching, globular masses. Gonad separated from liver, appearing in a few globular masses. Jaws covering whole pharynx. Radula with several laterals; median tooth may fail. Stomachal plates present. Nephroproct close inside anus. Eyes with very short optic nerves.
Fam. *Scyllaeidae*.

III. Back margin discontinuous, remaining only in the paired, generally compound, latero-dorsal cerata. Anus latero-dorsal. Jaws (when present) covering whole pharynx.

A. Rhinophore club with longitudinal plications. Cerata in the shape of lobes with a series of marginal papillae furnished with cnidosacs. Liver racemose. Velum distinct, bifid, with simple digitiform processes. Rhinophores with liver diverticula. Radula 1.1.1. Stomachal plates present. No prostata Fam. *Hancockiidae*.

B. Rhinophore club perfoliate. Cerata of different shape, dendriform or lobiform, without cnidosacs. Liver ramose, more or less compact, or tubuliform.

1. Cerata arborescent, with no special gills. Velum more or less distinct, with ramose processes. Radula 00.1.00. No stomachal plates. Bursa copulatrix vestigial, a secondary vesicula seminalis on the oviduct. Prostata present. Nephroproct close inside anus. Optical nerves elongated... .. Fam. *Dendronotidae*.

2. Cerata more or less branched, beset with gill tufts. Velum small, bifid, with simple papilliform (or digitiform) processes. Radula 00.1.00 (or reduced). Stomachal plates present. Bursa copulatrix well developed ⁽¹⁾. No prostata gland ⁽¹⁾. Nephroproct ⁽¹⁾ close in front of the anus. Optical nerves distinct. Cerata as a rule with liver diverticula Fam. *Bornelliidae*.

3. Cerata large, lobiform, with or without basal gills. Velum very wide, with fimbriate margin. Radula uniseriate or absent. Bursa copulatrix well developed. Nephroproct inside anus. Optical nerves very short Fam. *Fimbriidae*.

C. Rhinophore clubs smooth. Cerata simple or tuberculated (in rings), without cnidosacs, with or without gills. Liver racemose. Velum smooth, without processes. Radula 1.1.1 or 0.1.0. Rhinophores without liver diverticula. Bursa copulatrix and prostata well developed. Nephroproct close inside anus. Optic nerves distinct... .. Fam. *Dotonidae*.

IV. Back margin entirely reduced, as well as cerata. Anus lateral or dorsal. Liver consisting of two dorsal coeca (right and posterior liver) and one ventral (left anterior liver), all simple, tubuliform. Rhinophore club smooth (in contraction falsely laminated); sheaths very small. Jaws covering only frontal side of pharynx. Gonad in a few globular masses or flocculent stripes. No prostata and no bursa copulatrix (but a muscular vesicula seminis in the end of the oviduct). Nephroproct in the middle of the right side. Eyes with indistinct optic nerves... .. Fam. *Phylliroidae*.

⁽¹⁾ Unknown in *Pseudobornella*.

Fam. DUVAUCELIIDAE

The characteristic of this family is above all the compact, simple structure of the liver, which forms either a single mass with two hepatic ducts debouching into the stomach, what proves its composition of two fused parts, the left and the right liver portions; or two separate masses, representing the same parts, the right liver always smaller.

The primitive condition in the nudibranchs is, as mentioned above, that the liver originates at the larval stage as two distinct masses, one on each side of the stomach. In their phylogeny, however, the nudibranchs are supposed to have passed a process of detorsion. This, of course, was preceded by the torsion common to all gastropods. We may assume that the liver was made the subject of these processes in such a way that its original bipartition was obliterated by the earlier torsion, which made these portions fuse intimately with each other, whereas the detorsion activated the tendency to separate them anew. Where the detorsion has not been completed, as in the primitive opisthobranchs and even the Pleurobranchacea, the root of the nudibranchs, the liver still keeps this unity. According to this view we have to consider those forms of Duvauceliidae as the primitive ones, in which the liver remains a single mass composed by the fused right and left portions. To this section all genera belong except *Marionia* which shows a complete bipartition, inasmuch as its right liver is a distinct mass of its own. Just its position proves that the detorsion is less perfect, because in *Marionia* the right liver lies at the right side of the stomach, below the intestine, and debouches in the anterior stomach wall, whereas in *Duvaucelia* its position is to the left, on the upper side of the stomach and its mouth more medially; so in *Tritoniella*, too (cf. ODHNER 1934, figs. 58⁽¹⁾ and 63). *Marionia* has also another secondary character of organization, namely its stomachal plates. These thin, elevated, easily loosened laminae do not occur in the more primitive genera *Duvaucelia* and *Tritoniella*, but have originated from the pyloric folds in these forms by means of their increase and strong cuticularization.

The liver system thus offers in *Marionia* the first step towards a disintegration by separation of right and left liver portions, which is characteristic of all higher nudibranchs. This is so fundamental a character in *Marionia*, that its importance as generic mark must be esteemed far beyond others (stomachal plates, arborescent velar papillae, etc.). Together with the typical species, *M. berghi* VAYSSIÈRE 1877, which is synonymous with *Tritonia blainvillea* Risso 1828, the following species share the separate right liver: *cucullata* GOULD, *tessellata* BERGH, *chloanthes* BERGH, and the two new species described below (*pustulosa* and *granulosa*). Another species which has been placed in *Marionia*,

⁽¹⁾ The designations of the liver portions in the figure have been reversed: l_1 is the right liver, l_2 the left posterior one.

viz. *M. arborescens* BERGH 1890, synonymous, according to ELIOT 1908, with *Tritonia cyanobranchiata* RÜPPELL & LEUCKART 1828, has, however, mixed characters: stomachal plates are well developed as in *Marionia*, but the velar papillae are simple, and, above all, right liver is fused with left one as in *Duvaucelia*. The right liver duct debouches, as in *Marionia*, in the foremost wall of the stomach. Another character common to *Marionia* is the site of the nephroproct in front of the anus, whereas *Duvaucelia* has its nephroproct above the anus. The same chief characters are prevailing in a species described by RÜPPELL and LEUCKART 1828 as *Tritonia rubra*, which has not been refound and studied, but which I have identified and examined; it differs from *M. cyanobranchiata* in its composed velar papillae. Both species mentioned have a common characteristic in the site of the nephroproct immediately at the anus (as in *Duvaucelia*), but in front of it and not so remote from it as in *Marionia*. For these reasons I have established in 1934 for *M. cyanobranchiata* the new genus *Marioniopsis* with the following words: « Since it must be admitted that the liver system affords a much more important standard of subdivision and a more reasonable indication of relationship than the presence or absence of stomachal plates, I infer that the liver bipartition in *Marionia* is the essential characteristic of the genus... and that the presence of stomachal plates is of secondary significance. Consequently, the somewhat aberrant *M. cyanobranchiata* which cannot be referred to *Duvaucelia* on account of its stomachal plates, should at all events be excluded from *Marionia*; and then no other course is open than to make this species the type of a distinct genus, for which I propose the name *Marioniopsis*, a genus forming a transition between *Marionia* and *Duvaucelia*. » Further, some of the species from East Africa described by ELIOT as *Marionia*, and other forms, are here referred to this genus (cf. below).

Consequently, we have to consider *Marionia* as the most differentiated genus of the family connected with the more primitive genera by *Marioniopsis*. Except the condition mentioned we do not find any other specialization of the liver system apt to form a principle of classification of the family. The most primitive genera (*Duvaucelia*, *Tritoniella*, *Tritoniopsilla*), must be characterized, therefore, from other qualities, above all radula and external habitus. A unicuspid median tooth and a uniform shape of the laterals is a primitive sign of the radula, whereas a tricuspidate median tooth and a differentiation of the laterals so that the innermost one has got a peculiar shape, is to be considered as a secondary acquisition. We have already remarked the different site of the nephroproct as a good systematical character: it has a primitive site in front of the anus in *Tritoniella*, *Marioniopsis* and two species of *Tritoniopsilla*, whereas in *Tritoniopsilla elegans* it lies quite as in *Duvaucelia*, that is immediately above the anus.

To some extent also the genital organs offer a certain difference in distinct genera, but their uniformity in general is a striking feature. In *Tritoniella* and *Duvaucelia*, the spermatheca or bursa copulatrix is elongate, in *Tri-*

toniopsilla elegans it is spherical, but this character seems to be less constant. The genital opening, on the contrary, seems to lie constantly, in *Marioniopsis* below the second gill tuft, in *Marionia* beneath the 3rd or 4th gill.

A good discriminating character is afforded by the jaws, which have smooth margins, or a single row of coarse denticulations in it (*Marioniopsis*) or a microscopical serration of several series of microscopic hooks outside its edge (*Marionia*, *Duvaucelia*).

The genera of Duvauceliidae may therefore be classified according to the characters mentioned above and their distinctions expressed as in the following synopsis.

SYNOPSIS OF GENERA AND SPECIES OF DUVAUCELIIDAE

I. Liver fused into one mass, the right liver thus indistinct though having its own duct; this mass covering upper and left side of stomach.

A. Back margins with simple processes. Penis with an apical ring. No stomachal plates. Back with keels. Nephroproct in front of anus. Jaws with smooth margins. Radula with simple or tripartite median tooth. Bursa copulatrix elongate *Tritoniella* ELIOT 1907.

B. Back margin with branched processes (rarely absent). Penis simple, conical or flagelliform.

1. Median tooth of radula unicuspidate; first lateral undifferentiated. Gills of alternating size. No stomachal plates. Jaws smooth. *Tritoniopsilla* PRUVOT-FOL 1933 (= *Tritoniopsis* ELIOT 1905, non CARPENTER 1863).

2. Median tooth of radula tricuspidate; first lateral differentiated. Jaws with smooth or denticulate margin.

a. No stomachal plates. Nephroproct above anus. Back smooth or rugose. Bursa copulatrix elongate. Velar papillae simple. *Duvaucelia* RISSO 1826 (= *Tritonia* CUVIER 1803, non MEIGEN 1800).

b. Strong stomachal plates. Back as a rule granular. Nephroproct in front of anus. Gills of uniform, not alternating, size. Genital opening beneath 2nd gill. Jaws with a single series of strong denticles. Bursa copulatrix elongate. Velar papillae simple or branching *Marioniopsis* ODHNER 1934.

II. Liver in two masses, the right liver distinct, debouching in the frontal wall of the stomach, left liver part leaving the stomach free from covering. Gills of uniform, not alternating size. Nephroproct in front of anus. Stomachal plates present. Radula as in *Duvaucelia*. Genital opening beneath 3rd gill. Jaws with 3-6 series of very fine denticles. Bursa copulatrix spheric or elongate. Velar papillae compound *Marionia* VAYSSIÈRE 1877.

The genus *Mariana* PRUVOT-FOL 1930 b, too briefly described and referred by its author to Fam. Tritoniidae (= Duvauceliidae), is too incompletely characterized for being recognized or included in this survey. Moreover, the name

was preoccupied, what caused PRUVOT-FOL to change it (1931) to *Marianina*, without, however, to give further details on the characters. It may be possible that it is identical with *Aranucus* described below, but, since this is, unfortunately, impossible to decide from the meagre « diagnosis », which PRUVOT-FOL herself characterizes as incomplete, I am sorry to be obliged to consider this name as a *nomen nudum* with no chance to priority.

Tritoniella Eliot 1907.

Only two species have been referred to this genus, both established by ELIOT in 1907 from the Antarctic Region. The material collected by the British « Terra Nova » Expedition, 1910, studied by me and published in 1934, has enabled us to distinguish with certainty between these two species, the characters of which, according to the work mentioned, may be expressed as follows. *T. belli*, described as the first, may be chosen as the type.

I. Jaws with the masticatory margin emarginate in its upper half. Median tooth of radula with a broad anterior emargination and with a trace of tripartition; its breadth greater than its length; first lateral broader than the following ones, with a broad basal plate and a very short cusp. Max. L. of animal 63 mm.

T. belli ELIOT 1907 (= *T. sinuata* ODHNER 1926, non ELIOT 1907).

II. Jaws with a straight (not emarginate) masticatory margin. Median tooth with a narrow anterior emargination and without trace of tripartition; its length greater than its breadth; first lateral of about the same shape as the following ones, with comparatively narrow basal plate and distinct cusp. Max. length 30 mm.

T. sinuata ELIOT 1907.

Duvaucelia Risso 1926.

(= *Tritonia* Cuvier 1803, non Meigan 1800).

For the nomenclature of this genus I refer to IREDALE & O'DONOGHUE (1923) and ODHNER (1926), whereas PRUVOT-FOL's plea (1931) for CUVIER's original name cannot be accepted. I refer to my work of 1926 also for the classification of this genus with following additions. *D. undulata* O'DONOGHUE 1924 is to be added to the group of *D. diomedea* BERGH. *Sphaerostoma dakini* O'DONOGHUE 1924 is a *Marioniopsis* (cf. below). *Sphaerostoma aurantiacum* BARNARD 1927 may be akin to *Duvaucelia plebeia*, but is too meagerly described to be classified. *Tritonia incerta* BERGH 1904, from New Zealand, seems to be related to *D. pallida* and allies. *Tritonia irrorata* BERGH 1905 is a further member of this genus; BERGH speaks about « Hauptleber » and « Nebenleber », but he does not say the right liver to be distinct as in *Marionia*; he does not speak, neither, of stomachal plates and leaves unsettled if the 4 papillae (beside the tentacles) on each side of the velum are simple or composed. The *Duvaucelia irrorata* of BABA 1933 from Japan is certainly distinct and seems to be a *Marioniopsis*; in spite of its great size (60 mm) it has a narrower radula (25.1.1.1.25) than BERGH's *T. irrorata* of 32 mm length, which has 70.1.70 teeth in each row.

Tritoniopsilla Pruvot-Fol 1933.

(= **Tritoniopsis** Eliot 1905, non Carpenter 1863).

The type of this genus is *Tritoniopsis brucei* ELIOT 1905 from Gough Island (« Scotia » Exp. 1904), and it is of interest that the nearest relative is *Tritonia elegans* SAVIGNY 1826, which HAAS (1920) referred to the genus *Tritoniopsis* on account of the same shape of the median radula tooth. M^{me} PRUVOT-FOL (1933) has given some more details of the latter species (teeth, jaws, etc.), and I have here examined the anatomy of specimens from the Red Sea burrowed from the Berlin Museum and the Senckenberg Museum, Francfort-on-the-Main, and stated

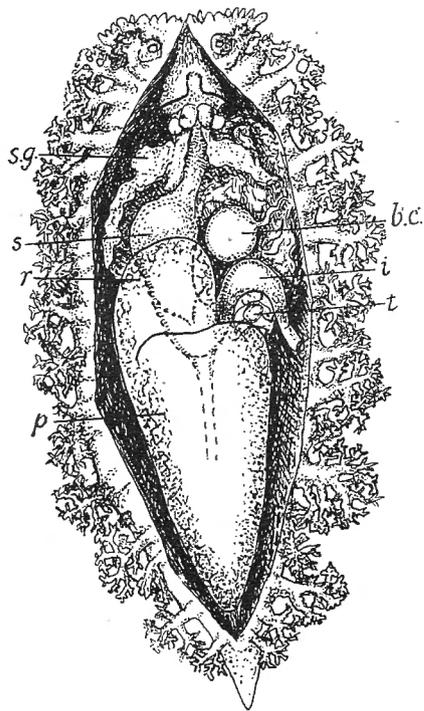


FIG. 12. — *Tritoniopsilla elegans*.
Anatomy.

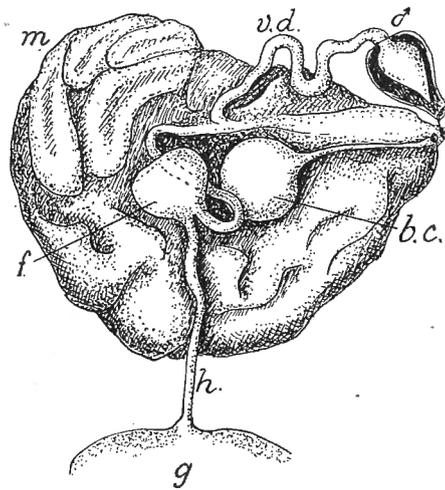


FIG. 13. — *Tritoniopsilla elegans*.
Genital organs.

liver, stomach and genitalia to be as in *Duvaucelia* (cf. figs. 12, 13). The intestine may be reflected on the upper side of the liver or not. Another specimen of *T. elegans* was from Pilai, Birma (L. 20 mm; Mus. Berlin). PRUVOT-FOL asks if *Tritoniopsis gravieri* VAYSSIÈRE 1912⁽¹⁾ may be identical with *T. elegans* or with *Tritonia cyanobranchiata* RÜPPELL & LEUCKART 1828, which has a similar colouration. This concordance in colour is, no doubt, occasional, since the habitual and anatomical characters of *T. gravieri* prove its identity with

(¹) The specimens from Ceylon reported by HAAS (1920) under the name of *Tritoniopsis gravieri* belong to *Marioniopsis cyanobranchiata* (*vide infra*).

T. elegans, whereas those of the latter species prove that this belongs to the different genus *Marioniopsis* (see below).

In addition to the species mentioned I referred in 1926 to the genus *Tritoniopsis* ⁽¹⁾ *Tritonia tetraquetra* PALLAS 1788 and *gigantea* BERGH 1904, which are certainly identical, on the base of the same character of the radula. O'DONOGHUE has (1922) completed our knowledge of the external habitus of this species, and it appears from his statement that it shares a character of the two remaining species, viz. that the numerous gills are of alternating size. As to the inner anatomy we have to consult BERGH's descriptions of this species, and we find from them that there are no stomachal plates and that the bursa copulatrix is pyriform with a short duct. BERGH states, further, the position of the nephroproct to be close in front of the anus. In *T. elegans* I found the site of the nephroproct just above the anus and the shape of the bursa copulatrix spherical.

The characters of the three species hitherto known may be tabulated as follows.

- I. Back with a median ridge sending out lateral ridges. Velum with 12-14 simple digitations. Rhinophore sheaths with 2-3 appendages in front. Gills 12-15. Radula about 30.1.30. Genital orifice between gills 5 and 6, anus between gills 7 and 8. Colour white. L. 22 mm. *T. brucei* ELIOT 1905 [*Tritoniopsis*].
- II. Back without ridges. Rhinophore sheaths without frontal appendages.
 - A. Back smooth or rugose. Velum with about 30 simple digitations. Rhinophore sheaths connected with gills or not. Nephroproct above anus, which lies behind gills 7 or 8; genital orifice below gills 4 or 5. Radula narrow, 7-9.1.7-9. Colour varying: bluish gray with dark blue or blackish gills, or with the gills reddish or green; or orange with a few blackish spots on the back and bluish gills. L. 50 mm. *T. elegans* SAVIGNY 1826 [*Tritonia*] (= *Tritonia glauca* and *glama* RÜPPELL & LEUCKART 1828; *Tritoniopsis gravieri* VAYSSIÈRE 1912).
 - B. Back tubercled. Velum smooth-margined, entire, not bilobed. Rhinophore sheaths with tubercled margins. Nephroproct close in front of anus. Radula broad, about 50 × 250.1.250. Colour brick red, at the edges sprinkled with brown, tubercles yellowish with white spots. L. up to 290 mm. living; (O'DONOGHUE) *T. tetraquetra* PALLAS 1788 [*Limax*] (= *Tritonia gigantea* BERGH 1904).

Marionia Vayssière 1877 and Marioniopsis Odhner 1934.

The type of *Marionia* is, as mentioned above, *M. berghi* VAYSSIÈRE 1877, which is identical with *Tritonia blainvillea* RISSO 1828. I have examined the

⁽¹⁾ PRUVOT-FOL (1933, p. 108) says nevertheless about *Tritoniopsis*: « Il est à noter qu'Odhner n'admet pas ce genre et n'en fait qu'un sous-genre » (evidently a confusion with *Tritoniodoxa*; cf. ODHNER 1926).

anatomy of the typical species and found it to concord with that of *M. cucullata* described by me in 1934. MISURI (1917) has given a correct figure of left liver, stomach, etc., but he has not observed the right one, though BERGH (Malac. Unters. 1884, p. 744, pl. LXXV, fig. 15) has clearly stated its presence.

A first list of the species of *Marionia* was given by BERGH (1884) (Malac. Unters., p. 703). He includes herein *M. blainvillea* as first member, and further *M. elegans* SAVIGNY, *M. cyanobranchiata* RÜPPELL & LEUCKART and *M. occidentalis* BERGH. As to *M. elegans* and *cyanobranchiata* he remarks in a note: « Ob alle diese letzteren Formen nun überhaupt Marionen sind, muss vorläufig dahingestellt bleiben ». In Malac. Unters. 1890, p. 891, and 1892, p. 1070, BERGH includes anew *elegans* and *cyanobranchiata* in *Marionia* and thinks them to be closely related to each other. The same lists then embrace the species mentioned above with the addition of *M. arborescens* BERGH. To these forms of *Marionia* ELIOT added 5 new species in 1904.

As to *M. elegans*, HAAS (1920) definitely referred this species to *Tritoniopsis* (cf. above). *M. cyanobranchiata*, however, was known only from the original diagnosis and figures, until ELIOT refound it in the Red Sea, examined it in detail (1908) and stated it to be a *Marionia* « on account of the armature of plates in the stomach ». ELIOT considered further that this species was identical with *M. arborescens* BERGH. In 1933 PRUVOT-FOL drew attention to the similar colour of *T. cyanobranchiata* and *Tritoniopsis gravieri* and said: « j'aurais été tentée de les regarder comme synonymes sans l'assertion d'Eliot que la *T. cyanobranchiata* est une *Marionia* et possède des plaques stomachales ». But already external characteristics prove the distinctness of the two species: *T. gravieri* shows much greater agreement with *T. elegans* in its branchiae which alternate with smaller ones, and in its cephalic veil with about 30 digitiform projections, whereas in *T. cyanobranchiata*, according to the description and figures (pl. 4, figs. 3a, 3b) of RÜPPELL & LEUCKART, there are 9 pairs of branchiae, all uniformly developed and no alternately small ones, and the veil has only 8 processes. In *M. cyanobranchiata* of ELIOT there are likewise 9 pairs of equally sized branchiae and no small ones between them; the velum has 10 processes; thus, with the latter slight difference, there is so good an agreement that ELIOT's specimen, as he remarks, « may be regarded as certainly identical with the *Tritonia cyanobranchiata* of RÜPPELL & LEUCKART », though no direct comparison with the type specimen has been made. Beside the similarities mentioned, the anus lies in *M. cyanobranchiata* beneath the 4th gill, quite as in the figure of the original, whereas, in *T. elegans*, still more branchiae (at least 5-7) precede the anus. I therefore do not hesitate in the correctness of ELIOT's identification and base the characters of *M. cyanobranchiata* on his description. It follows that this species is quite different from VAYSSIÈRE's above-mentioned species in spite of the strikingly similar colouration.

I identified with *M. cyanobranchiata* 2 specimens borrowed from the Zoolo-

gical Museum in Berlin, the one collected by HARTMEYER (Jan. 1902) in Gimsah Bay, Suez, and already correctly determined (L. 25 mm), the second collected by Stabsarzt Dr. SANDER at Zanzibar (L. 30 mm). The first had 4 papillae on each side of the velum (inclusively the tentacles) and a weak trace of a 5th mesial one on the right side; the second had 5 processes on each side (incl. tent.). There were 11 and 9 pairs of cerata respectively. Genital aperture below 2nd gill, anus below 4th. Nephroproct very close in front of anus.

An anatomical examination of these specimens revealed the fact, which made necessary the establishment of the genus *Marioniopsis*, namely that the right liver

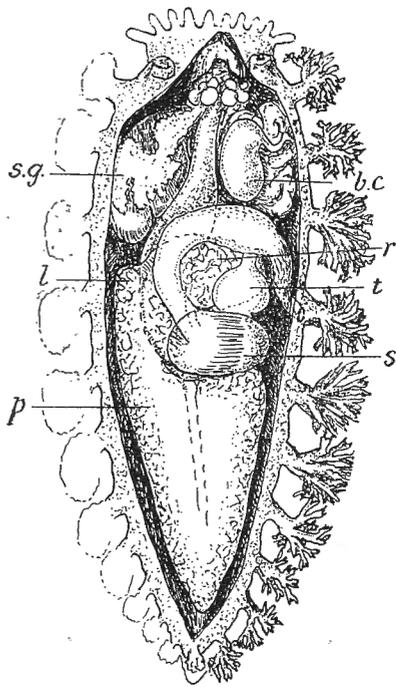


FIG. 14.
Marioniopsis cyanobranchiata.
Anatomy.

is fused with the left one (Fig. 14) which encloses

the stomach as in Duvaceliidae in general but aberrant from *Marionia*.

ELIOT (1908, p. 122) says about the liver in *M. cyanobranchiata*:

« The front part is hollowed out and forms two lobes which enclose the greater portion of the stomach...

An accessory portion of the liver lies under the intestine ». BERGH, in describing his *M. arborescens*, which ELIOT considers with right as synonymous, says about the liver (Malac. Unters, 1890. p. 893):

« Der untere linke Theil dieser Lebermasse [=posterior liver] setzt sich nach vorne in einen rechts gebogenen, 1-1.5 Cm (von links nach rechts) breiten, etwa 0.4 bis 0.6 Cm dicken Lappen fort; zwischen diesem Lappen und der Hauptleber liegt rechts der erste Magen, links der Kaumagen und der Darm welcher über die obere Seite des Magens verläuft.

In der Kniebiegung des Darmes liegt eine kleine, 8-4 mm lange Nebenleber. Die Hauptleber öffnet sich in den ersten Magen, der vordere Leberlappen, wie es schien in den Kaumagen und die Nebenleber, wie es schien, in den Darm. »

The

two liver portions are fused together in the specimens at my disposal, quite as typical in Duvaceliidae. Only two ducts lead into the stomach.

The genital organs were described by BERGH who found an elongate bursa copulatrix; ELIOT found it spherical. In the specimens at my disposal it has an elongate shape, but this may vary. It opens separately as in *Marionia*. An ampulla similar to that of *Marionia* debouches directly into the albumen gland; from here the short and wide vas deferens emerges; penis conical.

A further specimen (L. 25 mm) of *M. cyanobranchiata* belongs to Dr. TH. MORTENSEN's collections (Mus. Copenhagen) and comes from St. Cruz Island, Zamboanga, coral reef (25-28/2 1914). To this species also belong the specimens from Weligama, Ceylon, which HAAS (1920) reported under the name of *Trito-*

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niopsis gravieri (Mus. Senckenberg). *M. ramosa* ELIOT 1904 is no doubt identical with *cyanobranchiata*.

The second species which I refer to the genus *Marioniopsis* is one which was collected by Dr. MORTENSEN (Sept. 1925) at Cannoniers Point, Mauritius, in two specimens (Mus. Copenhagen). It has a rosy tint, 10-12 gill tufts on each side of the body, which is covered with low conical warts, and 6 processes on each side of the velum (except the tentacles), which are divided into several small twigs most in or below their tips. Because of these characters I refer these specimens, the largest of which attains 70 mm in length, to *Tritonia rubra* RÜPPELL & LEUCKART 1828 (pl. 4, fig. 1), a species from Tor, Red Sea, which has not been refound; I have not seen the type. PRUVOT-FOL (1933) thinks this species, listed by O'DONOGHUE (1929) as a *Sphaerostoma*, to be possibly identical with *Tritoniopsis elegans*; these are the single references existing beside the brief original description. One of the above specimens is figured on the plate, figs. 7, 8.

The rhinophorial clubs have 6 tripinnate filaments. The velar processes which are generally split up in their ends, the very slender body, the warty back and the colour forbid an identification with *T. elegans*, and the hindmost branchiae diminish in size much more rapidly than in that species. The radula of the present specimens show the characters of *Marionia*, and the jaws have a coarsely serrated margin as in *Marioniopsis cyanobranchiata*. The position of the openings is about the same as in the latter species; genital orifice below 2nd, anus just in front of 4th gill; nephroproct close in front of anus. Above all, however, the inner anatomy is quite in accordance with that species (Fig. 15), the liver is undivided in the same manner, the genital organs show a similar short and wide vas deferens and an elongate bursa copulatrix.

The jaws of *M. rubra* (Fig. 17) are reddish brown and very narrow in their upper ends, broadening towards below and much curved; their masticatory margin is coarsely serrated with one single series of about 120 denticles steadily increasing in size towards the under end of the processus masticatorius; only the 10 last ones decrease again rapidly. Length of jaws 12 mm. Radula 45 × 50-55.1.1.1.50-55; central tooth tricuspid (Fig. 19).

No direct observations on the liver being available it is somewhat uncertain which of the remaining species described as *Marionia* may belong to *Marioniopsis*. ELIOT (1904 a) has no particulars at all in this respect for *M. pellucida*, but for three of the remaining species described by him he talks about the stomach lying partly under or being included into the liver (*albotuberculata*, *viridescens*, *ramosa*). For *M. laevis*, ELIOT does not state these things, but I think this species is identical with *M. distincta* BERGH 1905 from the Paternoster Islands, because the coloured figures of BERGH (pl. IV, fig. 19) and ELIOT (pl. IV, fig. 4) show about the same main tint and similar transversal brown stripes and brown dots; further the back is smooth, and there are 9-10 pairs of branchiae, the three posterior ones rather small. BERGH, it is true, describes 11 velar papillae almost

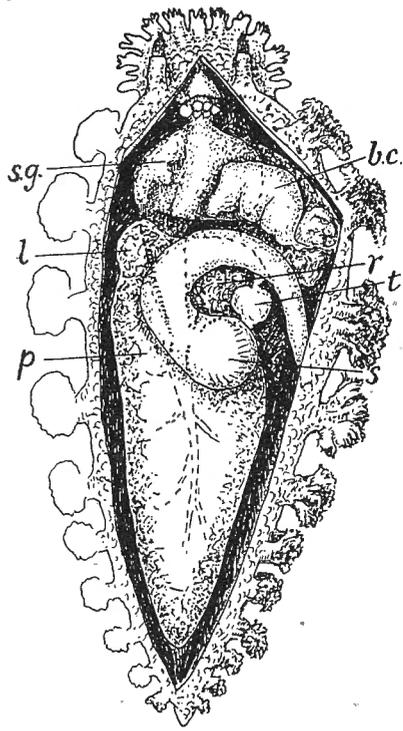


FIG. 15. — *Marionieopsis rubra*. Anatomy.

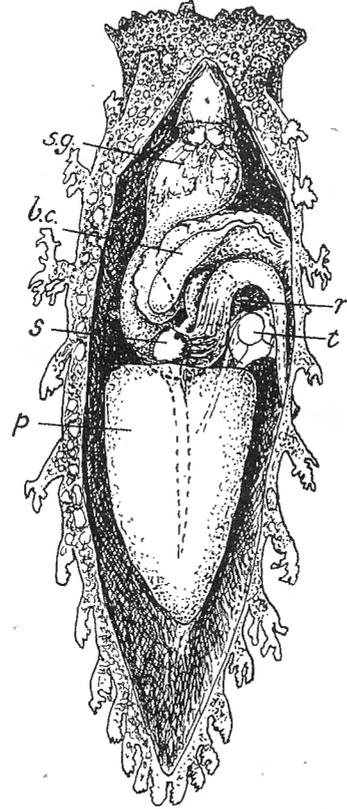


FIG. 16. — *Marionia pustulosa*. Anatomy.

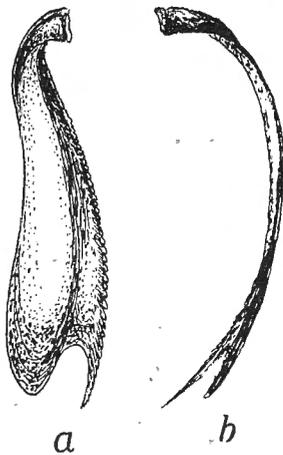


FIG. 17. — *Marionieopsis rubra*. Left jaw. a, from inside; b, from front margin. ×3.5.

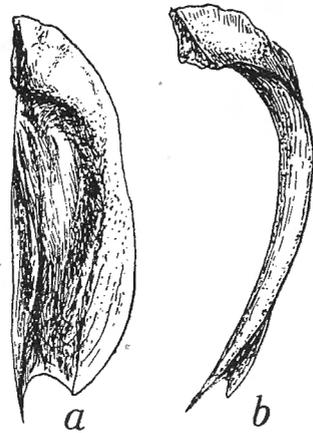


FIG. 18. — *Marionia pustulosa*. Left jaw. a, from outside; b, from front margin. ×3.

cylindric and tuberculate beneath, whereas ELIOT mentions 3 on each side, the two mesial ones simple (what is evident also in BERGH's fig.), and 4 branched ones; the difference may depend on different interpretation of the single papillae. In BERGH's specimen the mandibular margin has 14 strong denticles, in ELIOT's 20-30, which may depend on size or variation. BERGH says about the liver that it is 15 mm. in length including the accessory liver to the left, which seems to indicate that the liver parts are coalesced, thus a *Marioniopsis*. So we may be able to refer to that genus all the species mentioned above.

If we compare these species in other respects, we find that all possess a character which is not met with in any typical *Marionia*, viz. the denticulation of the jaw margin by means of a single row of coarse teeth. In *Marionia*, on the contrary, there are about 4-6 rows of small denticles without the smooth jaw margin, e. g. *M. cucullata* (cf. ODHNER 1934, fig. 65); at the naked eye the edges appear smooth. Further the jaws of *Marionia* are much broader in their upper part, in *Marioniopsis* much narrower above and dilated below. If this distinction holds good in all species of the two genera, we have a good means of separating them and to refer to respective genera also the remaining species of questionable systematic position. Thus *Marionia pellucida* ELIOT, which has 3-4 rows of denticles at the edge of the jaws, would be a true *Marionia*. Further, I suspected that *Sphaerostoma dakini* O'DONOGHUE, which has a single row of large denticles and a shape of jaw recalling that of *Marioniopsis rubra* though broader, would belong to the latter genus. Its reference to *Sphaerostoma* was to be doubted already on account of the description; for the oral veil « bears about six or seven dendriform processes on each side of the middle line » and the jaw is unlike every one of *Duvaucelia*. Though nothing is said about so important a character as the stomach armature or the liver, I did not hesitate to refer it to the genus *Marioniopsis*.

Through the kindness of Dr. CALMAN and Mr. ROBSON of the British Museum, a specimen of *Sphaerostoma dakini* was sent to me for réexamination. The liver proved at once to be quite as in *Marioniopsis*, and the stomach was armed with strong and high plates of a hyaline corneous colour. The back and body sides were warty. The velar processes were compound in a vertical plane as in *Marionia*. The nephroproct lies close in front of the anus. The jaws had about the same shape as in *M. rubra* (though less curved) and 40 regularly increasing denticles only half as densely set as in *M. rubra* (distance between the tips of denticles larger than their length; in *M. rubra* shorter than their length). The bursa copulatrix was elongate.

Duvaucelia irrorata of BABA 1933 is, as mentioned, different from the type of BERGH, it seems to be a *Marioniopsis* on account of velar processes and jaw margin. In want of detailed description I name it preliminarily *M. babai* n.

We are justified in supposing, then, that the characters of the jaws are generally distinctive in this group. As in *Duvaucelia*, the jaw has in *Marionia*

a thin and narrow masticatory process, and the whole masticatory margin is even and rounded, beset along its edge externally with 3-6 rows of small hooks. Where in certain species a different character of this margin is to be established, inasmuch as it bears a single series of teeth, as mentioned above (cf. BERGH 1905, pl. XIX, fig. 1), we have probably to do with a *Marioniopsis*. ELIOT (1904a) has expressed the opinion that possibly « the denticulation of the jaw varies with age », but no facts corroborating the view of a transition with age from one of these types into the other are available. The jaws may be worn, but then the edge becomes quite even also in cases where there is original serration in the edge; and the coarse serration cannot be the consequence of tearing, the less so, as it is quite typical in small specimens, too. In *Duvaucelia hombergi*, on the contrary, the denticulation of the jaw edge seems to be intensified by wearing, but here the denticles are of another kind than those of *Marionia* and *Marioniopsis*, inasmuch as they are composed of smaller hooks but with a stronger central one of greater resistance, which brings about a coarser serration after use.

Beside the structure of the jaws, we find a character distinguishing between *Marionia* and *Marioniopsis* in the position of the genital aperture; this lies beneath the 2nd gill in *Marioniopsis* and beneath the 3rd or further back in *Marionia*; so far known this seems to be a constant mark. Other taxonomic characters of a second range are found in the external habitus (back more or less warty) and the colour and radula. The number and branchment of the velar papillae seems to be conclusive for the discrimination of the species and gives perhaps also a generic distinction; in *Marioniopsis cyanobranchiata* the velar processes are all simple and not branched, in *M. rubra* and other congeneric species their branchment may be irregular, dendriform, except in *M. dakini*; in *Marionia blainvillea* and other species of *Marionia* and in *Marioniopsis dakini* their composition is quite regular, the smaller tubercles being set in vertical series.

According to the conclusions here arrived at I think it possible to comprise the species of *Marionia* and *Marioniopsis* in the following ways.

SYNOPSIS OF THE GENUS MARIONIOPSIS

- I. All velar processes simple. Median tooth of radula with 2 denticles on each side of the cusp. Jaw denticles more than 100. Velar processes about 5-7 on each side. Back, body sides and velum warty, rhinophore sheaths smooth. Gills 9-13 pairs. Anus beneath gill 4, genital opening beneath gill 2. Radula $60 \times 50.1.1.1.50$ (BERGH) or $45 \times 29.1.1.1.29$ (ELIOT, *M. ramosa*). Colour yellow, gill branches, velar margin and rhinophore bluish green; back with brown reticulations. L. 60 mm. (BERGH) *M. cyanobranchiata* RÜPPELL & LEUCKART 1828 [*Tritonia*] (= *Marionia arborescens* BERGH 1890, *M. ramosa* ELIOT 1904).
- II. All velar processes (as a rule) branched. Median tooth of radula with 1 denticle on each side of the cusp.
 - A. Back warty. Radula teeth less than 100 in half a row.
 1. Jaw denticles more than 100, gradually increasing in size towards below. Genital opening below gill 2. Velar processes 6 on each side.

- a. Gills 10-12 pairs. Rhinophore sheaths warty. Anus just in front of gill 4. Radula $45 \times 50-55.1.1.1.50-55$. Colour rosy, rhinophore clubs bluish green, gills and tips of velar papillae yellow. L. 70 mm. ... *M. rubra* RÜPPELL & LEUCKART 1928 [*Tritonia*].
- b. Gills 7 pairs. Radula $40 \times 25.1.1.1.25$. Colour (living) dark yellowish green sprinkled with dark brown, dark yellowish white, grayish white and dark reddish white mottles, bluish spots and dark reticulations; sides of body with grayish white granules, bluish spots and dark reticulations. L. 60 mm. *M. babai* n. n. (= *Duvaucelia irrorata* BABA 1933, non *Tritonia irrorata* BERGH 1905) ⁽¹⁾.
2. Jaw denticles fewer, 10 much larger than the rest. Radula with about 90 laterals in half a row.
- a. Radula $40 \times 95.1.1.1.95$. Velar processes 5 on each side. Gills 9 pairs. Genital aperture below gills 2-3. Colour white reticulated with red-brown; a small white tubercle in each mesh. L. 45 mm. ... *M. albotuberculata* ELIOT 1904 [*Marionia*].
- b. Radula $37 \times 90.1.1.1.90$. Velar processes 7 on each side. Gills 10 pairs. Colour reddish brown with greenish reticulations and white spots. L. 42 mm. *M. viridescens* ELIOT 1904 [*Marionia*].
- B. Back warty. Radula teeth more than 100 in half a row. Jaw denticles about 40, regularly increasing. Velar processes 6-7 on each side each with a vertical series of papillae. Gills about 13 pairs. Genital aperture below 2nd gill, anus below 3rd gill. Radula $67 \times 135.1.1.1.135$. Colour gray or pinkish marbled with brown. L. max. 88 mm. *M. dakini* O'DONOGHUE 1924 [*Sphaerostoma*].
- C. Back smooth. Radula teeth more than 100 in each half row. Velar processes 3 or 5 on each side, the 2 mesial ones simple. Gills 9-10 pairs. Radula $45-47 \times 80-100.1.1.1.80-100$ (ELIOT) or $52 \times 120-130.1.1.1.120-130$ (BERGH). Colour pale purplish brown with transversal stripes of darker brown; branchiae and rhinophores pink with dark red blotches (ELIOT). L. 36 mm. (BERGH) to 50 mm. (ELIOT) ... *M. laevis* ELIOT 1904 [*Marionia*] (= *Marionia distincta* BERGH 1905).

SYNOPSIS OF THE GENUS MARIONIA

I. Back with distinct polygenes, for the rest smooth or finely grainy. Gills 11-16 pairs.

A. Rhinophore sheaths and gill stems smooth.

1. Nephroproct close in front of the anus (distance equal to or smaller than anus diameter). Polygenes more or less filled with white spots within a reddish brown or orange reticulation. Velar processes 6-8 on each side. Gills 11-15 pairs. Radula $40-54 \times 30-54.1.1.1.30-54$ (BERGH) or $35-42 \times 18-36.1.1.1.18-32$ (MISURI). L. 45-95 mm. (MISURI)... *M. blainvillea* RISSO 1828 [*Tritonia*] (syn. *Tritonia gibbosa* RISSO 1828, *tethydea* DELLE CHIAJE 1829, *decaphylla* CANTRAINÉ 1840, *costae* VÉRANY 1852, *meyeri* VÉRANY 1852, *acuminata* COSTA 1866, *quadrilatera* SCHULTZ 1836; *Marionia berghi* VAYSSIÈRE 1877).

⁽¹⁾ Mr. BABA has kindly written me some completing characters of this species, but the chief generic one remains unsettled.

2. Nephroproct further in front of the anus (distance more than twice the anus diameter). Polygons greenish, body sides reddish or greenish with feebly elevated white spots. Velar processes 7-11 on each side. Gills 13-16 pairs. Radula $70 \times 60.1.1.1.60$ (ODHNER 1934). L. 90 mm.
M. cucullata GOULD 1852 [*Tritonia*].
3. Nephroproct? Polygons bright yellowish (in alcohol), main colour otherwise whitish. Velar processes 6 on each side. Gills 13 pairs. Radula with 35 series? (incompletely known). Jaws with 3 rows of hooks. Stomachal plates elevated (height=half the length). Anus below gill 5. L. 25 mm. *M. tessellata* BERGH 1905.
- B. Rhinophore sheaths and gill stems warty, the warts (whitish or yellowish in colour) growing larger to prominent polygons or low pustules on back, interlined with greenish brown; similar warts on velum and even inside the rhinophore sheaths. Velar processes 6-8 on each side. Gills 14-16 pairs. Radula about $80 \times 112.1.1.1.112$. L. 130 mm. *M. pustulosa* n. sp.
- II. Back without distinct polygons, but with distinct, though often scattered, tubercles.
- A. Velar processes 6 on each side, all 3-4-branched. Anus behind the 5th gill. Gills 14-16. Colour (in alc.) whitish; or reddish yellow with pale gray opaque vermiculations between the prickly yellow warts. Jaw margin with 4-6 rows of subequal small hooks. Radula $38 \times 50.1.1.1.50$ (L. of animal 37 mm.) or $34 \times 30.1.1.1.30$ (L. 22 mm.). Stomach plates elongate (height $\frac{2}{5}$ — $\frac{1}{3}$ of length) *M. granularis* n. sp.
- B. Velar processes 6 on each side, all, except 2 simple mesial ones, 3-branched. Anus between 4th and 5th gills. 12 gill pairs. Colour dark greenish gray. Jaws with 5-6 rows of small hooks at masticatory margin. Radula $40 \times 43.1.1.1.43$. L. 22 mm. *M. pambanensis* O'DONOGHUE 1932.
- C. Velar processes 5 on each side, thereof 43-branched. 13 gill pairs (first and last minute). Colour (living) sparsely reticulated with vermilion (in alc. yellowish) with white elevated spots or small tubercles (in alc. pale yellowish). Masticatory margin with 3-4 rows of hooks. Radula $25 \times 22.1.1.1.22$. L. 15 mm. (in alc.) *M. pellucida* ELIOT 1904.
- D. Velar processes 4 on each side, some ones with tubercles on under side. 9 gill pairs (large) and some intermediate smaller tufts. Colour yellowish white with a reddish tint and whiter warts; rhinophore sheaths and gillstems grass green. Masticatory margin with 5-6 rows of hooks. Radula $32 \times 44.1.1.1.44$. L. 20 mm. *M. chloanthes* BERGH 1902.

DESCRIPTION OF THE NEW SPECIES

***Marionia pustulosa* n. sp.**

(Plate, figs. 4, 5.)

Body large, lanceolate, depressed, L. 125 mm., br. 35 mm., h. 22 mm. Back with large, roundish, little elevated pustules, the largest in the median part, about 7 mm. in diameter, becoming smaller towards the margin and covering as warts the stems of the gills, the rhinophore sheaths (even inside), the velum (even under side) and the body sides. Velum with 6 papillae on each

side, composed (bearing 2-3 smaller knobs beneath). Rhinophore sheaths with thin even margin. Back margin prominent, with 15 pairs of cerata, mostly of uniform size, consisting of a thick stem 3 times pinnate into smaller and comparatively few branches, all directed backwards, the 5th and 7th largest, the anterior and posterior ones smaller. Genital aperture beneath 3rd gill, anus between 4th and 5th gill, nephroproct close in front of anus. Colour brownish green, deepening on the gills; pustulae yellowish, gradually passing into whitish in the marginal warts.

Jaws strong (Fig. 18), L. 17 mm., each $2\frac{1}{2}$ times as long as broad, with smooth margin. Radula (Fig. 20) with 80 series, the largest containing about 112.1.1.1.112 teeth, median tooth tricuspid, first lateral one little broader than following ones and with short and broad cusp (not contorted as in the rule in *Marionia*).

Stomach in its pyloric part with a girdle of about 25 strong and elongate

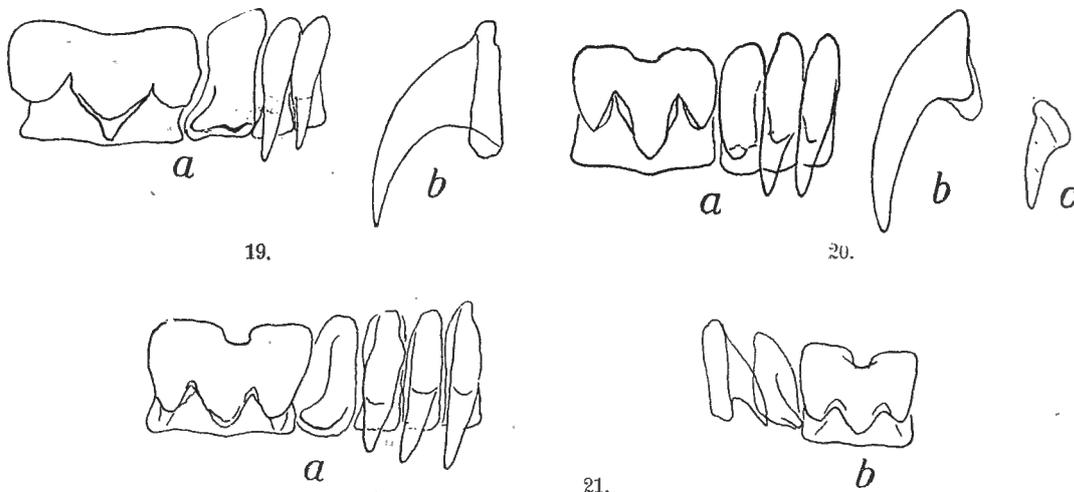


FIG. 19. — *Marionioopsis rubra*. Radula. *a*, median tooth and 3 innermost laterals; *b*, outmost marginal. $\times 80$.

FIG. 20. — *Marionia pustulosa*. Radula. *a*, median tooth and 3 innermost laterals; *b*, lateral from the middle of a series; *c*, outmost margin. $\times 80$.

FIG. 21. — *Marionia granularis*. Radula. *a*, from Formosa Channel; *b*, from Persian Gulf. $\times 125$.

folds each with a low cuticular hyaline crest, thus no true plate. Liver portions distinct, the right one small, debouching in right stomach wall, the left posterior one conic, leaving the stomach free (Fig. 16).

Genital organs with the short and wide vas deferens emerging from albumen gland, ending in a broadly conic, somewhat flattened penis; hermaphrodite duct widened to an elongate ampulla; bursa copulatrix with a stalk shorter than the vesicula and debouching in a separate opening.

Locality : Port Curtis, Queensland, 4-5 m., coll. MESSRS. MELBOURNE WARD & BOARDMAN (July 1929), 1 sp. (in Riksmuseum).

Marionia granularis n. sp.

(Plate, fig. 6.)

Body elongate, rather elevated, L. 37 mm., br. 10 mm., h. 6.5 mm. Back and body sides with small warts all over, very fine on rhinophore sheaths and velum. Margin of velum with 6 processes on each side, the largest compound of 4-5 vertically arranged papillae. Rhinophore sheaths with crenelate or minutely lobate margin. Back margin a little prominent, with 13-14 pairs of gills, not much branching. Genital opening beneath 3rd gill, anus between 5th and 6th gill. Nephroproct close in front of anus. Colour (in alc.) cream white. Jaws (L. 6 mm.), with 4-5 rows of small denticles. Radula 38 × 50.1.1.1.50 (Fig. 21a) median tooth tricuspid, with well marked deep emargination in front. Stomach with a girdle of strong hyaline plates with excentric apex (H. = 2/5 L.). Liver distinctly divided in one right small mass opening to the right into the stomach, and a conic posterior liver opening behind.

Penis short, conic; vas deferens short and broad coming from albumen gland. Ampulla typic, saucer-shaped.

The type belongs to the Uppsala Zool. Inst. and comes from Formosa Channel, 20°20'N., 121°30'E., 120 m. (Capt. SVENSEN), 1 sp.

To this same species I reckon a small specimen (L. 22 mm., br. 6 mm., h. 5.5 mm.) from the Persian Gulf (Brit. Mus. 98.12.5.89). It has a similar back, velum, rhinophore sheaths, site of anus and other openings, etc. but has a more reddish yellow tint and yellow warts. Its radula has 34 series with 30.1.1.1.30 teeth (Fig. 21b), and the stomachal plates are somewhat aberrant in having central apices and a height = a third of the length. Though a small specimen it has its genital organs well developed. Locality : Persian Gulf.

Fam. ARANUCIDAE

It was necessary to create a distinct family to accept the new genus *Aranucus* described below. Whereas in external habitus it bears a great similarity to a *Duvaucelia*, its liver, above all, differs from all Duvauceliidae inasmuch as a separation between the posterior liver and the anterior one (=right liver + anterior portion of left one) has taken place, which causes a type of liver like that of Scyllaeidae or still better some forms of Bornellidae (*Bornella excepta* and *Pseudobornella*). In *Aranucus* the two parts of the anterior liver send each a branch into the first pair of dorsal papillae, in *Pseudobornella* and *B. excepta* no such diverticula are developed. In the genital system, *Aranucus* differs from both Scyllaeidae and Bornellidae and agrees with Duvauceliidae in the fact that the vas deferens emerges rather from the distal main glandular mass, than from the hermaphrodite duct, and has no prostata.

DIAGNOSIS OF *ARANUCUS* N. GEN.

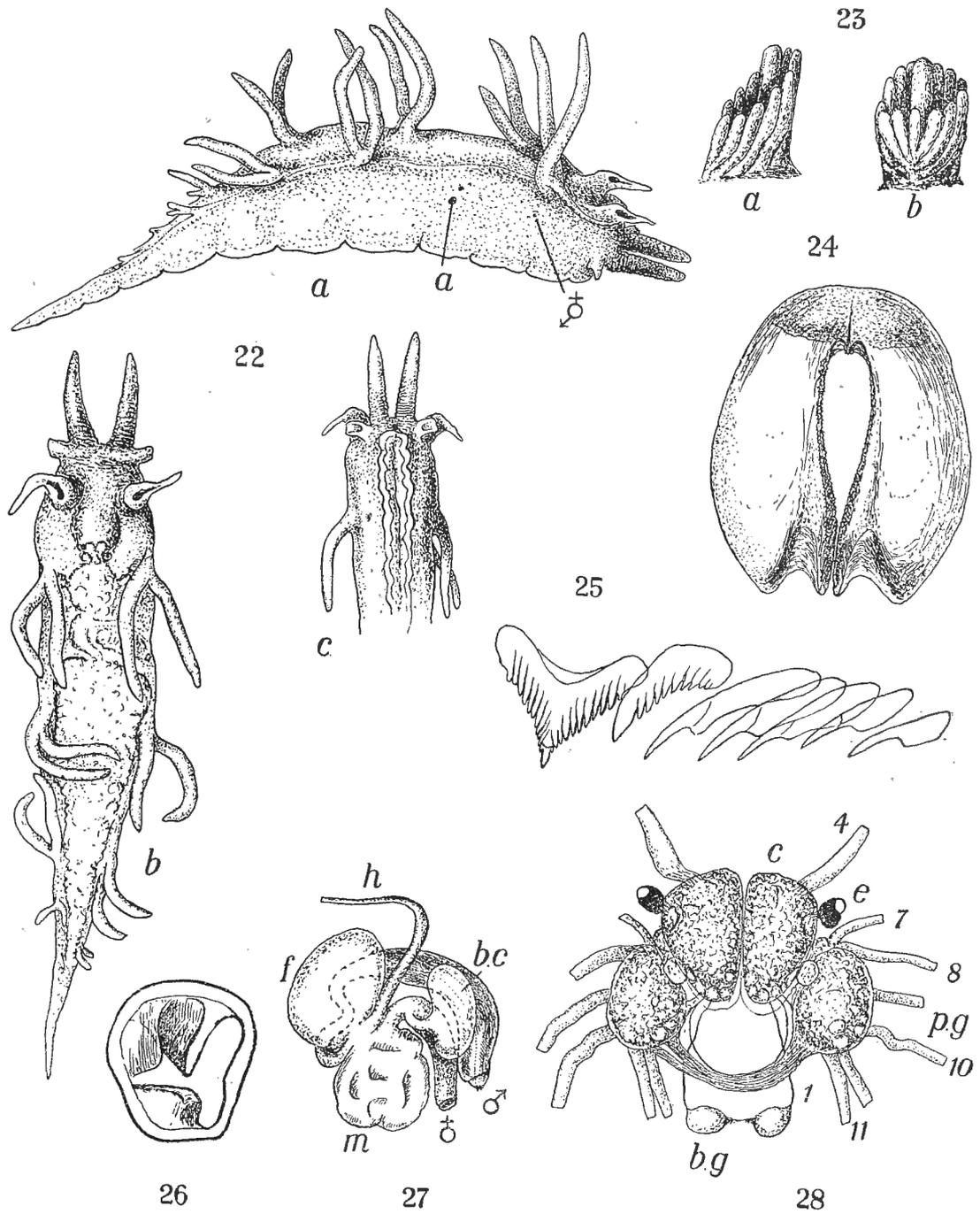
Body with thread-like back margin beset with a few pairs of erect bifid processes; rhinophore sheaths produced into a frontal lobe, club brush-like, with elongate simple papillae; velum with 2 median strong digitiform papillae directed forwards and a pair of short furrow-shaped tentacles laterally. Genital orifice beneath first papilla, anus lateral between 1st and 2nd papillae, nephroproct close above anus. Jaws with margin bearing several rows of minute grains. Radula with unicuspid median tooth, serrated in margins, first lateral with inner margin serrated, outer laterals smooth, few in number. Anterior liver with diverticula into the foremost pair of papillae, posterior liver unbranched. Stomach with cuticularized folds (no true plates).

Aranucus bifidus n. sp.

Body small, quadrangular in section, tapering to a narrow tail (Fig. 22). Margin of the smooth back faint but distinctly marked and continuous from the rhinophores to the tail root. Along each back margin a series of about 5 elongate bifid digitiform cerata without any ramifications; the foremost pair of cerata the longest, following cerata diminishing in length, the hindmost one a single median papilla. Rhinophores retractile within wide and moderately high sheaths with the hind margin entire but the anterior one with a tapering lobe projecting outwards. Base of the smooth sheaths with the back margin running up on the external side. Rhinophore clubs (Fig. 23) cylindrical, with a circlet of erect simply digitiform papillae, about 12 in number, shorter in front, the foremost ones diverging towards both sides from a very short rhachis. Head with a bifid velum bearing a pair of digitiform processes projecting forwards; the sides of the velum forming a pair of short furrow-shaped tentacles open beneath. Body sides smooth. Foot narrow, furrow-shaped, without prominent brim, rounded in front and with a simple anterior lip. Colour fulvous brown. Dimensions: Length 6.5 mm, breadth 1.5 mm, height 2 mm. Locality: Gilbert Islands, Aranuka, lagune, 1 sp. (S. BOCK coll. 10/10 1917, Riksmuseum).

ANATOMY. — The pharynx (L. 0.6 mm) is armed with a pair of strong yellowish jaws (Fig. 24) with well developed processus masticatorius; the latter, as well as the whole masticatory margin, bears crowded rows of small denticulations.

The small radula (Fig. 25) consists of a large number of series (at least 50), each with a median tooth and 6 lateral teeth. The median tooth is broadly triangular with both margins denticulated, the denticles are dense and diminish in size towards the apex of the cups, only a short tip of this is smooth. The first lateral recalls the half of the median tooth and is similarly denticulated in its outer margin. The 5 remaining laterals are smooth, with a short and



Aranucus bifidus.

- FIG. 22. — *a*, from the right; *b*, from the back; *c*, from beneath (foremost half). × 15.
 FIG. 23. — Left rhinophore club. *a*, from left side; *b*, from front. × 75.
 FIG. 24. — Jaws from front side. × 80.
 FIG. 25. — Radula, median tooth and all 6 laterals. × 750.
 FIG. 26. — Section through stomach.
 FIG. 27. — Genital organs.
 FIG. 28. — Central nervous system.

narrow slightly curved cusp and an elongate broad basal plate, which becomes shorter in the utmost teeth.

The salivary glands are compact and of a triangular shape.

Behind the short oesophagus is a simple sac-shaped stomach, which, in the specimen examined, was much contorted and displaced on account of the much swollen mucus gland. The walls of the stomach were folded into a small number of large cuticularized lamellae much intruding and forming a sort of rudimentary plates.

The dorsal surface of the stomach is covered by the anterior liver, which forms a single mass though debouching by means of two ducts at the right and the left sides of the stomach. From this liver portion a diverticulum sets out on each side to the first pair of cerata, into which they penetrate shortly.

From the posterior wall of the stomach a narrow intestine issues which runs in a slight curve to the right-sided anus. The inside of the intestine has no armature. To the left of the pylorus the posterior liver duct (from the posterior liver portion) debouches. This liver mass is simply conical and compact and sends no diverticula to the cerata. It is completely covered all round by the hermaphrodite gland.

In the hermaphrodite gland riping eggs were seen in the superficial follicles and bunches of spermatids in the deeper layers. A thin hermaphrodite duct runs beneath the intestine to the right side of the stomach, where the distal genital organs are lodged. Here the duct widens (Fig. 27*f*) to a bladder-like ampulla which, on one hand, communicates with the mucus and albumen glands (*m*), on the other hand gives off the short and slightly winding vas deferens; its starting point lies very close to these glands. The vas deferens widens to a saucer-shaped penis (*p*), which ends in a semi-spherical glans without armature; in its pore, however, a small cirlet of cuticular tufts was projecting, probably transformed vasal ciliae and perhaps representing a rudimentary armature.

The oviduct is furnished with an ovoid bursa copulatrix (*b.c.*) about equal to the ampulla in size and with a very short stalk.

Behind the intestine the heart appears superficially just below the cutis and to the right of it the initial portion of the kidney like an ovate sac with folded walls. The outer opening of the kidney is at the right body side somewhat above and in front of the anus.

In the central nervous system (Fig. 28) are to be remarked the sessile eyes recalling the conditions in the Eolidacea. Further, the four ganglia are rather concentrated, the pleural ganglia fused intimately with the cerebral, and the pedal ones being separated from each other only for a distance equal to the length of the cerebral ganglia. Traces of several statoliths were found in the statocysts.

RELATIONS. — That the genus *Aranucus* has its systematical position in the next vicinity of the Duvauceiliidae is evident from the lateral site of the anus, the

persistent margin of the back, the hermaphrodite gland superficially spread on the posterior liver, the shape of the rhinophore club, as well as the presence of velar tentacles. The new genus cannot be included in the same family because of the differences in cerata, liver and radula. The radula of Duvauceliidae is in the rule specialized as to the shape of the median teeth. In *Aranucus* the central tooth is unspecialized and similar to that of many genera of primitive nudibranchs, but a reduction of laterals has taken place. The radula has a great resemblance to that of *Bornella* or especially *Pseudobornella*, but this is probably merely an occasion phenomenon owing to little differentiation of the primitive type and reduction of laterals in both cases. Any close relation of *Aranucus* to Bornellidae is excluded because there are no gills on its cerata. In its nervous system *Aranucus* occupies a position between Duvauceliidae with their very long pedal commissure and other genera (e. g. *Bornella*, *Hancockia*, *Melibe*), with a short one. The genital organs are similar to those of Duvauceliidae in the lack of a prostata; the vas deferens, however, does not emerge from the albumen gland far from the hermaphrodite duct, but so closely to both, that a separation from the gland has just begun; in *Bornella*, *Hancockia*, etc., this separation has proceeded further. As to the liver, we have already spoken of the systematic facts indicated by its formation.

Fam. LOMANOTIDAE

Established on the single genus *Lomanotus* this family is quite distinct and well marked by external as well as internal characters. Unfortunately our knowledge of the anatomy and inner distinctions of the species is very limited and briefly treated only by ALDER & HANCOCK, BERGH, TRINCHESE and ELIOT, and

with no much holds for comparison. ALDER & HANCOCK have not been able to state with certainty fundamental conditions in liver and stomach, which were imperfectly made out and in part delineated by conjecture in their figure of *L. marmoratus*. In the preceding pages I have given some particulars on *L. genei*, and these seem to be so essentially different from corresponding characters of *L. marmoratus* that the two appear quite distinct. ELIOT (1910) supposes, however, that the latter species may be a young of the former one, and thinks this to be possible for *L. flavidus*, too. Till more observations have been made we must hold this alternative probable. ELIOT (1908) also thinks that the small *L. vermiformis* is

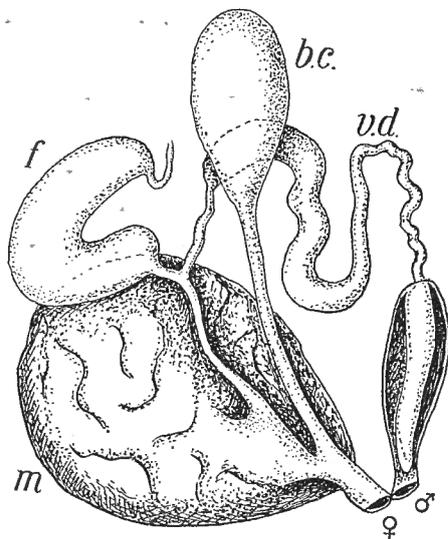


FIG. 29.
Lomanotus genei. Genital organs.

only a young form of a Mediterranean species that has, in recent time, invaded the Red Sea; but its characters seem to be distinct. I give a synopsis of the species as far as we know their characters, basing chiefly on ELIOT 1910, and only remark that the characters of the genus *Lomanotus* coincide with those of the family.

For the distal genital organs I examined *Lomanotus genei*. They differ essentially from those of Duvauceliidae in the bipartition of the ducts far before the glands. Vas deferens has a prostatic portion proximally, about as extended as the muscular distal part. Penis cylindro-conic. An elongate uterus leads to the albumen and mucus glands, and the short vagina bears a well-developed elongate bursa copulatrix with a long stalk.

Lomanotus Vérany 1844.

(= **Eumenis** Alder & Hancock 1845).

I. Anterior foot corners prolonged into tentaculiform processes. Oral veil with 4 digitations.

A. Back margin wavy.

1. Colour yellowish white suffused with brown, without white dots, or crimson with white spots. Papillae, about 30-32, in 8 undulations, 4 upwards and 4 downwards (largest papillae in each centre). Rhinophore sheaths with 5 processes. Radula $32 \times 36.0.36$ to $42 \times 58.0.58$; teeth with 4-10 denticles on each side of the cusp. Gonad encircling the posterior liver portion, which sends thick, little branching lobes to each inward undulation of the margin; anterior left liver and right liver fused. L. up to over 40 mm. *L. genei* VÉRANY 1846 (= *L. portlandicus* THOMPSON 1860; ? *L. hancocki* NORMAN 1877; *L. eisigi* TRINCHESE 1883; *L. varians* GARSTANG 1889).

2. Colour yellowish white with shades of brown and olive and quite small sandy spots; back lighter in centre; tips of cerata whitish, hepatic diverticula within them yellowish brown. Papillae about 22 in 4 indistinct undulations. Rhinophore sheaths with 4-5 processes or none. Radula $20 \times 8-10.0.8-10$; teeth with 12 denticles on each side of the cusp. Gonad above the posterior liver portion, which sends highly branching lobes to the back margin and into the papillae; anterior liver parts distinct? L. 17 mm. *L. mamoratus* ALDER & HANCOCK 1845 [*Eumenis*].

B. Back margin plain. Papillae, 3 large and about 20 small ones on each side, in a simple, not wavy row, white-tipped encircled with fulvous. Velum with 4 tubercular points. L. 6 mm. *L. flavidus* ALDER & HANCOCK 1846 [*Eumenis*].

II. Anterior foot corners rounded. Oral veil with 2 long processes. Rhinophore sheaths with 2-4 processes. Back margin plain, not wavy. Papillae concave, spoon-shaped, more than 20 on either side. Colour black with specks of white in two bands along the sides of the back; papillae translucent with white tips. Rhinophores brown or brown-spotted. Radula $17 \times 9.0.9$; teeth irregularly denticulated on both sides. L. 10 mm. *L. vermiformis* ELIOT 1908.

Fam. SCYLLAEIDAE

To this very characteristic family, for a long time comprising the single genus *Scyllaea*, a new genus was added by ELIOT when he established his remarkable *Crosslandia* in 1902; the genus *Nerea* LESSON 1830 is evidently identic with *Scyllaea*. A third very distinct genus of this family, *Notobryon*, will be described below; it is very characteristic in its radula with a broad naked rhachis. The three genera are related according to the synopsis given below.

As a general remark on these three genera may be said that they have all a liver divided into 2 or 3 globular masses which are quite smooth at their surface and do not branch. In the literature we meet with the statement that in *Scyllaea* liver branches are extended into the dorsal lobes, but this is not the case. What has been interpreted as liver branches are only the fine ramifications of

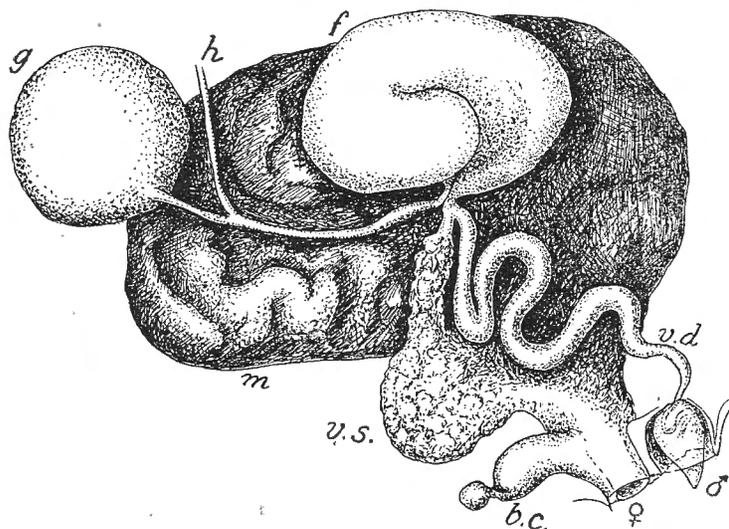


FIG. 30. — *Scyllaea pelagica*. Genital organs.

the kidney which spread among all the internal organs, gonads, liver, stomach, mucus gland, etc. They do not even enter the liver masses but end blindly on their external surface. ALDER & HANCOCK thought these canals to belong to the liver system and gave them this explanation in their figure, as mentioned above; and their real nature seems to have been unknown until present.

The kidney forms in *Scyllaea* as well as in *Notobryon* (fig. 31) a narrow tubular chamber with a lot of lateral ramifications in the shape of narrower canals giving off new branches which finally end blindly. In *Notobryon* the main urinary chamber extends on the upper side of the posterior liver and forms, behind its end, a large elongate conic vesicula. I have not seen a similar vesicula in *Scyllaea* where the kidney, in the posterior end of the body, terminates with branching canals like those in other parts of the body. In *Crosslandia* the liver

seems to share the unbranched shape of *Scyllaea*, and even here the kidney has a similar structure.

A genus character seems to be forwarded by the genital organs in fam. Scyllaeidae. In *Crosslandia* (cf. ELIOT 1902, text-fig. 4), the bursa copulatrix has an elongate stalk, and this is the case in *Notobryon*, too (cf. Fig. 31). In *Scyllaea*, however, the bursa has a peculiar shape (Fig. 30 *b.c.*). Its stalk is very broad and short distally, but in the fundus of this portion a narrow canal appears leading into a small vesicula, the pear-shaped bursa proper. It is evident that this organ is reduced. The oviduct, at the same time, has developed a dilatation (*v. s.*), still with muscular walls but, as it seems, with thinner parts as blisters in them. Thus we find in *Scyllaea* an interesting analogon or perhaps rudiment to the aberrant structure in *Dendronotus*.

Scyllaea is the single genus with more than one species, since ELIOT himself has withdrawn his second species of *Crosslandia* to be a mere colour variety of the first described typical *C. viridis*. We are able to discriminate three distinct species of *Scyllaea*, most of the names already given being merely synonymes of *Sc. pelagica*, the type species. Descriptions of colour of living specimens given by VERRILL (1878) and BARNARD (1927) prove that *S. edwardsi* of the first-mentioned author is the same as *Sc. pelagica*, and that the colour is quite alike on the coast of Maine and at the Cape. I here quote VERRILL's description of the colour, the most adequate one existing (1878, p. 21) : « Colour rich brownish yellow or orange, irregularly more or less spotted with deeper orange-brown blotches, and with opaque white specks, blotches and streaks. A band of deep yellowish brown runs along each side of the back interrupted by the dorsal lobes, and extending up their outer edges; edges of the dorsal lobes, tentacular sheaths and caudal lobe flake-white, which colour also borders the brown band. Along each side of the body, is a row of six or seven small, round, iridescent, purplish blue spots, and some smaller ones occur on the middle of the back. Anterior surface of tentacular sheath iridescent bluish. Along the sides is a row of small white papillae, and similar ones extend along the white line of the back. Tentacles orange, the plications edged with orange-brown, the tips white. »

For the discrimination of the species of *Scyllaea* the colour is not sufficient, though it was certainly the base of establishing new species, such as *Sc. viridis* ALDER & HANCOCK and *Sc. marmorata* A. & H., the type of which was reexamined, also anatomically, by ELIOT (1906 *d*). *Sc. viridis* of THIELE 1925, which I have examined for anatomy, proved, however, to be *Sc. pelagica*. The anatomy of *Sc. viridis* is thus unknown (even radula). The anatomy of *Scyllaea pelagica* has been described repeatedly by BERGH. The specific distinctions have been discussed briefly by ELIOT (1906 *d*); he remarks (p. 675) that the radula teeth are flat and bear only few denticles in *Sc. pelagica* and *marmorata*, but in *Sc. elegantula* and *bicolor* are erect and have more numerous denticles. I use in the synopsis also the number of gonads, which seems to be constant, and the number of liver masses, as classificatory marks.

SYNOPSIS OF GENERA OF SCYLLAEIDAE

- I. Radula with median tooth. Body sides with a row of small sparse papillae. Penis conical.
- A. One pair of dorsal lobes with a broad base. Anus lateral beneath the right lobe. Radula with the formula 30.1.30; a few denticles on all teeth. Liver in 2 compact masses (one anterior and one posterior). Rhinophores without elevated process, only with a weak margin behind, connected with the back margin... .. *Crosslandia* ELIOT 1902.
- B. Two pairs of well separated dorsal lobes. Anus latero-dorsal between the lobes. Liver consisting of 2 or 3 compact masses (right, left anterior, and posterior, the two former united or not). Rhinophore sheaths with an elevated posterior crest. Bursa copulatrix reduced in size, but with widened stalk. *Scyllaea* LINNÉ 1758.
- II. Radula without median tooth, rhachis naked, broad. Liver in 3 compact masses (right, left anterior, and posterior). Body sides smooth. Penis short, conical with flattened edge-shaped end bearing a small projecting lobe. Two pairs of dorsal lobes with long bases. Anus marginal between the right lobes. Rhinophores with an elevated posterior crest *Notobryon* n. gen.

SYNOPSIS OF SPECIES

CROSSLANDIA ELIOT 1902

Colour grass-green or Fucus-brown; a few sandy projections and coralline purple spots on sides; a brown marginal line on tail, body margin, rhinophores and velum. Lobes simple in adult specimens, bilobed and indented in young ones; a caudal crest in young specimens. Radula about 20 × 20-30.1.20-30. L. 38-50 mm;
C. viridis ELIOT 1902 (= *fusca* ELIOT 1902, 1908) (= *C. orientalis* THIELE 1925).

SCYLLAEA LINNÉ 1758 (**NEREA** LESSON 1830)

- I. Radula broad (at least 20 laterals on each side). Inner surface of the lobes and back surface with numerous gill tufts. Gonads 3-4 or 2.
- A. 3-4 gonads; liver in 2-3 isolated masses. Stomachal plates 15-26. Colour brownish (or greenish; BASEDOW & HEDLEY 1905), with green or bluish spots on the side. Radula 16-24 × 24-54.1.24-54; median and lateral teeth with 3-5 (6) denticles on each side. L. up to 60 mm. (BARNARD 1927)
Sc. pelagica LINNÉ 1758 (*Sc. ghomfodensis* FORSKÅL 1775, *Sc. quoyi* and *hookeri* GRAY 1850, *Sc. edwardsi* VERRILL 1878; *Sc. pel.* var. *marginata*, *sinensis*, *orientalis* BERGH 1875, ? *Sc. lamyi* VAYSSIÈRE 1917).
- B. 2 gonads. Stomachal plates 12. Colour brown marbled with yellow, with a row of yellow tubercles on each side of the body; branchiae whitish. Radula 16 × 27.1.27; median tooth with 4 denticles on each side; external laterals with 6 longish denticles on each side. L. 36 mm.
Sc. marmorata ALDER & HANCOCK 1864 (= *Sc. pelagica* of FARRAN 1905).
- C. Body slender, neck and tail much extended and longer than interjacent body part; rhinophorial crest short. Colour grass green with a few pale tubercles. Radula unknown. L. 25 mm. *Sc. viridis* ALDER & HANCOCK 1864.

II. Radula narrow (16-17 laterals on each side). Inside of the lobes with a few gill tufts. Gonads 2.

A. Liver in 2 masses. Insides of the lobes with 3-4 larger and 1-2 smaller gill tufts; 3-4 small tufts in a row at each side of the dorsal crest. Radula $18 \times 16.1.16$; median tooth with a short cusp and 4-6 lateral denticles; external marginals with more numerous denticles, those of external margin coarser and fewer than of the inner. One gonad to the left of anterior liver, one behind posterior liver. L. 14 mm. Stomachal plates of alternating size. Colour (in alc.) yellowish white *Sc. elegantula* BERGH 1875.

B. Liver in 3 isolated lobes. On each lobe 2 anterior and 2 posterior gill tufts and none elsewhere on back. Radula $24 \times 16-17.1.16-17$; median tooth with 4-5 denticles; external laterals with 5-7 denticles in inner margin and 4-5 coarser externally. Body dark olive green, sole and mouth pinkish yellow; rhinophore sheaths and lobes bordered with yellow. L. 16-35 mm. (ELIOT 1913). Stomachal plates of uniform size ... *Sc. bicolor* BERGH 1880.

SPURIOUS SPECIES

Scyllaea fulva QUOY & GAIMARD 1824; *Scyllaea (Nerea) punctata* LESSON 1830.

DIAGNOSIS OF NOTOBRYON N. GEN.

Body compressed bearing a low keel behind and 2 broadly triangular lobes, nearly contiguous at their bases, on back sides, with a single series of gill tufts on their upper surface. Rhinophores elevated, back margin running up as a continuous low crest, clubs laminated by several leaflets. Anus marginal between the two right lobes. Nephroproct just inside anus. Radula with broad naked rhachis, $14 \times 22-24.0.22-24$, inner laterals with short cusp, denticulated in inner margin, outer marginals with gradually stronger denticulation in outer margin; each tooth with a transversal process fitting into an excavation of its neighbour. Jaws with smooth margins. Salivary glands broadly triangular, flocculent. Stomach with a pyloric girdle of 8 thick plates. Liver in 3 globular masses, without ramifications. Gonads 2, globular, duct without ampulla, dividing into vas deferens and uterus which debouches into glandular mass; vagina with an elongate bursa copulatrix; no prostata; penis short conical with a flattened edge ending in 2 short cusps.

Notobryon wardi n. sp.

(Plate, figs. 1-3.)

Body slender, semitransparent, elevated, broad in front, much compressed in posterior third, with a dorsal crest slightly surpassing the level of the back. Inner surface of each lobe beset with a series of 4-8 gills, sometimes with smaller intermediate ones, on each side, about half-way to their edge. Back margin continuous forwards into a low list, with some few more elevated parts, running up and forming a marked crest on the elevated rhinophore sheaths. These with

funnel-shaped, smooth-edged opening directed forwards, and a perfoliate club with about 20 laminae and, on their frontal side, showing an angularity on each side of the rhachis (Fig. 31*b*). Head somewhat expanded round the mouth but forming no velum and bearing no processes nor tentacles. Foot a narrow furrow on the under side. Body surface quite smooth, but having the appearance as being microscopically grained by the presence of small subcutaneous glands. Colour (in alc.) whitish, here and there with traces of a light brown on lobes and gills. — Locality : Off Gatcombe Head, Port Curtis, Queensland, E. Australia, about 16 m depth, dredge (July 1929, M. WARD & W. BOARDMAN). Dimensions: Max. L. 60 mm, breadth across foremost lobes 25 mm, height 12 mm; 4 specimens (Riksmuseum).

ANATOMY. — The pharynx has a pair of horn-brown jaws (L. 4.3 mm) like those of *Scyllaea* and *Crosslandia*, thus elongate ovate, somewhat thickened along the masticatory process; this broad and with smooth margin.

The radula (Figs. 32, 33) is much aberrant from the normal one in

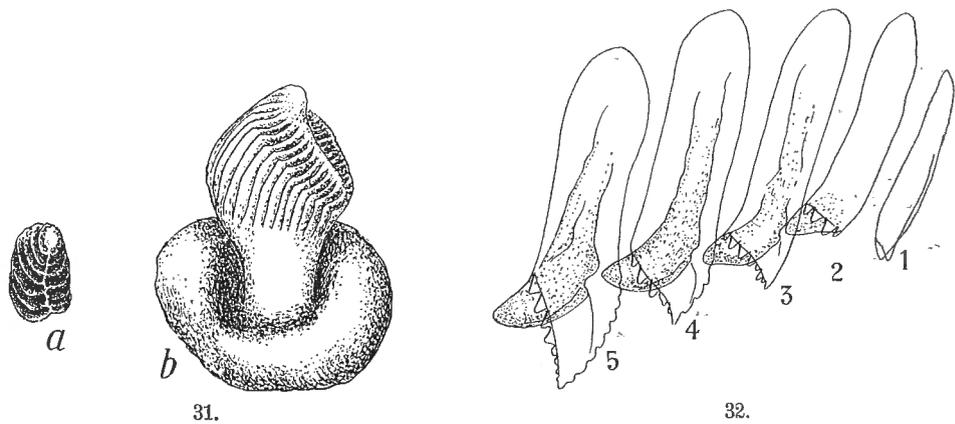


FIG. 31. — Rhizophore clubs of *Scyllaea pelagica* (a) and *Notobryon wardi* (b). $\times 20$.
FIG. 32. — *Notobryon wardi*. Radula, the 5 innermost teeth $\times 240$.

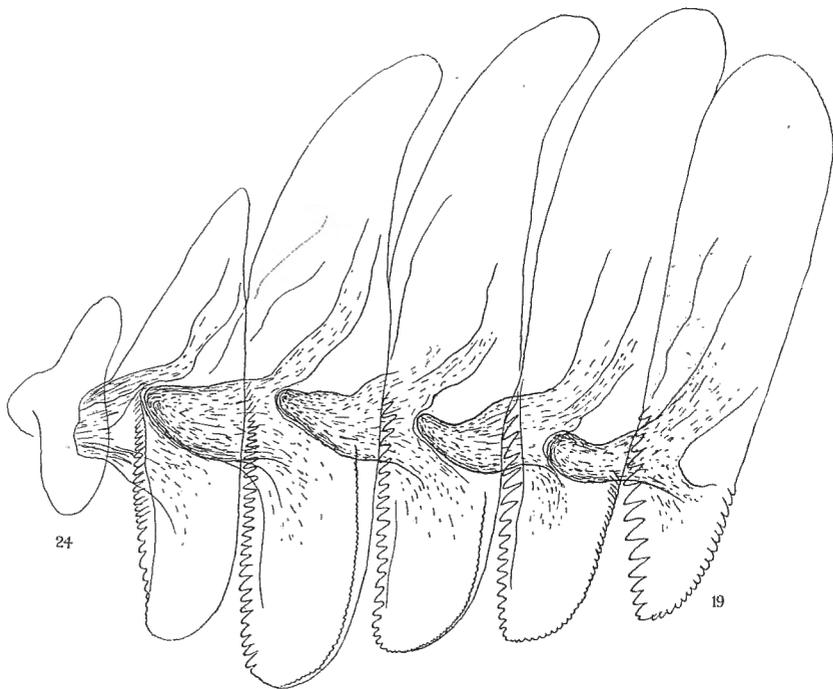
Scyllaeidae, above all because it lacks median plate. There is a broad naked rhachis, and the innermost laterals are quite vestigial showing that the whole median portion of the radula has been reduced. This part is also deeply infolded between the muscular halves of the tongue. The innermost tooth is very narrow, with a scarcely projecting cusp; the 2nd and 3rd have a denticulation of 4 and 7 denticles, respectively, in the outer margin, whereas their inner margin is smooth; in the 4th lateral also the inner margin is denticulated, and this shape of the teeth continues in the series to about the 17th or 18th tooth, at gradual increase in size of the tooth; the outer denticles increase at the same time in number, but the inner ones become indistinct; tooth 18 has 13-14 outer denticles, and the denticles of the inner margin appear as an indistinct serrulation and striation. The 2nd or (3rd) tooth from external margin is the largest one and has only external denticles (about 25); its cusp is rounded at

the inner side. A small vestigial utmost tooth with a short and smooth cusp may be present. All teeth are golden yellow. A peculiarity of the teeth is their transversal articulation within each row, mediated by a short conical process from the base which is lodged in an excavation in the next tooth. On the contrary, no articulation appears in a longitudinal direction; the basal plates of the teeth thin out forwards and do not touch the teeth of the next row.

The salivary glands surround the foremost part of the very wide oesophagus as a flocculent mass of fine, branching tubuli.

In the stomach the thick folds of the walls are raised and cuticularized forming a girdle of 8 thick plate-like elevations, broadly triangular in outline with elongate, relatively broad base at the fold and a central apex of cuticula substance (reddish brown in colour); the cuticula cover is thinner downwards. The top of the cuticula does not take the shape of a plate like those of *Scyllaea*, being not a lamella but rather a sort of elongate cap with quadrangular base and four blunt keels joining in the centre and forming the tip.

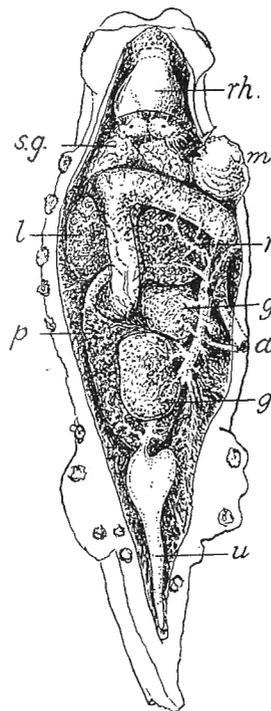
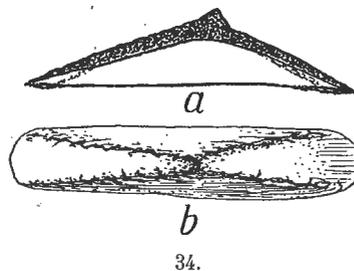
The contents of the stomach were a mass of animalic substance containing quantities of hydroid stocks.



33.

Notobryon wardi.

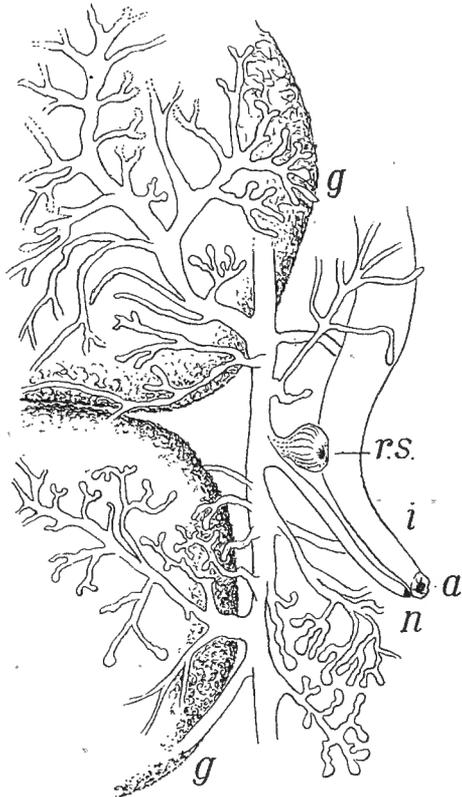
FIG. 33. — Radula. The outmost teeth. $\times 240$.
 FIG. 34. — Stomach plate. *a*, from side; *b*, from above. $\times 20$.
 FIG. 35. — Anatomy.



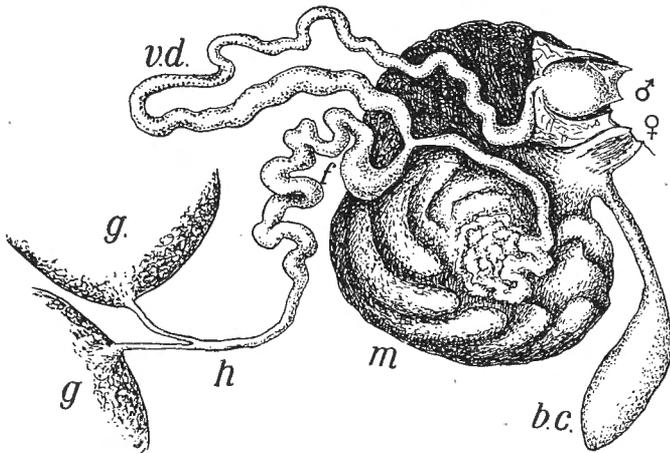
35.

On the upper side of the stomach the intestine is reflected forwards around the right liver (Fig. 35), and then it passes downwards and upwards again to the anus. The foremost half of the intestine has its inner wall faintly folded, a ventral fold, much larger than the others, extends to the end of the transversal part of the intestine. The liver is already described.

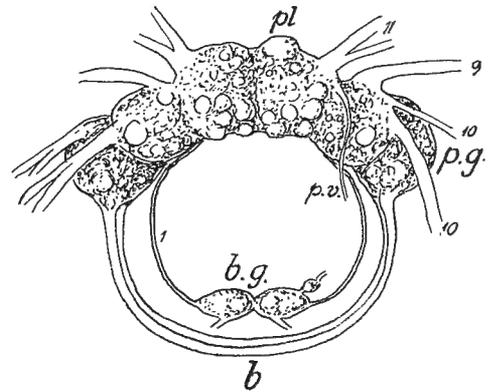
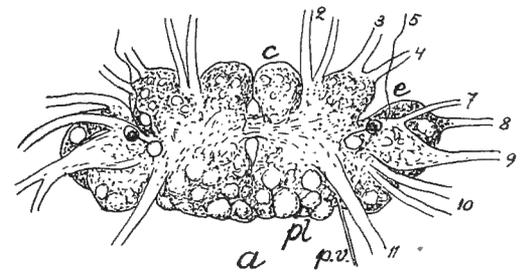
The heart lies behind the right liver, somewhat to the right of the median line of the body. In the ventral side of the pericardium appears the renal syrx, which leads into the tubular renal chamber (Fig. 36). This is branched all over and between the inner organs as a fine mesh-work covering them from salivary glands and stomach in front to liver and



36.



37.



38.

Notobryon wardi.

FIG. 36. — Central part of nephridium.

FIG. 37. — Genital organs.

FIG. 38. — Central nervous system. *a*, from above; *b*, from behind.

gonads behind. In the posterior end of the body a spacious urinary sac is lodged having an elongated coecum extended to the end of the body cavity.

The genital organs are already described. They exhibit (Fig. 37) two gonads lying on the upper side of the posterior liver mass. There is no ampulla (or this is only indicated as a widening of the duct) and no prostata, the vas deferens emerges far before the duct debouches into the glandular mass. The penis is singular in its short conical shape with its external margin compressed into an edge ending in a triangular lobe on the hind side of the glans.

In the central nervous system (Fig. 38) are the ganglia, compared with that of *Scyllaea*, much more distinct and separated in *Notobryon*, which agrees in this case with *Crosslandia* (ELIOT 1902, p. 67); the pedal ganglia in the last-named genus seem to concord with those of *Scyllaea* (« being ventral to the oesophagus »), but in *Notobryon* they lie much farther from each other, the pedal commissure being rather wide. There are very short optic nerves.

Fam. HANCOCKIIDAE

The genus *Hancockia* GOSSE (= *Govia* TRINCHESE) was first placed, by BERGH 1892, in the family Dotonidae. ELIOT (1910) included it in the fam. Lomanotidae, and MAC FARLAND (1923) created for it a separate family. This distinction, no doubt, is the better systematical arrangement on account of the peculiar organization in many respects pointed out by MAC FARLAND in his excellent work on this genus. *Hancockia* seems to have originated from a stem common to Duvauceliidae and Lomanotidae; its rhinophorial club recalls the former, and its cerata have an appearance recalling the undulating back margin of *Lomanotus*. As ELIOT remarks (1910), this papillation, the lamination of the rhinophorial club (which is vertical in *Hancockia* and rather oblique in *Lomanotus*) and the processes of the oral veil are characters approaching the genus to *Lomanotus* rather than to *Doto*. Only in the racemose liver ramification is concordance with *Doto*, but liver diverticula enter the rhinophores as in *Lomanotus*, in contradistinction to *Doto*.

One of the most peculiar organs of *Hancockia* is a median ptyaline gland described by both TRINCHESE and MAC FARLAND, much elongated (to about the end of the body cavity) and debouching in the bottom of the mouth together with the lateral ptyaline glands, which enter the rhinophores.

After MAC FARLAND, who has given a good description of this genus, we repeat its characteristics here: Animal elongate, foot narrow, linear, truncate in front, tapering to a short medially notched tail behind. Velum divided into a pair of palmate lateral processes. Rhinophores with vertically laminate clavus; sheath campanulate above round the club and here with fine ridges ending in small marginal denticulations. Back margin with a series (4-7) of

cerata, the foremost opposite to each other, the following alternating; each appearing as an outwardly turned stalked disc with digitate margin. Cerata and rhinophores with cnidocysts. Liver entirely cladohepatic, racemose, with 2 anterior and a posterior chief hepatic duct in body and liver mass in the distal ramifications. Lips with chitinous rodlets. Jaws with denticulate masticatory margin and process. Radula 1.1.1.; median tooth denticulate, laterals very broad, smooth. Salivary glands, ptyaline glands and a median much elongated ptyaline gland present. Hermaphrodite gland composed by numerous lobules lying above the liver duct, in the posterior body half. Penis conical, unarmed. Central nervous system highly concentrated; pedal commissure very short, optic nerves distinct, very short.

In order to judge if the characters of the genital organs of *Hancockia* as described by MAC FARLAND hold good of the genus as a whole, I examined *H. uncinata* from the Mediterranean ⁽¹⁾ and found here conditions quite different from those of *H. californica*, as already mentioned above, inasmuch as a typical bursa copulatrix is present and no secondary vesicula seminalis, whereas the contrary is the case in *H. californica*. These characters thus are not of generic range.

O'DONOGHUE constituted (1932) a genus *Iduliana* which he referred to fam. Dotonidae (=Iduliidae) but which, according to his description and his figure of the radula teeth of its type (*I. papillata*) is no doubt identical with *Hancockia*. The new species, which measures only 4 mm in length, comes from the Gulf of Manaar. O'DONOGHUE remarks that it cannot well be included in *Hancockia*, « because the lateral teeth are entirely different, the rhinophores are not provided with lamellae, and the swelling tubes and papillae on the dorsum are not found in that genus ». It is regrettable that no figure of the unusual habitus and back structure has been given, but in the radula, according to the figure, the laterals are quite like those described and figured by MAC FARLAND (1923) in *Hancockia californica*. I therefore place it in this genus as a good new species, though the description of O'DONOGHUE leaves one in doubt about the true nature of the papillation, the back « swelling » and « tube-like ridge », which may well be caused by contortion at preservation. The « papillation » is a mystical character and the whole description in some respects unclear.

M^{me} PRUVOT-FOL (1931) has had a good lot of specimens for examination at Banyuls and was able to decide that the European forms of *Hancockia* (described as *Doto uncinata* HESSE, *Hancockia eudactylota* GOSSE and *Govia rubra* and *viridis* TRINCHESE) are one single species, which, accordingly, should be named *Han-*

⁽¹⁾ One specimen, L. 10 mm. (in alc.) from St. Agata, Messina, 6-10 m., brown algae (BOVALLIUS 5/2, 1891) and one, L. 8 mm. in alc., 13 mm. living, from Rovigno in Istrien, brown algae (N. ODHNER 23/3, 1913; cf. ODHNER 1914), both in Riksmuseum.

cockia uncinata. This is, however, specifically well distinct from the Californian species, *H. californica* MAC FARLAND. The genus thus contains presently only three species which differ from each other chiefly in the following respects:

Hancockia Gosse 1877.

(*Govia* Trinchese 1885; *Iduliana* O'Donoghue 1932).

- I. Velar processes on each side 4, short, subequal. Colour greenish or reddish, dotted with white, seldom with bluish. Radula with 31-34 rows, median tooth with the lateral denticles (4 on each side) as large as the median cusp; lateral teeth with straight posterior margin and simple antero-interior corners. L. 7-13 mm.
H. uncinata HESSE 1872 [*Doto*] (= *H. eudactylota* GOSSE 1877, *Govia rubra* and *viridis* TRINCHESE 1885).
- II. Velar processes at least 6 on each side, of varying size. Colour reddish brown; tubercles of cerata and of rhinophores opaque white, often white spots along body sides. Radula with 50-62 rows; median tooth having its cusp stronger than the 3-5 denticles on each side of it; laterals with concave, in the middle bluntly projecting posterior margin and antero-interior corner bidentate. L. 21 mm.
H. californica MAC FARLAND 1923.
- III. Velar processes 6 on each side, digitiform. Colour dirty gray (in alcohol), no colour patterns. Radula with 51 rows, teeth similar to those of *H. californica* in size and shape, but laterals with small inner corners. Back with « an almost hemispherical vesicular swelling » sending a « tube-like ridge » backwards to the end and giving off lateral tubes to the cerata. In front of the swelling « two small pointed papillae, and a line of papillae 10-12 in number come off from the median ridge » (O'DONOGHUE). Cerata 7 on each side each with 8-9 knobs. L. 4 mm., width 12.5 mm. (preserved) *H. papillata* O'DONOGHUE 1932 [*Iduliana*].

Fam. DENDRONOTIDAE

Dendronotus Alder & Hancock 1845.

Since the genus *Campaspe* BERGH 1863, to which BERGH referred two species established by himself, cannot be separated from *Dendronotus* and is based on juvenile specimens of *D. frondosus* (cf. below), the family includes as single member the genus *Dendronotus*.

As I have remarked in a paper of 1926 (Nudibranchs and Lamellariids from the Trondhjem Fjord), the mandibulae and the radula are very variable in shape and dentition in this genus and thus not apt as base of the classification or description of the species of *Dendronotus*. The organization of the liver system is also subject of variation, inasmuch as the liver branches penetrate into the cerata in some individuals but do not in others (cf. ELIOT 1910). In specimens of *D. frondosus* from the Swedish West coast I have only seen the state represented in fig. 3, where the liver diverticula end at the base of the papillae, but in *D. iris* (= *giganteus*) from Nanaimo, British Columbia, the diverticula were found to

be attenuated as far as into the fine branches of the cerata, quite as ALDER and HANCOCK (1855, fig. 2, Fam. 3, pl. 2) draw their terminations.

The vestigial bursa copulatrix which was mentioned in the first chapter and which has not been noted previously in *Dendronotus*, is a generic character and

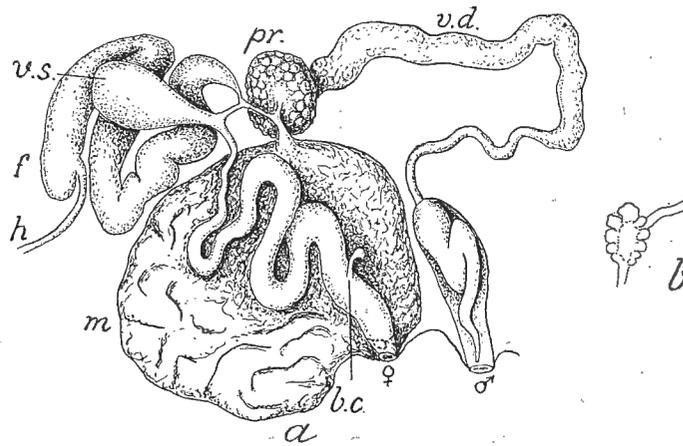
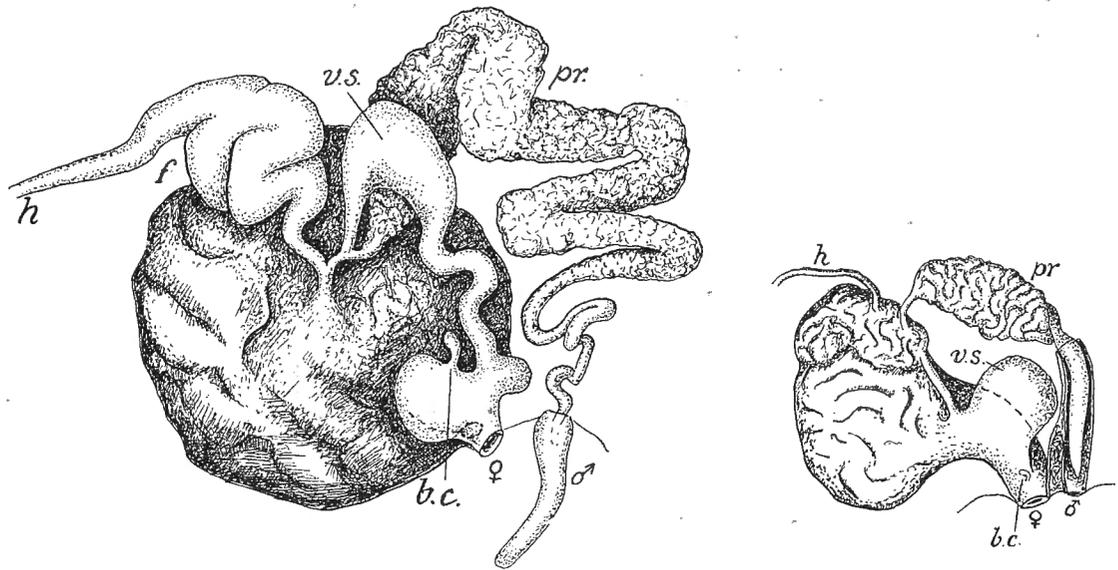


FIG. 39. — *Dendronotus*. Genital organs. a, of *D. frondosus*; b, prostata of *D. robustus*.



Dendronotus iris (= *giganteus*).

FIG. 40. — Genital organs.

FIG. 41. — Genital organs of young specimen.

not fit for discriminating the species. I have found it in *D. frondosus* from the Swedish coast (Fig. 39), in the same species from West Greenland (Baffin Bay), in *D. robustus* from the Gullmar Fjord, W. Sweden, and in *D. iris* (= *giganteus*) from British Columbia. At least two specimens were examined from each loca-

lity. In all cases the distal bursa showed the same position, and it seemed to be smallest in *D. frondosus*. As to the proximal vesicula seminalis, this existed in two shapes, but always with very thin walls, either as a swelling of the real apical end of the vagina, thus with the afferent canal debouching basally close at the side of the vaginal opening (a type present in *D. frondosus* and *D. robustus*, cf. fig. 39), or as a subapical dilatation of the vagina (*D. iris*) the afferent duct debouching into the opposite end of the vesicula (Fig. 40). A small specimen (about 30 mm) of *D. iris* (Fig. 41) not yet adult, proved that this vesicula originates as a large sac in the proximal end of the vagina, which was still rather short and bore, distally, a distinct though very small bursa copulatrix. In its proximal end the vagina narrowed again and was connected to the ampulla by means of a fine canal; on the other hand the vagina was in open communication with the mucus gland, from which it had not yet separated. The same condition, or the diaulic type of genital ducts, in the sense of ELIOT, was seen in a small specimen of *D. frondosus* from the Swedish coast. The ampulla, in the small *D. iris*, formed an intricate glomerus of the canal and gave off a side duct, vas deferens, which took its beginning in a likewise intricate prostata, the distal end of which showed the loose windings of the becoming muscular part of the vas. These observations place beyond every doubt that the proximal vesicula is a secondary formation of the vagina and that its existence makes superfluous the bursa, which therefore remains a rudiment even in the adult animal, though in *D. iris* it attains a trifle greater size than in the other species.

If the bursa copulatrix does not offer any specific distinctions, the vesicula, on the contrary, seems to do to some extent, but in still higher degree this is done by the prostata gland, which has a very different appearance in the different species. In *D. frondosus* it is a circular disc composed of numerous scattered vesiculae (Fig. 39a), in many circles; in *D. robustus* there is merely a single ring of vesicles in the prostata (Fig. 39b) (young specimens of *D. frondosus* hold an intermediate position with a few rings), and in *D. iris* the prostata is much elongated into a glandular thickened part of the vas deferens with vesiculose walls (Fig. 40). Thus we find in the prostata a good mark for characterizing the species, so that, when BERGH describes the prostata of *Campaspe major* as similar to that « in dem typischen Dendronotus » (1885, p. 24) we have a sufficient proof of their identity.

Further characters apt for taxonomy are to be found chiefly in the papillation of the frontal margin and the rhinophore sheaths. But the colouration, too, seems to offer, at least in some cases, useful marks. Thus O'DONOGHUE (1921), who has ventured to describe two new species of this genus so difficult in a taxonomic respect, remarks about the colour of his *D. giganteus* (1921), which he constitutes as a new species without, however, to take into consideration the previously known forms from the same coast of W. America, that its colour varies highly becoming in the cerata, « browner as they branch until

finally most of the tips are quite opaque, either a deep brown black or pale chrome yellow » and « around the edge of the foot is a narrow line of opaque white which starts at the edge of the veil ». This characteristic colour enables us to identify *D. giganteus* of O'DONOGHUE with the earlier described *D. iris* COOPER 1863, the diagnosis of which, together with the original remarks, I quote here in extenso in order to prove the correctness of this identification : « Pale purple, varying to orange red, foot narrowly edged with white, tentacles with white tips and a subterminal orange ring, branchial processes purple, the smaller ones sometimes olive near the base. Length of largest specimens 3, breadth 0.50 inch. Several found on the beach at Santa Barbara, May 5th, having been washed ashore by an unusually heavy sea, occurring at a very low stage of the tide. One, also, dredged on seaweed, from a depth of 28 fathoms, two miles off shore. This species seems more variable in colour than the other nudibranchiata of this coast, but I saw no reason for considering them of more than one species. Those washed ashore being somewhat injured although still alive, I made no drawing of them, and the more perfect one dredged was too small for this purpose. In the « Mollusca and Shells », of the U. S. Exploring Expedition under Commodore WILKES, Dr. GOULD mentions a species of *Dendronotus* collected at Puget Sound but does not name it or give any clue to its characters, except that the *branchiae* have white tips, unlike our specimens. It is very probable, however, that it belongs to the same species, as so many of the Mollusca of this coast have an equally wide range. »

Since *D. iris* (= *giganteus*) has never been figured, I reproduce a photograph of one specimen captured by Dr. MORTENSEN at Nanaimo, British Columbia, the type locality of *D. giganteus* (Plate, fig. 9).

D. rufus described by O'DONOGHUE (1921), on the other hand, has a colour which makes it a probable synonyme of *D. frondosus*, from which it cannot be separated (according to the description) in external characters. As a colour variety of the latter species we have certainly to regard also *D. lacteus* THOMPSON 1840, reported also by BECHER (1886) from Jan Mayen, just as are *D. luteolus* LAFONT 1871, *D. purpureus* BERGH 1879 and var. *aurantiaca* FRIELE 1879.

D. dalli BERGH 1879, on the contrary, was distinguished on its radula characters, but as I have shown in 1926 (Nudibr. fr. Trondhjems Fj.), these are too variable to serve as specific distinctions, and *D. dalli* cannot be maintained as separated from *D. frondosus*, and the same conclusion is valid for *D. lacteus* which BECHER thinks distinct on account of its radula; for particulars I refer to ELIOT (1910 and ODHNER 1926a). *D. elegans* VERRILL 1880 was established also chiefly on the radula characters (teeth 10.1.10; median tooth smooth), and is to be reduced to a synonyme of *D. frondosus*.

As a synonyme of *Dendronotus* I consider also the genus *Campaspe* BERGH 1863; *C. pusilla* BERGH 1863 and *C. major* BERGH 1886 are probably merely young specimens of *Dendronotus frondosus*.

With respect to these facts we may discriminate only 3 species of *Dendronotus* as valid, and these may be tabulated as follows.

- I. Velum obsolete; velar processes about 3-4, largest towards the median line of the body, smaller laterally.
- A. Rhinophore sheath round in section, without posterior crest, or bearing at most some small verrucae behind. Margin of rhinophore sheaths with about 5 subequal dendriform processes. Colour uniformly white, orange or red-brown, or marbled in these colours and with red and white spots. Prostata discoid, with several concentric series of vesiculae. Radula about $40 \times 9-15.1.9-15$. L. up to 75 mm. (ODHNER 1926)
D. frondosus ASCANIUS 1774 [*Amphitrite*] (= *Doris arborescens* MÜLLER 1776; *Dendronotus dalli* and *purpurascens* BERGH 1879, *D. elegans* VERRILL 1880).
- B. Rhinophore sheath with a posterior crest bearing a series of 3-5 small dendriform processes. Margin of rhinophore sheaths with 4-5 ramified processes. Colour purple, branchiae darker, foot edge with a line of opaque white. Prostata elongate, forming part of the vas deferens. Radula $35-40 \times 6-12.1.6-12$, median tooth projecting, with 11-13 denticles on each side, laterals smooth. L. up to 140 mm. (O'DONOGHUE 1921) *D. iris* COOPER 1863
 (= *D. giganteus* O'DONOGHUE 1921).
- II. Velum large, with 5 or more processes on each side, the largest laterally, smaller medially; external rhinophore process small. Margin of rhinophore sheaths with 4-5 ramified processes. Prostata with a single circle of vesiculae. Colour bright red, white dotted. Radula $35 \times 15.1.15$. L. up to 90 mm.
 (G. O. SARS). *D. robustus* VERRILL 1870 (= *D. velifer* G. O. SARS 1878).

Fam. BORNELLIDAE

Until 1932, when BABA described his remarkable *Pseudobornella*, this family contained the single genus *Bornella*. The ramification of the liver is described by ELIOT (1904 a, p. 100) as varying: « The ramification of the liver may be present or absent in the same species (*B. excepta*; see BERGH's two descriptions) and, when present, may not extend to all cerata. » ELIOT says about *B. digitata* from Zanzibar Harbour (l. c., p. 101): « The ramification of the liver appears to be very irregular and to vary in different specimens. In the largest the arrangement is as follows:— A single branch runs up into the tall tapering process behind each rhinophore; the first pair of cerata receive no branches at all; the second and third receive on the right hand a branch which bifurcates, and on the left a simple branch, which, in the third, stops at the base of the cera and does not enter it. The remaining cerata receive no branches. » In contrast to these statements VAYSSIÈRE (1917) describes and figures in *B. digitata* a liver branching to all the 3 foremost pairs of cerata, but without diverticula to the rhinophores. In 5 specimens of *B. digitata* at my disposal from the Marshall Islands (Jaluit and Ebon; coll. CHR. HESSLE, 1917), the liver branched as VAYS-

SIÈRE describes, thus sending diverticula to 1st, 2nd and 3rd pairs of cerata, but none to the posterior pairs and none to the rhinophores; only a very short lobe pointing forwards may be present in the right liver.

In *B. simplex*, according to ELIOT 1904*a*, p. 104, the liver « sends off diverticula into the process behind the rhinophores and all four pairs of cerata ».

In *B. excepta*, BERGH states the absence of every branchment (1884) (cf. Fig. 42) : in a specimen examined in 1902 he found « diverticula rising into the papillae; from the right liver a similar branch stretches along the body-wall forwards, but no similar on the left side » (cf. BERGH, 1902*a*, pl. III, fig. 4).

This variation in branchment of the liver is analogous with that stated in *Dendronotus* and does not imply any specific distinctions. These are, as it

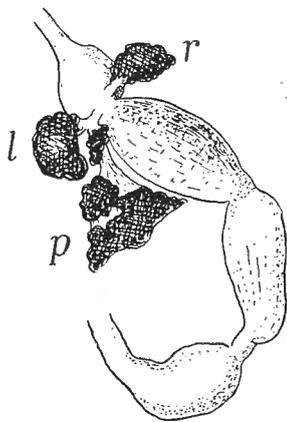


FIG. 42. — *Bornella excepta*. Liver portions.
(After BERGH, 1884, pl. VIII, fig. 9.)

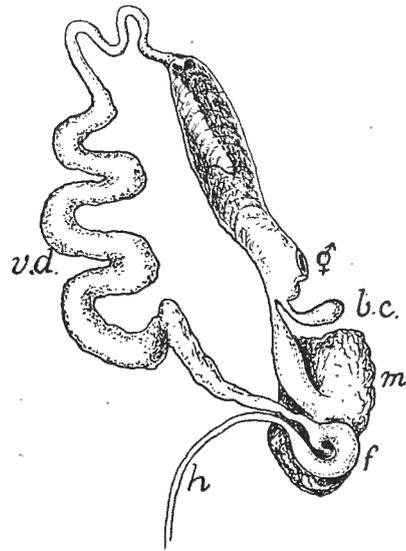


FIG. 43. — *Bornella digitata*. Genital organs.

seems, to be deduced, in the genus *Bornella*, from external characters : the shape of cerata, the papillation of the velum and the rhinophore sheaths. The small number of specimens still known to a sufficient degree does not permit us to form a definite opinion about the value of these distinctions. BERGH (1892*a*) and ELIOT (1904*a*) give a list of the species described, many of them being synonyms. ELIOT (1904*a*) hesitates if *B. arborescens* PEASE 1871 is a distinct species or identical with (or a variety of) *B. digitata* ADAMS & REEVE 1848; it has most of its cerata bifid, a character which BERGH (1874, Mus. Godeffroy) states as specific of *B. arborescens*. BERGH himself describes, however, a variation in this respect (p. 98), as well as in the number of velar papillae (8-16; p. 97), *B. arborescens* evidently includes *B. marmorata* COLLINGWOOD 1878, which has likewise part of the cerata (2nd-4th pairs) bifid and only 5-6 papillae on each side of the deeply incised velum, but forms itself a synonym of the typical *B. digitata*, the charac-

ters mentioned scarcely being constitutive for the species. A critical estimation of the species is presently impossible to undertake, and I give a synopsis in next agreement with ELIOT's opinion as to their delimitation.

If the genital organs offer any distinguishing characters is uncertain.

In *B. digitata* I found the same features as VAYSSIERE (1917) : a small bursa; vas deferens emerging from the ampulla, and with lengthened prostatic portion (Fig. 43).

The genus *Pseudobornella* with the type *orientalis* established and made the subject of a thorough investigation by BABA in 1932, has afterwards (1933) been examined anew by the same author; from both descriptions its characters have been quoted here.

SYNOPSIS OF GENERA

- I. Gills at the inner base of the cerata; these cleft into long processes diminishing in number towards behind. Body slender. Foot narrow. Rhinophore sheaths with elongate marginal processes. Jaw with smooth margins, without masticatory process. Radula 7-14.1.7-14, the median tooth denticulated, the laterals smooth. Hermaphrodite gland dissolved into a number of more or less separated globules lying above the posterior liver *Bornella* GRAY (in ADAMS & REEVE) 1848.
- II. Gills along inner side of each dorsal papilla. Rhinophore sheaths with 3 long processes (the posterior much elongate and slender). Body stout. Foot broad. Velar processes 2-4 on each side, the lateral ones much elongated, the mesial short. Cerata simple, not branched nor cleft. Jaws with denticulate masticatory process. Radula 2.1.2. median tooth denticulated, inner lateral denticulated or smooth, the outer one smooth. Hermaphrodite gland a single mass at the right side of the posterior liver *Pseudobornella* BABA 1932.

SYNOPSIS OF SPECIES

BORNELLA GRAY (in ADAMS & REEVE) 1848

- I. Velum with a series of tubercles on each side.
 - A. Rhinophore bases without papillae; rhinophore sheaths with 4 marginal processes. Median tooth of radula denticulate.
 1. Posterior process of rhinophore margin simple. Dorsal papillae deeply cleft, with 1-3 gills on inside. Generally 6 (7) pairs of dorsal papillae with 4, 3, 2 branches (the hindmost simple). Velum with 10-12 (or 5-6) short processes on each side (in a single or 2 or more rows). Colour white with orange or red reticulation, cerata white-tipped and orange-ringed. Radula 33-45 × 8-14.1.8-14. L. up to 50 mm.
B. digitata GRAY (in ADAMS & REEVE) 1848 (syn. *B. adamsi* GRAY 1850, *B. hancockiana* KELAART 1859, *B. hermanni* ANGAS 1864, *B. semperi* CROSSE, 1870, *B. arborescens* PEASE 1871, *B. caledonica* CROSSE 1875, *B. marmorata* COLLINGWOOD 1878).
 2. Posterior process of rhinophore margin 4-digitate. Dorsal papillae cleft only apically. Gills 2 on the inside and 2, basal, on the outside of the

cerata, the latter gills protected each by one small papilla. Velum with 7-11 processes on each side. Colour whitish, reticulated with orange. Radula $41 \times 17-19.1.17-19$ or $34 \times 16.1.16$. L. 30-60 mm.
B. excepta BERGH 1884.

B. Rhinophore bases with posterior papilla or papillae; sheath margins with 6 processes. Dorsal cerata 7 pairs, deeply cleft, 1st cera 4-partited, with gills at base and between parts. Velum with a few elongated processes on each side. Colour yellowish white. Radula $41 \times 11.1.11$; median tooth smooth. L. 65 mm.
B. calcarata MÖRCH 1863.

II. Velum with a single tubercle on each side. Rhinophore sheaths with six short digitations and a larger rounded knob behind. Cerata 4 pairs, each 4-divided (except the simple hindmost one) and with one pair of gills (anterior and posterior). Colour transparent white, an orange net-work on back and a row of opaque white dots on sides. Radula $21 \times 9.1.9$, median tooth with 7-8 strong denticles (little smaller than median cusp). L. 12 mm.
B. simplex ELIOT 1904.

PSEUDOBORNELLA BABA 1932

Cerata 4 pairs. Rhinophore sheaths with the posterior papilla elongated to as much as 5 times the length of the body. Foot large, expanded. Colour translucent yellow with chocolate-brown mottlings and yellowish white striations. L. 10 mm.
B. orientalis BABA 1932.

Fam. FIMBRIIDAE

BERGH (1892a) gave this family the name of Tethymelibidae, an ethymology which has no support in the rules of nomenclature. THIELE (1931) therefore changed it into Tethyidae after the typical genus *Tethys* (auct.). But this name was given by LINNÉ in 1758 for two species which he later on (1767) called *Aplysia* at the same time reserving the name *Tethys* to the nudibranch ever since designated so by most of the authors; LINNÉ called the type *Tethys fimbria*, accepting as specific name a genus established by BOHADSCH in 1761. The fact that *Tethys* LINNÉ 1758 has to replace *Aplysia* LINNÉ 1767 was recalled in actuality by PILSBRY 1895 and left the nudibranch genus without name. For the latter the name *Tethys* is impossible to take up, even if *Aplysia* should be preserved as a nomen conservandum and *Tethys*, in the original sense of LINNÉ 1758, dropped. The nudibranch genus, consequently, has to take another name. I think our best way out of this nomenclatural dilemma is to accept the proposal made by O'DONOGHUE 1926, that is, name the genus in question *Fimbria*. This name may stand, though BOHADSCH was not a binominalist, since « LINNÉ had used the same name for the same animal in the specific sense » (O'DONOGHUE 1929, p. 758), and its type thus, should be named *Fimbria fimbria* LINNÉ 1767 in analogy with so many other tautonomic names, e. g. in ornithology such as *Pica pica* LINNÉ.

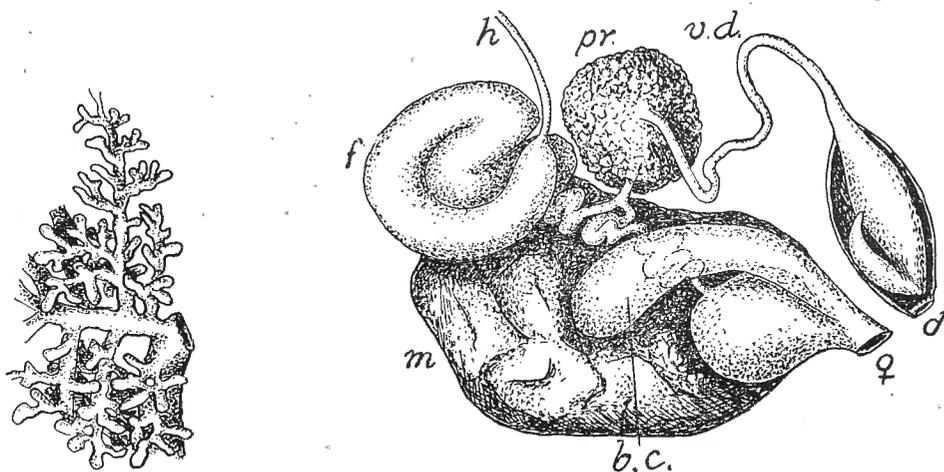
Besides the genus *Fimbria*, this family comprises only the genus *Melibe* (syn. *Chioraera* GOULD 1853 and *Jacunia* DE FILIPPI (1867) ⁽¹⁾). A common characteristic of these two genera is the absence of the radula, a condition seemingly in correlation with the unusual differentiation of the nutrition organs. The velum has developed into a large cowl or catching net apt for the capturing of small crustaceans or even fishes being the prey of these nudibranchs. It is impossible to state other common characters besides, however, that the cerata are larger than generally in nudibranchs. Jaws are absent in *Fimbria* and *Melibe leonina*, but are observed in other species and are perhaps occasionally wanting in *M. fimbriata*. The cerata have basal branchiae in *Fimbria* but none in *Melibe*, where, on the contrary, the whole surface of the cerata and that of the body is covered, generally, with tubercles and filaments; it is smooth in *M. leonina*. The foot is broad in *Fimbria* and in *Melibe japonica* and *mirifica* but in most other species of *Melibe* it is very narrow. As to the inner organization, no gastral plates are extant in *M. leonina*, whereas, in all remaining species, there are. The liver is subject to great polymorphy. Its chief posterior portion is compact in *Fimbria* having also its duct united with that from the left anterior portion, as described above. In *Melibe* the liver is generally flocculent (Fig. 44) and the left anterior gall duct is generally entirely independent, though in *M. leonina* the same condition prevails as in *Fimbria*. The most differentiated liver is that of *Melibe leonina* which has been transformed into a net-work of tubes (cf. AGERSBORG 1923, pl. 27, fig. 2); in other species these tubes are frequently beset with tufts of shorter tubes or with vesiculae. Separation of different genera cannot be made on the base of the liver structure.

The rhinophoria exhibit two different types: as a rule they are pillar-shaped with a funnel-like dilatation at tip round the club (most species of *Melibe*), or are laterally compressed as to resemble the cerata and with the club immersed in the anterior edge of the lamelliform organ. This type is to be found in *Fimbria* and in *Melibe leonina*. Recently (1929) O'DONOGHUE described similar rhinophoria in a species from the Red Sea which he identified as *M. bucephala* of BERGH 1902; the same species was identified and reported also by ELIOT (1908). A direct comparison of BERGH's type with ELIOT's description enabled me to decide that they are identical, though no trace of rhinophores were seen. *M. bucephala*, according to ELIOT and O'DONOGHUE, shares the characteristic rhinophores with *M. leonina*.

Several species of *Melibe* have been described but their delimitation is not sharply defined in all cases. BERGH, who established *M. vexillifera* in 1880, is in 1884, inclined to consider the same as a synonyme of *M. papillosa*, and with

(¹) ALLAN established in 1932 a new genus *Propemelibe* on a new interesting species with very broad foot; in other respects, however, no distinct characters can be adduced, and it seems impossible to maintain that genus unless further characters are known.

right; for the characters constituting *vevillifera* seem to be due to distortion, as ELIOT (1907) thinks. A probable synonymy is also, as ELIOT (1907) suggests, *P. pilosa*=*papillosa*. For the taxonomy the shape of the cerata comes in first place, as well as the shape of the cowl, if entire and circular or incised in anterior or posterior margin. The foot is generally narrow but a broad foot is characteristic of *M. japonica* ELIOT and *M. mirifica* ALLAN. To some degree the jaws and the stomachal plates are of value for the taxonomy. The fan-shaped organ, a dilatation of the uterus, seems to be a variable feature. I found it only feeble in *M. papillosa* (Fig. 45).



Melibe pilosa (= *papillosa*).

FIG. 44. — Part of left liver with duct.

FIG. 45. — Genital organs.

Of the genus *Fimbria* the generally known type *fimbria* inhabits the Mediterranean Sea. BERGH's statement (1890) that it occurs at the Canary Islands is certainly due to confusion with *Tethys* (= *Aplysia*) *leporina*. In this same work BERGH, however, described a specimen of *Fimbria* from the vicinity of Dominica, West Indies, 250 m depth, under the name of *Tethys leporina* L. var. It differs from the Mediterranean type in its colour (large black spots on the back) and in anatomy: the salivary glands are extended to the liver, the right and left anterior part of which spreads over the stomach, the halves meeting medially; further, the genital organs offer some differences. On account of these discrepancies there is no doubt that the West Indian form is to be considered as a distinct species, for which I propose the name *Fimbria occidentalis*.

SYNOPSIS OF THE GENERA

- I. Body flattened. Cerata smooth, each with one pair of basal gills. No jaws. Stomach without plates. Liver with posterior part compact, surrounded by the gonad.
Fimbria BOHADSCH 1761 (*Tethys* auct., non LINNÉ 1758).

- II. Body usually narrow and elevated. Cerata as a rule tubercled or fimbriated, with no basal gills. Jaws generally present, small. Stomach with a girdle of plates. Liver diffuse, tubulose or flocculent. Gonad forming glandular masses beneath liver.
Melibe RANG 1829 (*Chioraera* GOULD 1853, *Jacunia* DE FILIPPI, *Propemelibe* ALLAN 1932).

SYNOPSIS OF SPECIES

FIMBRIA BOHADSCH 1761

- I. Colour pale yellowish or hyaline grayish yellow with dense white dots in sinuous bands; velar margin black or black-spotted beneath. Foot sole yellowish white. Cerata white, their upper surface with black spots. Cerata in 6-8 pairs. Salivary glands very short. Right and left anterior liver only little spread on the stomach. Penis with an accessory sac. L. 160-210 mm.; br. of velum 100-140 mm. ...
F. fimbria LINNÉ 1767 [*Tethys*] (= *Tethys leporina* auct., non LINNÉ 1758).
- II. Colour of velum yellowish white of dense dots confluent towards the margin to irregular spots; under side black; marginal cirri yellowish white. Rhinophore sheaths black with large yellowish white spots, club whitish with black base. Back yellowish white with large black spots on neck and margins; gills whitish; foot yellowish, sole brownish gray. Cerata in 7 pairs. Right and left anterior liver spread over stomach and meeting medially, each with 2 branches, the anterior towards rhinophore sheath, the posterior to 1st papilla. Salivary glands elongated backwards as far as to the liver. Penis without accessory sac. L. 43 mm. ...
F. occidentalis n. n. (= *Tethys leporina* L. var., BERGH 1890).

MELIBE RANG 1829

- I. Rhinophores stalked, cup-shaped, without posterior crest.
- A. Foot narrow. Velum circular, with entire margin.
1. Cerata claviform, tapering and rounded at top, covered with large nodules.
- a. Body with simple conical or spherical (generally not branched) tubercles scattered all over.
- + . Inside and outside of velum nodulose. Body with fine nodules. Cerata 7-9 pairs with a few (3-5 in half its periphery) large nodules. Velar margin with 2-4 series of cirri. Rhinophore clubs with about 12 lamellae. Jaws with about 12 coarse denticles and a short masticatory process. Stomach plates 8 (1-3 smaller intermedian), with a high crest. Colour white to yellowish red. L. 40 mm. ...
M. rosea RANG 1829.
- + + . Inside of velum finely grained or smooth. Body warty.
- a¹. 7-9 pairs of cerata, everywhere covered with dense nodules. Velum with 2 rows of marginal cirri. Rhinophore club with 10-11 laminae. Jaws with 25-30 fine denticles. Stomach plates 26-31, thin, with high crest. Colour greenish white. L. 85 mm. *M. rangi* BERGH 1875.

*a*². 5-6 pairs of cerata (unknown to shape and appearance). Velum with 4 rows of marginal cirri. Rhinophore club with 7-8 lamellae. Jaws with 22-23 coarse denticles. Stomach plates 10, rounded above, with no crest. Colour pale yellowish white. L. 12 mm.

M. capucina BERGH 1875.

*a*³. 3 pairs of cerata. Velum with 2 (3) rows of cirri. Rhinophore club with 10 laminae. Jaws smooth. Stomach plates 24, with high crest. Colour grayish with dense whitish-green dots; tubercles on body sides black with fine greenish white dots in centre. L. 60 mm.... ..

M. ocellata BERGH 1888.

b. Body smooth except for ramified processes along middle line of back. 4 pairs of roundish cerata with perforations on top. Colour yellowish white, cerata orange, white-topped. L. 32 mm.

M. australis ANGAS 1864 [*Melibaea*].

2. Cerata wedge-shaped (with thin edge at top), covered with small tubercles or fimbriated (as body in general), set in 5-7 pairs. Stomach plates about 20.

a. Rhinophore sheath expanded and wavy, generally with a posterior process on margin. Cerata and body with soft irregular tubercles and fine thread-like (not arborescent) appendages. Inside of velum nodose. Rhinophore club with 6-8 laminae. Colour yellowish or reddish brown with dark shades and mottles or grayish green or blue dotted by olive in the tips of the cerata and on body. L. 60-100 mm. (BABA 1933)

M. pilosa PEASE 1860 (= *Jacunia papillosa* DE FILIPPI 1867; *M. vexillifera* BERGH 1880).

b. Rhinophore sheath rounded, smooth. Cerata and body tomentose all over with arborescent filaments. Rhinophore club with 9-10 laminae. Colour bright yellow to ashy gray, usually with irregularly placed spots and blotches of black, gray or sandy. Inside of velum shagreened. L. up to 200 mm. (ELIOT 1902).

M. fimbriata ALDER & HANCOCK 1864.

B. Foot broad. Velum notched in posterior margin below mouth. Jaws with thin undulated edge.

1. Velum entire in front margin, with 9-10 rows of cirri at the sides, 2-3 rows above the mouth. Cerata 10 pairs, covered with irregular tufts. On the sides of the velum small scattered papillae; inside of velum with small papillae and tufts. Rhinophore sheaths with a tuberculate process behind. Stomach plates 24, black, triangular. Colour transparent yellow with a reddish tinge in parts. L. 150 mm. *M. japonica* ELIOT 1913.

2. Velum incised in the front margin, with about 4 rows of cirri. Cerata 5-7 pairs, with rounded pustules and a few branched fimbriae. Stomach plates about 40, lengthened and rounded above, more like folds than laminae. Colour transparent pinky-blue; velar cirri rose-pink (upper-

most row white); pustules on back rose-pink or white; filaments smoky reddish gray and tipped with white. L. above 300 mm.

M. mirifica ALLAN 1932 [*Propemelibe*].

II. Rhinophores blade-like, similar to the cerata in shape, with the club in the anterior edge.

A. Cerata (in 5-6 pairs) and back (as well as rhinophores) tubercled. Velar margin with 3-4 (5) rows of cirri; inside with very fine papillae, almost smooth. Jaws small with thin wavy margin. Stomach plates 20 with high crest. Colour transparent white, with a light tinge of brownish and plenty of opaque white dots; small lateral warts red. L. 90 mm. Liver flocculent; left and posterior ducts separate. *M. bucephala* BERGH 1902.

B. Cerata (in 6 pairs), back and rhinophores smooth. Velar margin with 2 rows of cirri. No jaws. Posterior liver duct and left one united. Liver tubular. Stomach with a corneous lining but no cuticularized folds or plates. Colour pale yellowish or whitish gray with a fine white net-work. L. about 60 mm. (O'DONOGHUE 1921) *M. leonina* GOULD 1853 [*Chioraera*] (= *M. pellucida* BERGH 1904; *M. dalli* HEATH 1917).

Fam. DOTONIDAE

For the nomenclature of this family and its typical genus, *Doto* OKEN 1815, which, according to IREDALE & O'DONOGHUE (1923) should be, as preoccupied, abandoned in favour of *Idulia* LEACH 1852, I refer to M^{me} PRUVOT-FOL who (1931) has raised weighty objections to this change of names (cf. ODHNER 1934). I keep *Doto* as a valid name. Its type is designated by GRAY (1847) to be *Doris muculata* MONTAGU 1804 (= *Doris coronata* GMELIN 1791). *Idulia* LEACH and *Dotona* IREDALE are to be considered as synonymes. To these must be added *Bornellopsis* O'DONOGHUE (1929), which cannot be kept even as a section, since its characteristic, the gills on the inside of the cerata, exists also in *D. coronata*, though less distinctly. In reality we can observe in *D. coronata*, at the base of the inner side of the large papillae, a modification of the tubercles, inasmuch as three of them, at least, have coalesced to a gill and do not contain any liver diverticulum (Fig. 46a). TRINCHESE (1881) has figured a similar condition in *D. cornaliae* (l. c., pl. LXI, fig. 1e), which he explains as « eminenza papillare senza ramo epatico. Essa è situata sulla faccia interna della papilla ». In his habitus figure of this species (l. c., pl. LIV), however, no trace of this singularity is observable. In reality, there seems to be a transition between normal papillae and those modified into gills. In small papillae of *D. coronata*, normal tubercles, but smaller, are at the place where in large papillae the gills develop. In *D. fragilis* a similar gill formation takes place (Fig. 46b) : the small basal papillae coalesce in a longitudinal direction and bud further in vertical stripes and laterally. In *D. pinnatifida* (2 specimens, L. 12 mm, from Asia Shoal, Plymouth, 10 m, on Antennularia; coll. T. GISLÉN 27/6 1925; Riksmuseum) a gill precisely as large and elaborate as in *Bornellopsis* was present on each papilla. Therefore

it seems not likely that a classification of the genus *Doto* may be based on these papilla formations, which may be of varying stage of development; in 2 specimens of *D. fragilis* taken together with the above-mentioned *D. pinnatifida* and measuring 17 mm (contracted), these gills were much less distinct; in the new species *D. japonica* and *apiculata* (Fig. 46c), on the contrary, they are quite as striking as in *D. kabretiana*, which O'DONOGHUE described as *Bornellopsis* but which has nothing to do with *Bornella*; cf. also PRUVOT-FOL, 1933, p. 133.

Very little accession has been made to our knowledge of the *Dotonidae* since BERGH's time, and no new valid genera have been established; on the contrary, the genera then existing have been degraded to mere sections by THIELE (1931), and with right, for the distinctions may be effaced in certain cases; thus *D. paulinae* has indistinct tubercles on its papillae and mediates the transition to the

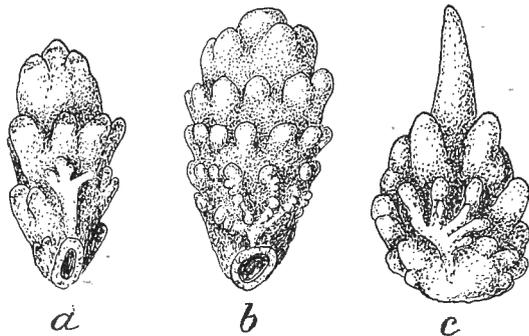


FIG. 46. — Dorsal papillae of *Doto coronata* (a); *D. fragilis* (b), and *D. apiculata* (c), showing the basal tubercles on inside modified into gills.

tubercles; single species *luctuosa* BERGH 1870), and *Heromorpha* in 1873 (with *H. antillensis* as monotype) characterized by a velum like that of *Doto* though somewhat produced laterally, and simple papillae (?) (2).

The more abundant in species is the genus *Doto* sensu stricto. The classification of the about 20 species which prove valid, offers great difficulties, since only slight differences exist and these are above all to be found in the colouration, which remains in essential degree even in preserved specimens. A classification of *Doto* must base upon this character, as I have pointed out in 1922 and 1934, at least for the present. As it is of importance for further study of the genus that a synopsis is at hand, I have put one together comprising all known species arranged as to their colour and rendering also other characteristics of value for identification.

(1) Cf. ELIÖT (1910, p. 166); this species is not mentioned by VAYSSIÈRE (1913, Moll. de France).

(2) Only the last papilla on one side remained in the type specimen examined by BERGH, and this was simple; the last papilla may, however, be not only smaller but also simpler than the preceding ones. (Cf. TRINCHESE, 1881, pl. LVIII, *D. paulinae*.)

section *Gellina* GRAY 1850 (with the single species *affinis* d'ORBIGNY 1837 described as *Tergipes*, from Rochelle, but not refound) (1) which is characterized in having all papillae simple. *Iduliella* THIELE (1931), = *Dotilla* BERGH 1871, non STIMPSON 1858, differs only in having lateral teeth (the single species *D. pygmaea* BERGH 1871 may be identical with *Doto floridicola* SIMROTH 1888). The remaining original genera of *Dotonidae* are established by BERGH: *Caecinella* in 1870. (anterior papillae simple, last pair with 2-3 rings of

SYNOPSIS OF SPECIES

DOTO OKEN 1815, s. s.

I. Papillar tubercles with dark (red, brown, blue, black) apical spots or subapical rings.

A. Papillae in 6-8 (9) pairs, each with 4-5 (6) rows of tubercles. Rhinophore sheaths usually with smooth or crenulate margin.

1. Colour whitish yellow with crimson spots and dots, tubercles with red dots and rings. Radula with above 100 teeth. L. 10-12 mm.
D. coronata GMELIN 1791 [*Doris*] (= *costae* TRINCHESE 1881).
2. Colour pale ochraceous with dark-brown spots, an apical brown spot above a whitish ring in each tubercle; 5-6 rows of tubercles. L. 10 mm.
D. pinnatifida MONTAGU 1804 [*Doris*] ⁽¹⁾.
3. Papillae yellow-brown with dark-blue tips to the tubercles. Radula with 70 teeth. L. 3 mm. (preserved). *D. africana* ELIOT 1904.
4. Colour reddish brown, gray or black, papillae red-brown with black or dark-gray tubercles. Radula with 72 teeth. Rhinophore sheaths with anterior margin expanded and prolonged. L. 7 mm.
D. obscura ELIOT 1906.
5. Colour brownish, papillae yellowish with spherical black tubercles. Radula with 70 teeth, median cusp much elongated. L. 10 mm.
D. racemosa RISBEC 1928.

B. Papillae in 4-5 pairs.

1. Papillae globose with distinct tubercles in 4 rows. Margin of rhinophore sheath even or slightly crenulate.
 - a. Colour yellowish white, velar margin and rhinophores gray, a black ring below the white apex of each tubercle. Radula? L. 9 mm. (in alc.) *D. annuligera* BERGH 1905.
 - b. Colour dirty yellow, black-spotted on back; velum and rhinophore sheath with white-spotted margin. Tubercles with a dark band below the white tip. L. 4 mm. (preserved).
D. nigromaculata ELIOT 1906 [*D. cinerea* var. *nigr.*]
 - c. Colour grayish or pale grayish yellow with black streaks. Velum with a few short papillae. Radula with 86-96 teeth. L. 14 mm.
D. columbiana O'DONOGHUE 1921.
2. Papillae elongate with produced, subcylindrical tops; tubercles indistinct in 2-3 rows, each tubercle with a brown subapical spot. Body cinereous with a brown band on back. L. 6 mm.
D. paulinae TRINCHESE 1881 ⁽²⁾.

⁽¹⁾ ELIOT (1910, p. 124) discriminates var. *splendida* TRINCHESE 1881 (whitish with distinct, not confluent, dark spots), var. *nigra* ELIOT 1910 (deep dark-gray; rhinophore-sheaths with jagged margin), and var. *papillifera* ELIOT 1910 (back and body sides with papillae in rows; rhinophore sheaths with 2-3 papillae).

⁽²⁾ PRUVOT-FOL (1931, p. 752) remarks that this form may be a young *D. coronata*, because its tubercles are still little distinct quite as in young specimens of *D. coronata*, though these have dark-dotted tips of tubercles.

- C. Papillae in 11 pairs, each with a distinct gill on inside; tubercles in 5-6 circlets. Colour dark olive green, tubercles paler, grayish yellow green, each with a black spot (in preserved specimens often hidden under the opaque epidermis). Radula with 140 teeth. L. 9 mm. (in alc.) *D. japonica* n. sp.
- II. Papillar tubercles with apical spots paler than general colour; no subapical rings. Papillae in at most 8 pairs, without distinct gills.
- A. Colour uniform, without spots. Rhinophore sheaths with lobated or crenelated margin.
1. Rhinophore sheath with an external longitudinal crest. Colour grayish brown. Papillae 7 pairs, brown with yellow tips and grayish tubercles in 3-4 rows. Radula with 96 teeth. L. 12 mm. (living), 5.5 mm. (preserved). *D. indica* BERGH 1888.
 2. Rhinophore sheaths smooth, without crest, and short and wide; club annulated. Colour yellowish brown. Papillae in 6 pairs, with yellowish white tubercles, in 3 rings. L. 6 mm. *D. crassicornis* M. SARS 1870.
 3. Rhinophore sheaths smooth, without crest, elongated; club smooth.
 - a. Papillae in 8 pairs. Body translucent white, tubercles in 6-7 circlets, white-topped. L. 13 mm. ... *D. formosa* VERRILL 1875 [*Doris*].
 - b. Papillae in 6-7 pairs, tubercles in 4 circlets. Colour uniform pale yellowish white or yellowish brown. Radula with 83 teeth. L. 11 mm. *D. antarctica* ELIOT 1907.
- B. Colour pale with darker spots. Rhinophore sheaths with even margin. Papillae in 6 pairs, tubercles in 5-6 circlets.
1. Colour cinereous with irregular brown spots, velar and rhinophore margins white-spotted, tubercles brown with white ends. L. 8 mm. *D. cinerea* TRINCHESE 1881.
 2. Colour yellowish, brown-spotted; papillae pale reddish, white-spotted, with tubercles. L. 8 mm. *D. rosea* TRINCHESE 1881.
- III. Papillar tubercles (elongate and pointed) without apical spots, of the same uniform colour as the body.
- A. Papillae in 8-9 pairs, each with 8-9 circlets of tubercles. Colour brownish yellow, tubercular yellow spots on back and white spots on sides. Radula with above 100 teeth. L. up to 25 mm. *D. fragilis* FORBES 1838 [*Melibaea*].
- B. Papillae in 4-6 pairs, with at most 7 circles of tubercles.
1. A distinct gill on the inside of the large papillae.
 - a. 5-6 pairs of papillae with 5-6 circlets of tubercles; top of papillae of the same size as the tubercles (or little larger). Colour dirty greenish gray. Radula with 85 teeth. L. 5.25 mm. (preserved). *D. kabretiana* O'DONOGHUE 1929 [*Bornellopsis*].
 - b. 4 pairs of papillae with 6-7 circlets of tubercles and the top elongated at least to twice the length of the tubercles. Colour yellowish, along each body-side a blackish blue band and a thinner similar one beneath, corners of velum with a spot of similar colour. Radula with 145 teeth, L. 10 mm. (preserved) *D. apiculata* n. n. (= *Doto* sp. BERGH 1904).

2. No distinct gill on the papillae; each papilla with 4 circlets of tubercles.
 - a. Papillae in 6 pairs. Rhinophore sheaths with lobated margin. Colour white or yellowish, spotted with pink or purplish. L. 6 mm. (preserved) *D. cuspidata* ALDER & HANCOCK 1862.
 - b. Papillae in 5 pairs. Rhinophore sheaths with lobated margin. Colour yellow with a net-work of black or violaceous lines on back. L. 8 mm. *D. aurea* TRINCHESE 1881.
 - c. Papillae in 5 pairs. Rhinophore sheaths with entire margin. Colour dark olive, each papilla with a rosy ring round its base; each tubercle with 2 white longitudinal lines. L. 10 mm. *D. cornaliae* TRINCHESE 1881.

SPURIOUS SPECIES

For the names of *Doto* given by HESSE 1872 I refer to PRUVOT-FOL 1931. *Melibaea arbuscula* AGASSIZ is a nomen nudum; GOULD & BINNEY (1871) list it as a synonym of *Doto coronata*. *Melibaea minuta* FORBES 1843, from the Aegean, has not been refound nor recognized.

DESCRIPTION OF NEW SPECIES

Doto japonica n. sp.

(Plate, figs. 11-16.)

Back with 11 pairs of papillae decreasing in size backwards. Tubercles on the largest papillae in 5 or 6 rows with 5 or 6 in each row, often forming longitudinal straight or feebly spiral series. Tubercles with truncated (or rounded, not pointed) ends and of the same size as the top of the papilla. Rhinophore sheaths with even margin wider in front but not lobated. In front of each rhinophore one distinct small papilla. Genital aperture below 1st papilla; anus projecting as a tube between 1st and 2nd papilla; nephroproct close inside the anal tube.

Body sides quite smooth, without any papillae.

Colour dark olive-green, almost black over the whole body; foot margin in one specimen whitish; one single specimen with fine spots of dark red. Rhinophore sheaths uniformly pale yellowish green, clubs black with white tip (in the dotted specimen wholly white). Papillae paler than body, grayish yellow-green, with pale grayish tubercles each having a black spot on top.

The largest papillae with the basal tubercles of the inside transformed and fused together to a gill attaining a height of half the papilla; the smaller papillae with similar, smaller, gills. No liver diverticula in the gill processes.

Radula uniseriate, with about 140 teeth of the usual shape with a small median cusp and 4 lateral denticles (Fig. 47).

Locality : Japan, Sagami, Moroiso, 2-10 m, stones, algae (T. GISLÉN, 29/6 1930) 4 specimens, max. L. (contracted) 9 mm, br. 2.5 mm, h. 4 mm, h. of largest papilla 5.5 mm.

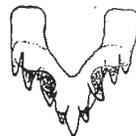


FIG. 47.
Doto japonica.
Radula tooth. ×750.

Among 4 small young specimens of *Doto* taken at the same locality in the surface on piles, one specimen belonged to *D. japonica* and showed a black body with black rhizophore sheaths and the tubercles on the elongated papillae black, the others had uniformly grayish rhizophore sheaths and papillae, the latter of a shorter shape; their body was pale with dots and vermiculate paintings of black. Either they represent a distinct species (too inadult to be described) or a pale variety; the tubercles were often indistinct and the papilla top elongated as in *D. paulinae*.

***Doto apiculata* n. n.**

Through a kind loan from the Zool. Museum at Copenhagen, mediated by Dr. R. SPÄRCK, I could reexamine BERGH's *Doto* sp. described in 1904 and give here some particulars in addition to this description. There are no spots on the papillae at all, and the tubercles are pointed; the tip of each papilla is at least twice as elongated as the tubercles (Fig. 45c). On the inside of the papillae a gill similar to that of *D. kabretiana*, *japonica* and *pinnatifida* is developed from modified tubercles. That the colour of the body appears as a band on each side may be occasional with respect to the various colour of *D. japonica*. The velum and foot were margined with pale yellow. The rhizophore sheaths bore a large lobe on the anterior inner side. Genital opening, anus and nephroproct as in *D. japonica*. The somewhat dried specimen did not allow more details to be observed, but those known, especially the elongated tips of the papillae, justify the establishment of a distinct species for this form, which was taken in 24° 43' N 119° 31' E.

Fam. PHYLLIROIDAE

Though much has been written on the morphology of this family, there are still some points to elucidate, above all the systematical relation of these animals and the delimitation of the species of respective genera.

A means of judging the relationship is given us also in this case by the liver. This consists of 3-4 tubiform coeca without ramifications. FISCHER (1892, p. 316) remarks that there are three liver openings in the stomach⁽¹⁾ and says: « Ce cas se ramène donc à celui des Aeolidiens », a fact that cannot be denied; moreover, the liver as a whole recalls much that of a young eolid according to the interesting figures and facts given by FISCHER (*l. c.*, pl. XV, figs. 65-67; cf. VESSICHELLI, 1906, p 127). This does not mean that *Phylliroe* has any immediate relationship to the eolids, which all have a much ramified liver, but that both groups have a common origin; and *Phylliroe* stands closer

⁽¹⁾ I never observed the two upper diverticula debouch by means of a common duct, as d'ORBIGNY (1835) maintains to be characteristic of his *Phylliroe rosea*, a statement no doubt due to same misinterpretation.

to the root than do the eolids, in having unbranched liver coeca (¹). A somewhat similar main liver organization is realized in the Scyllaeidae, and, besides, the spherical gonads of *Phylliroe* offer great similarity to those of Scyllaeidae. The liver of *Phylliroe* can easily be derived from that of *Scyllaea*, if the globular masses here are thought extended in length. The dorsal liver tube of *Phylliroe* is homologous of the right liver, as is proved by its position in front of the heart and its entrance to the right distinctly remote from the remaining liver ducts. The ventral liver coeca are then homologous with the left anterior liver, and the posterior coecum, of course, of the posterior liver; these two open close to each other. The fact that the right and left liver portions have attained a position on the dorsal and ventral side respectively may be explained from the supposition that still a slight amount of torsion remains in the situs viscerum; for a similar case I refer to the genus *Telarma* in which the liver portions show an incomplete detorsion, too (cf. ODHNER, 1934, fig. 42), I therefore think that the Phylliroidae may be derived from a stem common to the Scyllaeidae — the latter have developed their back margin, progressively, into lobes, whereas the former have reduced it completely except for the rhinophorial sheaths, into which the smooth rhinophores can be retracted or rather contracted to their whole extent. The next affinity as to external habitus is exhibited by *Notobryon* with its semitransparent body; its nephridium, i.a., has a renal chamber which may be said to intermediate, to some extent, between the highly branched rein of *Scyllaea* and the tube-like simple one of *Phylliroe* and *Cephalopyge*.

No nephridial apparatus is said to be extant in the genus *Acura* ADAMS 1850, the single species of which, *A. pelagica*, was described at some length by BERGH (1873). Such an organization, however, seems to be absurd, and that species, which in other respects agrees with *Ph. atlantica*, is certainly based on mutilated specimens of the latter one. The genus *Acura* thus is to be withdrawn as a synonym of *Phylliroe*.

There is no divergence of opinion about the distinctness of the genus *Cephalopyge*, which shows the more primitive characteristic of a distinct though small foot. This may in certain cases be retracted (cf. ODHNER 1931, p. 46), which causes the appearance as if it is absent or little developed (as is said about *C. orientalis* and *Ctilopsis*). The last-mentioned genus shares the most important characters of *Cephalopyge* (dorsal anus, flocculent gonads, 3 liver coeca) and has, besides, large and thick rhinophores which are united at base. The latter character has, however, no generic range; on the contrary, it causes a suspicion of some aberration, the more so, as nothing is said about any rhinophorial sheaths. For these reasons I think it better not to maintain *Ctilopsis* but consider it a synonym of *Cephalopyge*, which has been much enriched in this respect (cf. ODHNER 1931).

(¹) VESSICHELLI (1906) has observed a few cases where the coeca bore a few small diverticula, and one case where they were totally atrofied.

Whereas the delimitation of the genera of Phylliroidae offers no difficulties, the distinction between the species of *Phylliroe* has been subject of much discussion. A least two species must be considered as distinct, *Ph. bucephala* and *atlantica*, but their synonymies are not quite settled. *Ph. bucephala* PÉRON and LESUEUR is, however, different from *Ph. bucephala* SOULEYET 1852, which, as already BERGH (1873) states, is *Ph. atlantica* BERGH; and VESSICHELLI (1906) shows that the two species have been confounded even by LANG (1900), because his figure of *Ph. bucephala* (fig. 21, p. 14) is the form of SOULEYET, thus *Ph. atlantica* BERGH; and from this book the mistake has been repeated in later manuals (THIELE 1931, fig. 539; HOFFMANN 1933, fig. 73 B). A very good figure of *Phylliroe bucephala* PÉRON & LESUEUR is given by VESSICHELLI (1906, pl. 5, fig. 1).

In 1931 I made an attempt to separate *Ph. rubra* QUOY & GAIMARD as a form of *atlantica* on the assumption that the concentration of the gonads, which had been displaced towards the stomach, was a distinguishing mark; in the typical *atlantica* they lie namely more towards behind. A closer investigation of specimens with a concentration of this kind, however, shows that here the gonads have much contorted ducts, just as if they had been forced forwards, and I think this has been the case, indeed, as a result of the preservation. This concentration of the gonads, thus, is artificial, and the forma *rubra*, as I have tried to explain it, seems to have no justification in the zoological system.

Afterwards (1934) M^{mo} PRUVOT-FOL examined the type of *Ph. rubra* of QUOY and GAIMARD but could not find any distinguishing characters, and I therefore think that this form may be due to some occasional aberration — PRUVOT-FOL thinks that the « plaque rouge », which is spoken of in the diagnosis and which has « rien de commun avec les gonades », may be a parasitic formation. Thus also *Ph. rubra* should be considered as a synonym of *Ph. atlantica*.

The last-mentioned species, according to VESSICHELLI (1906), is a synonym of *Ph. amboinensis* QUOY & GAIMARD, a supposition that I could corroborate, when PRUVOT-FOL sent me a typical specimen of QUOY & GAIMARD's lot which proved to share the characters of *Ph. atlantica* (cf. PRUVOT-FOL 1934, p. 82). In the figure (pl. 28, fig. 10) of QUOY & GAIMARD there are three gonads, two lying behind, the foremost beneath the anus. In my work of 1931, the characteristic of *Ph. atlantica* was said to be « 3 Gonade, die hinterste dicht links und unter dem Anus, die beiden anderen weiter unten und vorn liegend », each of the gonads may, however, be divided into two. *Ph. bucephala*, on the contrary, has two gonads, both lying behind and beneath the anus. The more anterior position of the gonads in *Ph. atlantica* may, however, as in the case of the above-mentioned forma *rubra*, be due to secondary replacement caused by the preservation. *Ph. amboinensis* is therefore no doubt identical with *Ph. atlantica*. On the other hand, a still earlier name is *Eurydice lichtensteini* ESCHSCHOLTZ 1825. The figure (pl. 5, fig. 6) accompanying the description is very good for the time and shows 3 gonads, the hindmost just behind and below the anus, the 2 remaining ones farther in front, and the liver coeca, too, are like those of

Ph. atlantica; consequently we have to substitute the name *Ph. lichtensteini* for *atlantica*.

Of the two genera of Phylliroidae, *Cephalopyge* is certainly the more primitive one because of the permanency of the distinct foot and the dorsal site of the anus which is to be well distinguished from the secondary dorsal position in many nudibranchs as a result of the replacement of the anus from a lateral site into the interhepatic space or still farther back. The male apparatus with its simpler penis is also a sign of primitivity in *Cephalopyge*, and the liver coeca have not attained so complete a stage of symmetry as in *Phylliroe*. The distinguishing characters may be tabulated thus :

- I. Body elongate lanceolate, with distinct foot. Anus dorsal, close behind rhinophores. Gonads flocculent, in stripes or clusters of folliculi. Liver coeca usually 3 (a single dorsal one, a single ventral, as a rule, and a posterior). Head with disc. Jaws without processus masticatorius. Radula often obliterated. Penis conical, unarmed. *Cephalopyge* HAEL 1905 (*Ctilopsis* ANDRÉ 1906, *Dactylopus* BONNEVIE 1921 non Gill 1859, nec CLAUS 1862, *Nectophylliroe* HOFFMANN 1922, *Boopsis* PIERANTONI 1923, *Bonneviia* PRUVOT-FOL 1931).
- II. Body elliptical, without foot. Anus lateral, dextral. Gonads in spherical globuli. Liver coeca 4 (2 superior and 2 inferior ones). Head without disc. Jaws with processus masticatorius. Radula well developed, with a few lateral teeth denticulated in the inner edge, and a median tooth denticulated on both sides. Penis cylindrical, tube-like; its glans armed with conical papillae and with a large sub-apical lobe *Phylliroe* PÉRON & LESUEUR 1810 (*Eurydice* ESCHSCHOLTZ 1825, *Philyrine* MENKE 1844; *Acura* H. & A. ADAMS 1850).

SYNOPSIS OF SPECIES

CEPHALOPYGE

- I. No ventral anterior liver coecum. Gonad folliculi tubular.
 - A. Dorsal anterior liver coecum well developed.
 - 1. Body elongate elliptic. Gonads 5 : 2 posterior between the liver coeca, 1 median just behind stomach, 2 ventral. Colour red, hyaline. L. 7-10 mm., height 2 mm. Radula vestigial *C. trematoides* CHUN 1888 [*Phylliroe*].
 - 2. Body elongate-spatulate. Gonads 2, string-like, short, between the liver coeca, and 1 ventral, longer. Colour hyaline white. Radula with 12-14 series. L. 15-18 mm., h. 2 mm. *C. mediterranea* PIERANTONI 1923 [*Boopsis*].
 - B. Dorsal anterior liver coecum very short, vestigial. Body elongate elliptic.
 - 1. Gonads 4 : 2 between the liver coeca, 2 ventral, somewhat shorter. Colourless, hyaline. No radula. Rhinophore elongate. L. 7-8 mm., h. 1.3 mm. *C. orientalis* BABA 1933.
 - 2. Gonads 3, 1 between posterior liver coeca and 2 ventral (together larger than the upper). Radula well developed (1.1.1). Rhinophores short and thick; united at base. Colour? L. 10 mm., h. 2.7 mm. *C. picteti* ANDRÉ 1906 [*Ctilopsis*].

- II. A ventral anterior coecum (short). Dorsal coecum? Gonad folliculi spherical, gonads 2, the ventral longer. Body elongate spatulate? Colour (in alc.) pale grayish, little translucent. L. 15 mm., h. about 6 mm. No radula.
C. michaelsarsi BONNEVIE 1921 [*Dactylopus*].

SYNOPSIS OF SPECIES

PHYLLIROE

- I. Gonads 2, behind and beneath the anus, yellowish-white on their under side. Liver coeca curved, constricted in their middle. Radula 15-22 × 1-6.1.1-6. Colour dirty hyaline white with reddish head. L. up to 26 mm.
Ph. bucephala PÉRON & LESUEUR 1810 (= ? *Ph. punctulatum* QUOY & GAIMARD 1833; = *Ph. sanzoi* SPARTA 1925; non *Ph. bucephala* SOULEYET 1852).
- II. Gonads 3 (rarely 2), simple or bipartited, with reddish-brown under side. Liver coeca straight, of about uniform breadth throughout. Radula (14—) 22-29 × 1-6.1.1-6. Colour pale or dark grayish red all over, with brown, blackish dots; back and ventral margin spotted with white or yellow. L. up to 30 mm.
Ph. lichtensteini ESCHSCHOLTZ 1825 [*Eurydice*] (= *Ph. amboinensis* QUOY & GAIMARD 1833, = ? *Ph. rubra* QUOY & GAIMARD 1833, = *Ph. rosea* d'ORBIGNY 1836, = *Ph. bucephala* SOULEYET 1852, non PÉRON & LESUEUR 1810, = *Ph. atlantica* BERGH 1871, = *Acura pelagica* ADAMS 1850, BERGH 1871).

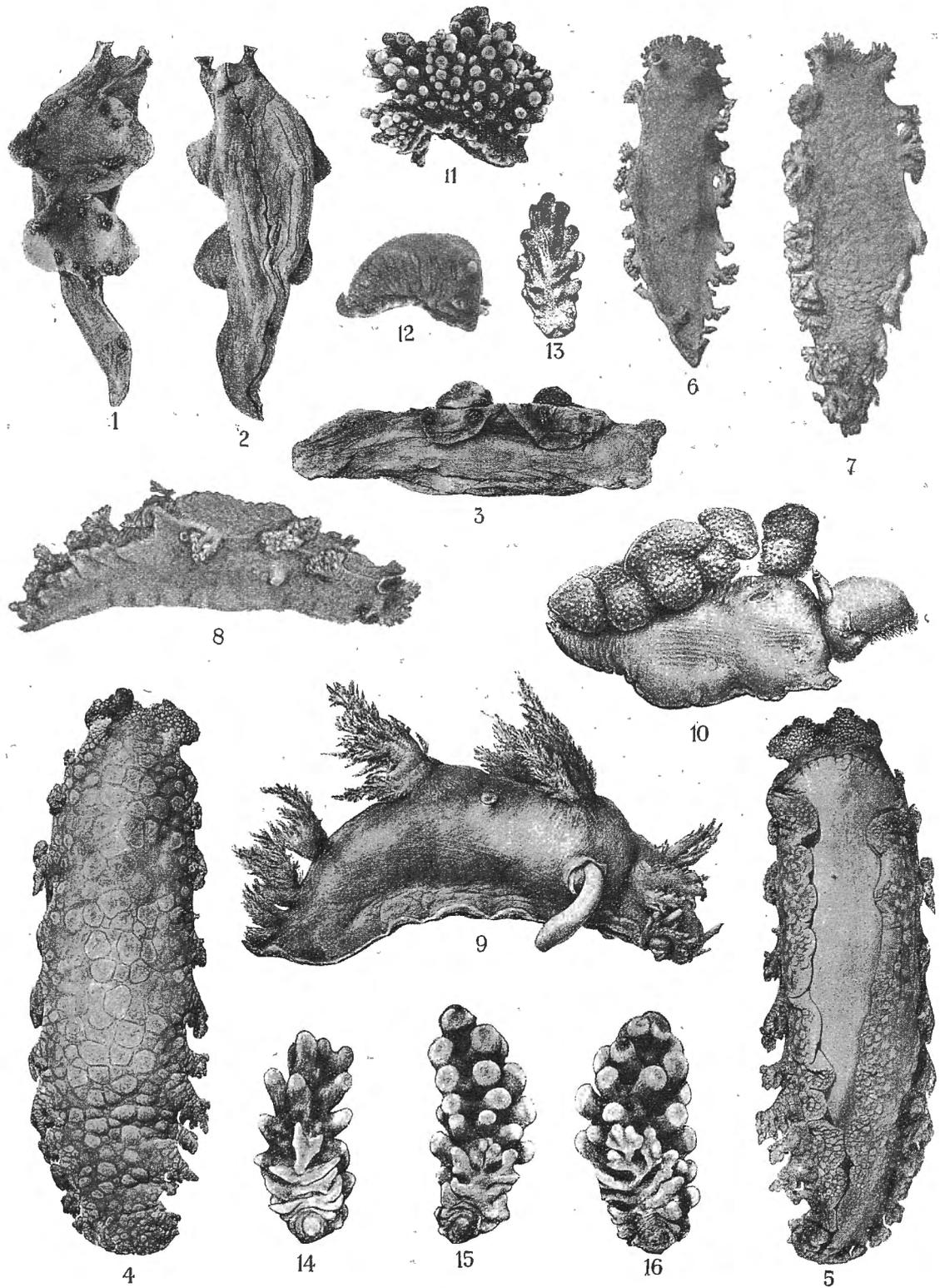
Ph. lanceolata BERGH 1873, described from a sketch by SEMPER, is spurious and may be a mutilated or aberrant *Ph. lichtensteini*.

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FIGS. 1-3. — *Notobryon wardi* n. gen. n. sp. Almost nat. size.

FIGS. 4, 5. — *Marionia pustulosa* n. sp. $\frac{3}{4}$ of nat. size.

FIG. 6. — *Marionia granularis* n. sp. $\times 1 \frac{1}{2}$.

FIGS. 7, 8. — *Marioniopsis rubra* RÜPPELL & LEUCKART. Almost nat. size.

FIG. 9. — *Dendronotus iris* COOPER. $\frac{3}{4}$ of nat. size.

FIG. 10. — *Melibe pilosa* PEASE. $\frac{3}{4}$ of nat. size.

FIGS. 11, 12. — *Doto japonica* n. sp. $\times 3$

FIGS. 13-16. — *Doto japonica*. n. sp. Dorsal papillae from inside. $\times 7$.