

Sub-order 2.—Ceratona.

Characters.—The typical Molluscan ctenidium is not developed; upon the dorsal area is developed a more or less numerous series of cylindrical or branched processes (the cerata) into each of which the intestine usually sends a process; anus dorsal, median, or right-sided.

Family 7.—Tritoniadae. Genera: Tritonia, Cuvier; Scyllasa, L.; Tethys, L. (fig. 62, B); Dendronotus, A. and H.; Doto, Oken.

Family 8.—Eolidae. Genera: Eolis, Cuvier (fig. 62, A); Glaucus, Forster; Fiona, A. and H. (fig. 67); Embletonia, A. and H.; Proctonotus, A. and H.; Antiopa, A. and H.; Hermesa, Loven; Alderia, Allman.

Sub-order 3.—Haplomorpha.

Characters.—No ctenidia, cerata, mantle-skirt, or other processes of the body-wall; degenerate forms of small size.

Family 9.—Phyllirhoidea. Genera: Phyllirhoë, Peron and Lesueur (fig. 58); Acura, Adams.

Family 10.—Elysiadae. Genera: Elysia, Risso (fig. 62, D, E); Acteonina, Quatref.; Centia, A. and H.; Limapontia, Johnston; Rhodops, Köll.

Further Remarks on the Opisthobranchia.—The Opisthobranchia present the same wide range of superficial appearance as do the Azygobranchiate Streptoneura, forms

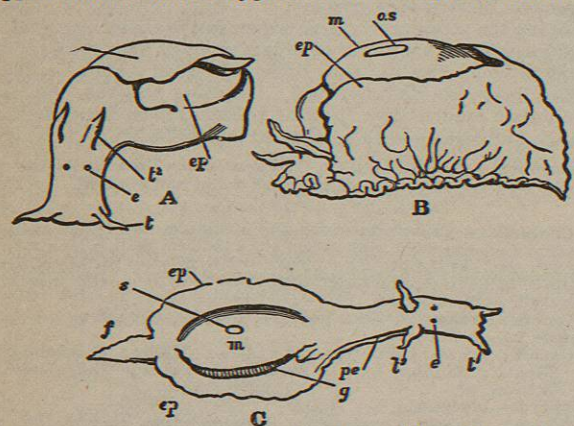


FIG. 56.—Three views of Aplysia sp., in various conditions of expansion and retraction. A, anterior cephalic tentacles; B, posterior cephalic tentacles; C, eyes, f, metapodium; ep, epipodium; g, gill-plume (ctenidium); m, mantle-skirt reflected over the thin oval shell; os, s, orifice formed by the unclosed border of the reflected mantle-skirt, allowing the shell to show; pe, the spermatheca. (After Cuvier.)

carrying well-developed spiral shells and large mantle-skirts being included in the group, together with flattened or cylindrical slug-like forms. But in respect of the substitution of other parts for the gill which the more degenerate Opisthobranchia exhibit, this order stands alone. Some Opisthobranchia are striking examples of degeneration (some Haplomorpha), having none of those regions or processes of the body development which distinguish the archaic Mollusca from such flat-worms as the Dendrocoel Planarians. Indeed, were it not for their retention of the characteristic odontophore we should have little or no indication that such forms as Phyllirhoë and

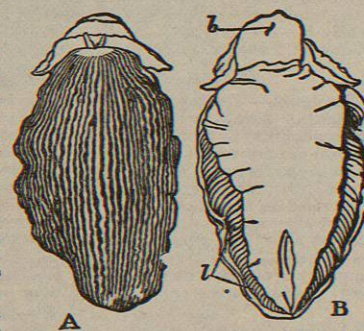


FIG. 57.—Dorsal and ventral view of Pleurophyllidia lineata (Otto), one of the Phyllidobranchiate Palliate Opisthobranchia. B, the mouth; l, the lamelliform sub-pallial gills, which (as in Patella) replace the typical Molluscan ctenidium. (After Kieferstein.)

Limapontia really belong to the Mollusca at all. The interesting little Rhodops Veranyi, which has no odontophore, has been associated by systematists both with these simplified Opisthobranchs and with Rhabdocel Planarians (29).

In many respects the Sea-Hare (Aplysia) of which several species are known (some occurring on the English coast), serves as a convenient example of the fullest development of the organization characteristic of Opisthobranchia. The woodcut (fig. 56) gives a faithful representation of the great mobility of the various parts of the body.

The head is well marked and joined to the body by a somewhat constricted neck. It carries two pairs of cephalic tentacles and a pair of sessile eyes. The visceral hump is low and not drawn out into a spire. The foot is long, carrying the oblong visceral mass upon it, and projecting (as metapodium) a little beyond it (f). Laterally the foot gives rise to a pair of mobile fleshy lobes, the epipodia (ep), which can be thrown up so as to cover in the dorsal

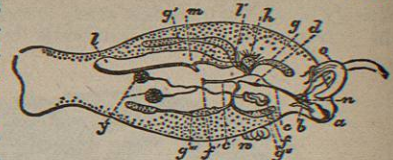


FIG. 58.—Phyllirhoë ducephala, twice the natural size, a transparent pisciform pelagic Opisthobranch. The internal organs are shown as seen by transmitted light. a, mouth; b, radular sac; c, oesophagus; d, stomach; e, intestine; f, anus; g, g, g, g, the four lobes of the liver; h, the heart (atrium and ventricle); i, the renal sac (nephridium); j, the ciliated communication of the renal sac with the pericardium; m, the external opening of the renal sac; n, the cerebral ganglion; o, the cephalic tentacles; p, the genital pore; q, the ova-testes; r, the parasitic hydromedusa Mesocera, usually found attached in this position by the aboral pole of its umbrella. (After Kieferstein.)

The head is well marked and joined to the body by a somewhat constricted neck. It carries two pairs of cephalic tentacles and a pair of sessile eyes. The visceral hump is low and not drawn out into a spire. The foot is long, carrying the oblong visceral mass upon it, and projecting (as metapodium) a little beyond it (f). Laterally the foot gives rise to a pair of mobile fleshy lobes, the epipodia (ep), which can be thrown up so as to cover in the dorsal

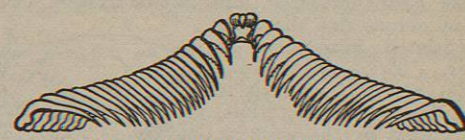


FIG. 59.—Acura bullata. A single row of teeth of the radula. (Formula, x.l.x.) surface of the animal. Such epipodia are common, though by no means universal, among Opisthobranchia. The torsion of the visceral hump is not carried out very fully,

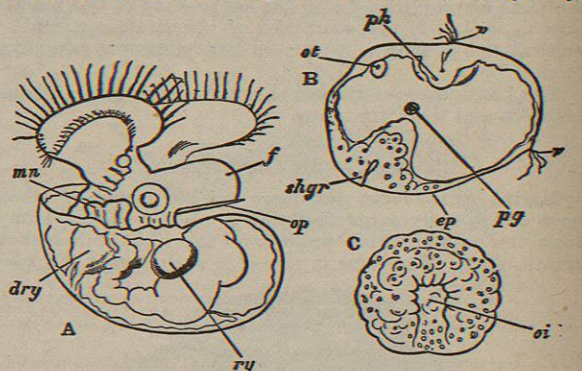


FIG. 60.—A, Veliger-larva of an Opisthobranch (Pelecypoda). f, foot; ep, operculum; mn, anal papilla; ry, dry, two portions of unabsorbed nutritive yolk on either side the intestine. The right otocyst is seen at the root of the foot. B, Trochosphere of an Opisthobranch (Pelecypoda) showing: shgr, the shell-gland or primitive shell-sac; v, the cilia of the velum; pb, the commencing stomodaeum or oral invagination; ot, the left otocyst; pg, red-coloured pigment spot. C, Diblastula of an Opisthobranch (Pelecypoda) with elongated blastopore ot. (All from Lankester.)

the consequence being that the anus has a posterior position a little to the right of the median line above the metapodium, whilst the branchial chamber formed by the overhanging mantle-skirt faces the right side of the body instead of lying well to the front as in Streptoneura and as in Pulmonate Euthyneura. The gill-plume which in Aplysia is the typical Molluscan ctenidium is seen in fig.

63 projecting from the branchial sub-pallial space. The relation of the delicate shell to the mantle is peculiar, since it occupies an oval area upon the visceral hump, the extent of which is indicated in fig. 56, C, but may be better understood by a glance at the figures of the allied genus Umbrella (figs. 54, 55), in which the margin of the mantle-skirt coincides, just as it does in the Limpet, with the margin of the shell. But in Aplysia the mantle is reflected over the edge of the shell, and grows over its upper surface so as to completely enclose it, excepting at the small central area s where the naked shell is exposed. This enclosure of the shell is a permanent development of the arrangement seen in many Streptoneura (e.g., Pyrula, Ovulum, see figs. 38 and 41), where the border of the mantle can be, and usually is, drawn over the shell, though it is withdrawn (as it cannot be in Aplysia) when they are irritated. From the fact that Aplysia commences its life as a free-swimming Veliger with a nautiloid shell not enclosed in any way by the border of the mantle, it is clear that the enclosure of the shell in the adult is a secondary process. Accordingly, the shell of Aplysia must not be confounded with a primitive shell in its shell-sac, such as we find realized in the shells of Chiton and in the plugs which form in the remarkable transitory "shell-sac" or "shell-gland" of Molluscan embryos



FIG. 61.—Polyera cristata, one of the Pygobranchiate Opisthobranchs (dorsal view). a, anus; b, the ctenidium peculiarly modified so as to encircle the anus; c, cephalic tentacles. External to the branchial ctenidium are seen ten club-like processes of the dorsal wall, these are the "cerata" which are characteristically developed in another sub-order of Opisthobranchs, the Ceratona (see fig. 62, A). (From Gegenbaur, after Alder and Hancock.)

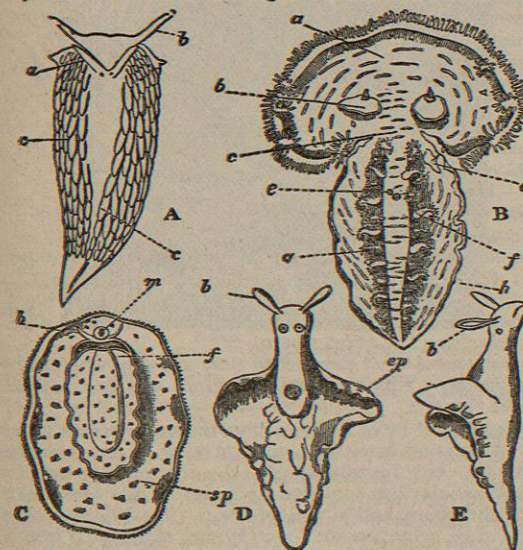


FIG. 62.—A, Eolis papillosa (Lin.), dorsal view. a, b, posterior and anterior cephalic tentacles; c, the dorsal "cerata" (hence Ceratobranchia). B, Tethys leporina, dorsal view. a, the cephalic hood; b, cephalic tentacles; c, neck; d, genital pore; e, anus; f, large cerata; g, smaller cerata; h, margin of the foot. C, Doris (Achinocyclus) tuberculatus (Cuv.), seen from the pedal surface. m, mouth; b, margin of the head; f, sole of the foot; ep, the mantle-like epipodium. D, E. Dorsal and lateral view of Elysia (Actaeon) viridis. ep, epipodial out-growths. (After Kieferstein.)

(see figs. 7, 68, and 72\*\*\*). Aplysia, like other Mollusca,

develops a primitive shell-sac in its trochosphere stage of development (fig. 68), which disappears and is succeeded by a nautiloid shell (fig. 60). This forms the nucleus of the adult shell, and, as the animal grows, becomes enclosed by a reflexion of the mantle-skirt. In reference to the possible comparison of the enclosed shell of Aplysia and its allies with those of some Slugs and of Cuttle-fishes, the reader is referred to the paragraphs dealing especially with those Molluscs. When the shell of an Aplysia enclosed in its mantle is pushed well to the left, the sub-pallial space is fully exposed as in fig. 63, and the various apertures of the body are seen. Posteriorly we have the anus, in front of this the lobate gill-plume, between the two (hence corresponding in position to that of the Azygobranchia) we have the aperture of the renal organ. In front, near the anterior attachment of the gill-plume, is the osphradium (olfactory organ) discovered by Spengel, yellowish in colour, in the typical position, and overlying an olfactory ganglion with typical nerve-connexion (see fig. 20). To the right of Spengel's osphradium is the opening of a peculiar gland which has, when dissected out, the form of a bunch of grapes; its secretion is said to be poisonous. On the under side of the free edge of the mantle are situated the numerous small cutaneous glands which, in the large Aplysia camelus (not in other species), form the purple secretion which was known to the ancients. In front of the osphradium is the single genital pore, the aperture of the common or hermaphrodite duct. From this point there stretches forward to the right side of the head a groove—the spermatheca—down which the spermatheca fluid passes. In other Euthyneura this groove may close up and form a canal. At its termination by the side of the head is the muscular introverted penis. In the hinder part of the foot (not shown in any of the diagrams) is the opening of a large mucous-forming gland very often found in the Molluscan foot.

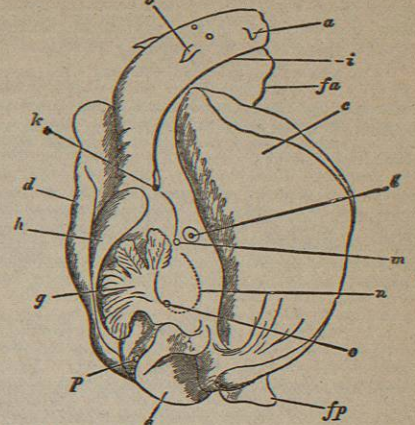


FIG. 63.—Aplysia leporina (camelus, Cuv.), with epipodia and mantle reflected away from the mid-line. a, anterior cephalic tentacle; b, posterior do.; between a and b, the eyes; c, right epipodium; d, left epipodium; e, hinder part of visceral hump; fp, posterior extremity of the foot; fa, anterior part of the foot underlying the head; g, the ctenidium (branchial plume); h, the mantle-skirt tightly spread over the horny shell and pushed with it towards the left side; i, the spermatheca; k, the common genital pore (male and female); l, orifice of the grape-shaped (supposed poisonous) gland; m, the osphradium (olfactory organ of Spengel); n, outline of part of the renal sac (nephridium) below the surface; o, external aperture of the nephridium; p, anus. (Original.)

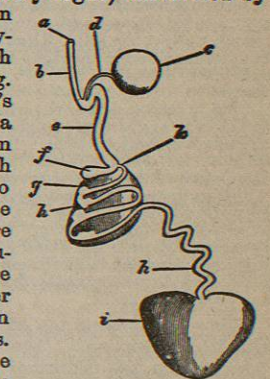


FIG. 64.—Gonad, and accessory glands and ducts of Aplysia. a, ova-testis; b, hermaphrodite duct; c, albuminiferous gland; d, vesicula seminalis; e, opening of the albuminiferous gland into the hermaphrodite duct; f, spermatheca; g, uterine duct; h, its duct; i, genital pore. (Original.)



With regard to internal organization we may commence with the disposition of the renal organ (nephridium), the external opening of which has already been noted. The position of this opening and other features of the renal organ have been determined recently by Mr. J. T. Cunningham, Fellow of University College, Oxford, who writes as follows from Naples, February 1883:—

"There is considerable uncertainty with respect to the names of the species of *Aplysia*. There are two forms which are very common in the Gulf of Naples, and which I have used in studying the anatomy of the renal organ in the genus. One is quite black in colour, and measures when outstretched eight or nine inches in length. The other is light brown and somewhat smaller, its length usually not exceeding seven inches. The first is flaccid and sluggish in its movements, and has not much power of contraction; its epipodial lobes are enormously developed and extend far forward along the body, it gives out when handled an abundance of purple liquid, which is derived from cutaneous glands situated on the under side of the free edge of the mantle. In the Zoological Station this form is known as *Ap. leporina*; but according to Blochmann it is identical with *A. Camelus* of Cuvier. The other species is *A. depilans*; it is firm to the touch, and contracts forcibly when irritated; the secretion of the mantle-glands is not abundant, and is milky white in appearance. The kidney has similar relations in both genera, and is identical with the organ spoken of by many authors as the triangular gland. Its superficial extent is seen when the folds covering the shell are cut away and the shell removed; the external surface forms a triangle with its base bordering the pericardium and its apex directed posteriorly and reaching to the left-hand posterior corner of the shell-chamber. The dorsal surface of the kidney extends to the left beyond the shell-chamber beneath the skin in the space between the shell-chamber and the left epipodium.

"When the animal is turned on its left-hand side and the mantle-chamber widely opened, the gill being turned over to the left, a part of the kidney is seen beneath the skin between the attachment of the gill and the right epipodium (fig. 63). On examination this is found to be the under surface of the posterior limb of the gland, the upper surface of which has just been described as lying beneath the shell. In the posterior third of this portion, close to that edge which is adjacent to the base of the gill, is the external opening (fig. 63, o).

"When the pericardium is cut open from above in an animal otherwise entire, the anterior face of the kidney is seen forming the posterior wall of the pericardial chamber; on the deep edge of this face, a little to the left of the attachment of the auricle to the floor of the pericardium, is seen a depression; this depression contains the opening from the pericardium into the kidney.

"To complete the account of the relations of the organ: the right anterior corner can be seen superficially in the wall of the mantle-chamber above the gill. Thus the base of the gill passes in a slanting direction across the right-hand side of the kidney, the posterior end being dorsal to the apex of the gland, and the anterior end ventral to the right-hand corner.

"As so great a part of the whole surface of the kidney lies adjacent to external surfaces of the body, the remaining part which faces the internal organs is small; it consists of the left part of the under surface; it is level with the floor of the pericardium, and lies over the globular mass formed by the liver and convoluted intestine.

"Here dissection does not give sufficient evidence concerning such communications as these of the kidney in *Aplysia*. I studied the external opening by taking a series of sections through the surrounding region of the gland; to demonstrate the internal aperture injected a solution of Berlin blue into the pericardium; it did not fill the whole kidney easily, but ran down into the part adjacent to the base of the gill.

Thus the renal organ of *Aplysia* is shown to conform to the Molluscan type. The heart lying within the adjacent pericardium has the usual form, a single auricle and ventricle. The vascular system is not extensive, the arteries soon ending in the well-marked spongy tissue which builds up the muscular foot, epipodia, and dorsal body-wall.

The alimentary canal commences with the usual buccal mass; the lips are cartilaginous, but not armed with horny jaws, though these are common in other Opisthobranchs; the lingual ribbon is multidentate, and a pair of salivary glands pour in their secretion. The cesophagus expands into a curious gizzard, which is armed internally with large horny processes, some broad and thick, others spinous, fitted to act as crushing instruments. From this we pass to a stomach and a coil of intestine embedded in the lobes of a voluminous liver; a caecum of large size is given off near

the commencement of the intestine. The liver opens by two ducts into the digestive tract.

The generative organs lie close to the coil of intestine and liver, a little to the left side. When dissected out they appear as represented in fig. 64. The essential reproductive

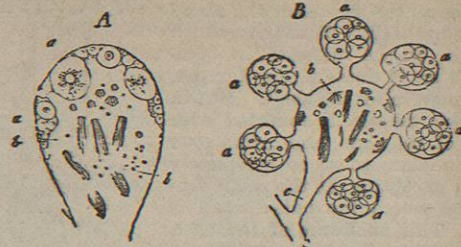


FIG. 65.—Pollicles of the hermaphrodite gonads of Euthyneurous Anisopleura. A, of *Helix*; B, of *Eolidia*. a, ova; b, developing spermatozooids; c, common efferent duct.

organ or gonad consists of both ovarian and testicular cells (see fig. 65). It is an ovo-testis. From it passes a common or hermaphrodite duct, which very soon becomes entwined in the spire of a gland—the albuminiferous gland. The latter opens into the common duct at the point x, and here also is a small diverticulum of the duct y. Passing on, we find not far from the genital pore a glandular spherical body (the spermatheca z) opening by means of a longish duct into the common duct, and then we reach the pore (fig. 63, k). Here the female apparatus terminates. But when the male secretion of the ovo-testis is active, the seminal fluid passes from the genital pore along the spermatheca (fig. 63, z) to the penis, and is by the aid of that eversible muscular organ introduced into the genital pore of a second *Aplysia*, whence it passes into the spermatheca, there to await the activity of the female element of the ovo-testis of this second *Aplysia*. After an interval of some days—possibly weeks—the ova of the second *Aplysia* commence to descend the hermaphrodite duct; they become enclosed in a viscid secretion at the point where the albuminiferous gland opens into the duct intertwined with it; and on reaching the point where the spermatheca debouches they are impregnated by the spermatozoa which escape now from the spermatheca and meet the ova.

The development of *Aplysia* from the egg presents many points of interest from the point of view of comparative embryology, but in relation to the morphology of the Opisthobranchia it is sufficient to point to the occurrence of a trochophore and a veliger stage (fig. 60), and of a shell-gland or primitive shell-sac (fig. 68, *shs*), which is succeeded by a nautiloid shell.

The nervous system of *Aplysia* will be found on comparison of fig. 20, which represents it, with our schematic Mollusc (fig. 1, D) to present but little modification. It is in fact a nervous system in which the great ganglion-pairs are well developed and distinct. The Euthyneurous visceral loop is long, and presents only one ganglion in *Aplysia camelus*, but two distinct ganglia joined to one another in



FIG. 66.—Enteric canal of *Eolidia papillosa*. ph, pharynx; m, mid-gut, with its hepatic appendages; h, hind gut; an, anus. (From Gegenbaur, after Alder and Hancock.)

*Aplysia hybrida* of the English coast), placed at its extreme limit, representing both the right and left visceral ganglia and the third or abdominal ganglion, which are so often separately present. The diagram (fig. 20) shows the nerve connecting this abdomino-visceral ganglion with the olfactory ganglion of Spengel. It is also seen to be connected with a more remote ganglion—the genital. Such special irregularities in the development of ganglia upon the visceral loop, and on one or more of the main nerves connected with it, are, as the figures of Molluscan nervous systems given in this article show, very frequent. Our figure of the nervous system of *Aplysia* does not give the small pair of buccal ganglia which are, as in all Glosso-phorous Molluscs, present upon the nerves passing from the cerebral region to the odontophore.

For a comparison of various Opisthobranchs, *Aplysia* will be found to present a convenient starting-point. It is one of the more typical Opisthobranchs, that is to say, it belongs to the section Palliata, but other members of the Palliata, namely, *Bulla* and *Tornatella* (figs. 52 and 53), are less abnormal than *Aplysia* in regard to their shells and the form of the visceral hump. They have naked spirally-twisted shells which may be concealed from view in the living animal by the expansion and reflexion of the epipodia,

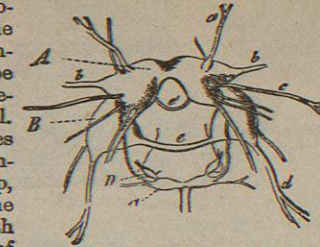


FIG. 67.—Central nervous system of *Piona* (one of the Ceratonotus Opisthobranchs), showing a tendency to fusion of the great ganglia. A, cerebral, pleural, and visceral ganglia united; B, pedal ganglion; C, buccal ganglion; D, cesophageal ganglion connected with the buccal; a, nerve to superior cephalic tentacles; b, nerve to inferior cephalic tentacles; c, nerve to generative organs; d, pedal nerve; e, pedal commissure; e', visceral loop or commissure (?). (From Gegenbaur, after Bergh.)



FIG. 68.—Young veliger larva of an Opisthobranch (Pleurobranchidium). m, mouth; c, ciliated band marking off the velum; ng, cerebral ganglion developing from epiblast, within the velar area; ot, otocyst also developing from epiblast; f, foot; i, intestine; ry, residual nutritive yolk; shs, primitive shell-sac or shell-gland. (From Lankester.)

but are not enclosed by the mantle, whilst *Tornatella* is remarkable amongst all Euthyneura for possessing an operculum like that of so many Streptoneura.

The great development of the epipodia seen in *Aplysia* is usual in Palliate Opisthobranchs; it occurs also in *Elysia* (fig. 62, D) among Non-Palliata; in *Doris* it seems probable that the mantle-like fold overhanging the foot is to be interpreted as epipodium, the mantle-skirt being altogether absent, as shown by the naked position of the gills and anus on the dorsal surface (figs. 61 and 62, C). The whole surface of the body becomes greatly modified in those Non-Palliata forms which have lost, not only the mantle-skirt and the shell, but also the ctenidium. Many of these (Ceratonota) have peculiar processes developed on the dorsal surface (fig. 62, A, B), or retain purely

negative characters (fig. 62, D). The chief modification of internal organization presented by these forms, as compared with *Aplysia*, is found in the condition of the alimentary canal. The liver is no longer a compact organ opening by a pair of ducts into the median digestive tract, but we find very numerous hepatic diverticula on a shortened axial tract (fig. 66). These diverticula extend usually one into each of the dorsal papillae or "cerata" when these are present. They are not merely digestive glands, but are sufficiently wide to act as receptacles of food, and in them the digestion of food proceeds just as in the axial portion of the canal. A precisely similar modification of the liver or great digestive gland is found in the Scorpions, where the axial portion of the digestive canal is short and straight, and the lateral ducts sufficiently wide to admit food into the ramifications of the gland there to be digested; whilst in the Spiders the gland is reduced to a series of simple caeca.

The typical character is retained by the heart, pericardium, and the communicating nephridium or renal organ in all Opisthobranchs. An interesting example of this is furnished by the fish-like transparent *Phyllirhoë* (fig. 58), in which it is possible most satisfactorily to study in the living animal, by means of the microscope, the course of the blood-stream, and also the reno-pericardial communication. With reference to the existence of pores placing the vascular system in open communication with the surrounding water, see the paragraph as to Mollusca generally. In a form closely allied to *Aplysia* (*Pleurobranchus*) such a pore leading outwards from the branchial vein has been precisely described by Lacaze Duthiers. No such pore has been detected in *Aplysia*. In many of the Non-Palliata Opisthobranchs the nervous system presents a concentration of the ganglia (fig. 67), contrasting greatly with what we have seen in *Aplysia*. Not only are the pleural ganglia fused to the cerebral, but also the visceral to these (see in further illustration the condition attained by the Pulmonate *Lirnaeus*, fig. 22), and the visceral loop is astonishingly short and insignificant (fig. 67, e'). That the parts are rightly thus identified is probable from Spengel's observation of the oesophagus and its nerve-supply in these forms; the nerve to that organ, which is placed somewhat anteriorly—on the dorsal surface—being given off from the hinder part (visceral) of the right compound ganglion—the fellow to that marked A in fig. 67. The Ceratonotus Opisthobranchs, amongst other specialities of structure, are stated to possess (in some cases at any rate) apertures at the apices of the "cerata" or dorsal papillae, which lead from the exterior into the hepatic caeca. This requires confirmation. Some amongst them (*Tergipes*, *Eolis*) are also remarkable for possessing peculiarly modified epidermic cells placed in sacs at the apices of these same papillae, which resemble the "thread-cells" of the Planarian Flatworms and of the Coelentera. The existence of these thread-cells is sufficiently remarkable, seeing that the Non-Palliata Opisthobranchs resemble in general form and habit the Planarian worms, many of which also possess thread-cells. But it is not conceivable that their presence is an indication of genetic affinity between the two groups, rather they are instances of homoplasy. The development of many Opisthobranchia has been examined—e.g., *Aplysia*, *Pleurobranchidium*, *Elysia*, *Polycera*, *Doris*, *Tergipes*. All pass through trochophore and veliger stages, and in all a nautiloid or boat-like shell is developed, preceded by a well-marked "shell-gland" (see figs. 60 and 68). The transition from the free-swimming veliger larva with its nautiloid shell (fig. 60) to the adult form has not been properly observed, and many interesting points as to the true nature of folds (whether epipodia or mantle or velum) have yet to be cleared up by a knowledge of such development in forms like *Tethys*, *Doris*, *Phyllidia*, &c.



As in other Molluscan groups, we find even in closely-allied genera (for instance, in *Aplysia* and *Pleurobranchidium*, and other genera observed by Lankester) the greatest differences as to the amount of food-material by which the egg-shell is encumbered. Some form their *Diblastula* by emboly (fig. 7), others by epiboly (fig. 5); and in the later history of the further development of the enclosed cells (arch-enteron) very marked variations occur in closely-allied forms, due to the influence of a greater or less abundance of food-material mixed with the protoplasm of the egg.

#### Order 2 (of the Euthyneura).—Pulmonata.

**Characters.**—Euthyneurous Anisopleurous Gastropoda, probably derived from ancestral forms similar to the Palliate Opisthobranchia by adaptation to a terrestrial life. The ctenidium is atrophied, and the edge of the mantle-skirt is fused to the dorsal integument by concrescence, except at one point which forms the aperture of the mantle-chamber, thus converted into a nearly closed sac. Air is admitted to this sac for respiratory and hydrostatic purposes, and it thus becomes a lung. An operculum is never present; a contrast being thus afforded with the operculate Pulmonate Streptoneura (*Cyclostoma*, &c.), which differ in other essential features of structure from the Pulmonata. The Pulmonata are, like the other Euthyneura, hermaphrodite, with elaborately-developed copulatory organs and accessory glands. Like other Euthyneura, they have very numerous small denticles on the lingual ribbon. The ancestral Pulmonata appear to have retained both the right and the left osphradia (Spengel's olfactory organs), since in some (*Planorbis*, *Auricularia*) we find the single osphradium to be that of the original left side, whilst in others (*Limnæus*) it is that of the original right side.

In some Pulmonata (Snails) the foot is extended at right angles to the visceral hump, which rises from it in the form of a coil as in Streptoneura; in others the visceral hump is not elevated, but is extended with the foot, and the shell is small or absent (Slugs).

The Pulmonata are divided into two sub-orders according to the position of the cephalic eyes.

##### Sub-order 1.—Basommatophora.

**Characters.**—Eyes placed medially of the cephalic tentacles at their base; the embryonic velar area retained in adult life as a pair of cephalic lobes (fig. 70, v); male and female generative apertures separate, placed (as is typical in Anisopleura) on the right side of the neck; visceral hump well developed, with a well-developed shell; aquatic in habit.

##### Family 1.—Limnæidae.

Genera: *Limnæus*, Lam. (figs. 3, 4, &c.); *Chilinia*, Gray; *Physa*, Draparn.; *Ancylus*, Geoff.; *Planorbis*, Müll., &c.

##### Family 2.—Auriculidae.

Genera: *Auricula*, Lam.; *Conovulus*, Lam.; *Pitharella*, Wood, &c.

##### Sub-order 2.—Stylommatophora.

**Characters.**—Eyes placed on the summit of two hollow tentacles; visceral hump well or not at all developed; shell large and coiled, or minute or absent; almost exclusively terrestrial.

##### Family 1.—Helicidae.

Genera: *Helix*, L. (figs. 69, A; 72\*); *Vitrina*, Draparn.; *Succinea*, Draparn.; *Bulinus*, Scopoli; *Achatina*, Lam.; *Pupa*, Lam.; *Clausilia*, Draparn., &c.

##### Family 2.—Limacidae (Slugs).

Genera: *Limax*, L.; *Inciliaria*, Benson; *Arion*, Ferrussac (fig. 69, D); *Parmacella*, Cuvier; *Testacella*, Cuvier (fig. 69, C), &c.

##### Family 3.—Onchidiidae.

Genera: *Onchidium*, Buchanan; *Peronia*, Blainv. (fig. 72); *Vaginulus*, Ferrussac, &c.

**Further Remarks on Pulmonata.**—The land-snails and slugs forming the group Pulmonata are widely distinguished from a small set of terrestrial Azygobranchia, the Pneumochlamyda (see above), at one time associated with them on account of their mantle-chamber being converted, as in

Pulmonata, into a lung, and the ctenidium or branchial plume aborted. The Pneumochlamyda (represented in England by the common genus *Cyclostoma*) have a twisted

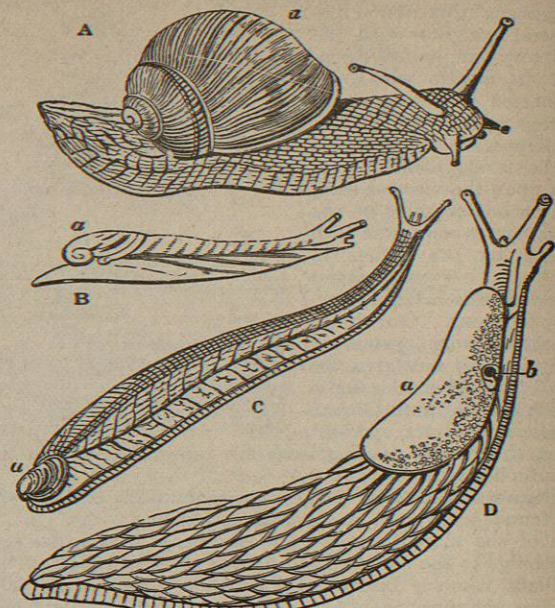


FIG. 69.—A series of Stylommatophorous Pulmonata, showing transitional forms between snail and slug.  
A, *Helix pomatia* (from Keferstein).  
B, *Helicophanta brevipes* (from Keferstein, after Pfeiffer).  
C, *Testacella haitioides* (from Keferstein).  
D, *Arion ater*, the great Black Slug (from Keferstein).  
a, Shell in A, B, C, shell-sac (closed) in D; b, orifice leading into the subpallial chamber (lung).

visceral nerve-loop, an operculum on the foot, a complex rhipidoglossate or tænioglossate radula, and are of distinct sexes; they are, in fact, Azygobranchiate Streptoneura. The Pulmonata have a straight visceral nerve-loop, never an operculum (even in the embryo), and a multidenticulate

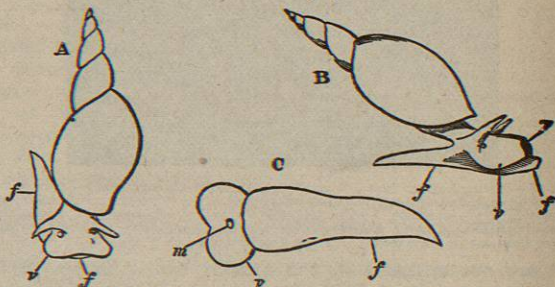


FIG. 70.—A, B, C, Three views of *Limnæus stagnalis*, in order to show the persistence of the larval velar area v, as the circum-oral lobes of the adult. m, mouth; f, foot; v, velar area, the margin v corresponding with the ciliated band which demarcates the velar area or velum of the embryo Gastropod (see fig. 4, D, E, F, H, I, v). (Original.)

radula, the teeth being equi-formal; and they are hermaphrodite. Some Pulmonata (*Limnæus*, &c.) live in fresh-waters although breathing air. The remarkable discovery has been made that in deep lakes such *Limnæi* do not breathe air, but admit water to the lung-sac and live at the bottom. The lung-sac serves undoubtedly as a hydrostatic apparatus in the aquatic Pulmonata, as well as assisting respiration. It is not improbable that here, and in other air-breathing animals, the hydrostatic function was the primary one, and the respiratory a later development.

The same general range of body-form is shown in Pulmonata as in the Natant Azygobranchia and in the Opisthobranchia; at one extreme we have Snails with coiled visceral hump, at the other cylindrical or flattened Slugs (see fig. 69). Limpet-like forms are also found (fig. 71, *Ancylus*). The foot is always simple, with its flat crawling surface extending from end to end, but in the embryo *Limnæus* (fig. 4, H) it shows a bilobed character, which leads on to the condition characteristic of Pteropoda.

The adaptation of the Pulmonata to terrestrial life has entailed little modification of the internal organization. The vascular system appears to be more complete in them than in other Gastropoda, fine vessels and even capillaries being present in place of lacunæ, in which arteries and veins find their meeting-point. The subject has not, however, been investigated by the proper methods of recent histology, and our know-

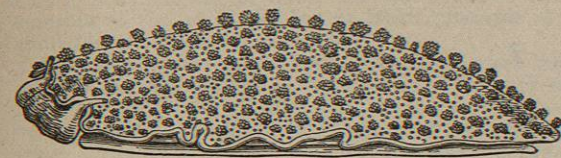


FIG. 72.—*Peronia Tongae*, a littoral Pulmonate, found on the shores of the Indian and Pacific Oceans (Mauritius, Japan).

ledge of it, as of the vascular system of Molluscs generally, is most unsatisfactory. In one genus (*Planorbis*) the plasma of the blood is coloured red by hæmoglobin, this being the only instance of the presence of this body in the blood of Glossophorous Mollusca, though it occurs in corpuscles in the blood of the bivalves *Arca* and *Solen* (Lankester, 31).

The generative apparatus of the Snail (*Helix*) may serve as an example of the hermaphrodite apparatus common to the Pulmonata and Opisthobranchia (fig. 72\*). From the ovo-testis, which lies near the apex of the visceral coil, a common hermaphrodite duct *v.e.* proceeds, which receives the duct of the compact white albuminiferous gland *E.d.*, and then becomes much enlarged, the additional width being due to the development of glandular folds, which are regarded as forming a uterus *u.* Where these folds cease the common duct splits into two portions, a male and a female. The male duct *v.d.* becomes fleshy and muscular near its termination at the genital pore, forming the penis *p.* Attached to it is a diverticulum *fl.*, in which the spermatozoa which have descended from the ovo-testis are stored and modelled into sperm ropes or spermaphores. The female portion of the duct is more complex. Soon after quitting the uterus it is joined by a long duct leading from a glandular sac, the spermatheca (*R.f.*). In this duct and sac the spermaphores received in copulation from another snail are lodged. In *Helix hortensis* the sperma-



FIG. 72\*.—Hermaphrodite reproductive apparatus of the Garden Snail (*Helix hortensis*). *v.*, ovo-testis; *v.e.*, hermaphrodite duct; *E.d.*, albuminiferous gland; *u.*, uterine dilatation of the hermaphrodite duct; *d.*, digitate accessory glands on the female duct; *p.s.*, calciferous gland or dart-sac on the female duct; *R.f.*, spermatheca or receptacle of the sperm in copulation, opening into the female duct; *v.d.*, male duct (vas deferens); *p.*, penis; *fl.*, flagellum.

theca is simple. In other species of *Helix* a second duct (as large in *Helix aspersa* as the chief one) is given off from the spermathecal duct, and in the natural state is closely adherent to the wall of the uterus. This second duct has normally no spermathecal gland at its termination, which is simple and blunt. But in rare cases in *Helix aspersa* a second spermatheca is found at the end of this second duct. Tracing the widening female duct onwards we now come to the openings of the digitate accessory glands *d.*, which probably assist in the formation of the egg-capsule. Close to them is the remarkable dart-sac *ps.*, a thick-walled sac, in the lumen of which a crystalline four-fluted rod or dart consisting of carbonate of lime is found. It is supposed to act in some way as a stimulant in copulation, but possibly has to do with the calcareous covering of the egg-capsule. Other Pulmonata exhibit variations of secondary importance in the details of this hermaphrodite apparatus.

The nervous system of *Helix* is not favourable as an example on account of the fusion of the ganglia to form an almost uniform ring of nervous matter around the oesophagus. The Pond-Snail (*Limnæus*) furnishes, on the other hand, a very beautiful case of distinct ganglia and connecting cords (fig. 22). The demonstration which it affords of the extreme shortening of the Euthyneurous visceral nerve-loop is most instructive and valuable for comparison with and explanation of the condition of the nervous centres in Cephalopoda, as also of some Opisthobranchia. The figure (fig. 22) is sufficiently described in the letter-press attached to it; the pair of buccal ganglia joined by the connectives to the cerebrals are, as in most of our figures, omitted. Here we need only further draw attention to the osphradium, discovered by Lacaze Duthiers (32), and shown by Spengel to agree in its innervation with that organ in all other Gastropoda. On account of the shortness of the visceral loop and the proximity of the right visceral ganglion to the oesophageal nerve-ring, the nerve to the osphradium and olfactory ganglion is very long. The position of the osphradium corresponds more or less closely with that of the vanished right ctenidium, with which it is normally associated. In *Helix* and *Limax* the osphradium has not been described, and possibly its discovery might clear up the doubts which have been raised as to the nature of the mantle-chamber of those genera. In *Planorbis*, which is dextrotropic (as are a few other genera or exceptional varieties of various Anisopleurous Gastropods) instead of being leiotropic, the osphradium is on the left side, and receives its nerve from the left visceral ganglion, the whole series of unilateral organs being reversed. This is, as might be expected, what is found to be the case in all "reversed" Gastropods. It is also the case in the Pulmonate *Auricula*, which is leiotropic.

The shell of the Pulmonata, though always light and delicate, is in many cases a well-developed spiral "house," into which the creature can withdraw itself; and, although the foot possesses no operculum, yet in *Helix* the aperture of the shell is closed in the winter by a complete lid, the "hibernaculum," more or less calcareous in nature, which is secreted by the foot. In *Clausilia* a peculiar modification of this lid exists permanently in the adult, attached by an elastic stalk to the mouth of the shell, and known as the "clausilium." In *Limnæus* the permanent shell is preceded in the embryo by a well-marked shell-gland or primitive shell-sac (fig. 72\*\*\*), at one time supposed to be the developing anus, but shown by Lankester to be identical with the "shell-gland" discovered by him in other Mollusca (*Pisidium*, *Pleurobranchidium*, *Neritina*, &c.). As in other Gastropoda Anisopleura, this shell-sac may abnormally develop a plug of chitonous matter, but normally it flattens out and disappears, whilst the cap-like rudiment of the permanent shell is shed out from the dome-like surface