MOLLUSCA

THE Mollusca form one of the great "phyla," or sub-kingdoms of the Animal Pedigree or Kingdom.

Literary History of the Group.—The shell-bearing forms belonging to this group which were known to Linnæus were placed by him (in 1748) in the third order of his class Vermes under the name "Testacea," whilst the Echinoderms, Hydroids, and Annelids, with the naked Molluscs, formed his second order, termed "Zoophyta." Ten years later he replaced the name "Zoophyta" by "Mollusca," which was thus in the first instance applied, not to the Mollusca at present so termed, but to a group consisting chiefly of other organisms. Gradually, however, the term Mollusca became used to include those Mollusca formerly placed among the "Testacea," as well as the naked Mollusca.

It is important to observe that the term μαλάκια, of which Mollusca is merely a Latinized form, was used by Aristotle to indicate a group consisting of the Cuttle-fishes only.

The definite erection of the Mollusca into the position of one of the great primary groups of the animal kingdom is due to George Cuvier (1788-1800), who largely occupied himself with the dissection of representatives of this type (1).[1] An independent anatomical investigation of the Mollusca had been carried on by the remarkable Neapolitan naturalist Poli (1791), whose researches (2) were not published until after his death (1817), and were followed by the beautiful works of another Neapolitan zoologist, the illustrious Delle Chiaje (3).

The "embranchement" or sub-kingdom Mollusca, as defined by Cuvier, included the following classes of shell-fish:—1, the cuttles or poulps, under the name CEPHALOPODA; 2, the snails, whelks, and slugs, both terrestrial and marine, under the name GASTROPODA; 3, the sea-butterflies or winged-snails, under the name PTEROPODA; 4, the clams, mussels, and oysters, under the name ACEPHALA; 5, the lamp-shells, under the name BRACHIOPODA; 6, the sea-squirts or ascidians, under the name NUDA; and 7, the barnacles and sea-acorns, under the name CIRRHOPODA.

The main limitations of the sub-kingdom or phylum Mollusca, as laid down by Cuvier, and the chief divisions thus recognized within its limits by him, hold good to the present day. At the same time, three of the classes considered by him as Mollusca have been one by one removed from that association in consequence of improved knowledge, and one additional class, incorporated since his day with the Mollusca with general approval, has, after more than forty years, been again detached and assigned an independent position owing to newly-acquired knowledge.

The first of Cuvier's classes to be removed from the Mollusca was that of the Cirrhopoda. Their affinities with the lower Crustacea were recognized by Cuvier and his contemporaries, but it was one of the brilliant discoveries of that remarkable and too-little-honoured naturalist, J. Vaughan Thompson of Cork, which decided their position as Crustacea. The metamorphoses of the Cirrhopoda were described and figured by him in 1830 in a very complete manner, and the legitimate conclusion as to their affinities was formulated by him (4). Thus it is to Thompson (1830), and not to Burmeister (1834), as erroneously stated by Keferstein, that the merit of this discovery belongs. The next class to be removed from Cuvier's Mollusca was that of the Nuda, better known as Tunicata. In 1866 the Russian embryologist Kowalewsky startled the zoological world with a minute account of the developmental changes of Ascidia, one of the Tunicata (5), and it became evident that the affinities of that class were with the Vertebrata, whilst their structural agreements with Mollusca were only superficial. The last class which has been removed from the Cuvierian Mollusca is that of the Lamp-shells or Brachiopoda. The history of its dissociation is connected with that of the class, viz., the Polyzoa or Bryozoa, which has been both added to and again removed from the Mollusca between Cuvier's date and the present day. The name of J. Vaughan Thompson is again that which is primarily connected with the history of a Molluscan class. In 1830 he pointed out that among the numerous kinds of "polyps" at that time associated by naturalists with the Hydroids, there were many which had a peculiar and more elaborate type of organization, and for these he proposed the name Polyzoa (6). Subsequently (7) they were termed Bryozoa by Ehrenberg (1831).

Henri Milne-Edwards in 1844 demonstrated (8) the affinities of the Polyzoa with the Molluscan class Brachiopoda, and proposed to associate the three classes Brachiopoda, Polyzoa, and Tunicata in a large group "Molluscoidea," coordinate with the remaining classes of Cuvier's Mollusca, which formed a group retaining the name Mollusca. By subsequent writers the Polyzoa have in some cases been kept apart from the Mollusca and classed with the "Vermes;" whilst by others (including the present writer) they have, together with the Brachiopoda, been regarded as true Mollusca. The recent investigation by Mr. Caldwell (1882) of the developmental history of Phoronis (9), together with other increase of knowledge, has now, however, established the conclusion that the agreement of structure supposed to obtain between Polyzoa and true Mollusca is delusive; and accordingly they, together with the Brachiopoda, have to be removed from the Molluscan phylum. Further details in regard to this, the last revolution in Molluscan classification, will be found in the article POLYZOA.

As thus finally purified by successive advances of embryological research, the Mollusca are reduced to the Cuvierian classes of Cephalopoda, Pteropoda, Gastropoda, and Acephala. Certain modifications in the disposition of these classes are naturally enough rendered necessary by the vast accumulation of knowledge as to the anatomy and embryology of the forms comprised in them during fifty years. Foremost amongst those who have within that period laboured in this group are the French zoologists Henri Milne-Edwards (20) and Lacaze Duthiers (21), to the latter of whom we owe the most accurate dissections and beautiful illustrations of a number of different types. To Kölliker (22), Gegenbaur (23), and more recently Spengel (24), amongst German anatomists, we are indebted for epoch-making researches of the same kind. In England, Owen's anatomy of the Pearly Nautilus (10), Huxley's discussion of the general morphology of the Mollusca (11), and Lankester's embryological investigations (12), have aided in advancing our knowledge of the group. Two remarkable works of a systematic character dealing with the Mollusca deserve mention here—the *Manual of the Mollusca* by the late Dr. S. P. Woodward, a model of clear systematic exposition, and the exhaustive treatise on the Malacozoa or Weichthiere by the late Professor Keferstein of Göttingen, published as part of Bronn's *Classen und Ordnungen des Thier-Reichs*. The latter work is the most completely illustrated and most exhaustive survey of existing knowledge of a large division of the animal kingdom which has ever been produced, and, whilst forming a monument to its lamented author, places the student of Molluscan morphology in a peculiarly favourable position.

[1] These figures refer to the bibliography at the end of the article, p. 695.

Classes of the Mollusca.—The classes of the Mollusca which we recognize are as follows:—

Phylum MOLLUSCA.

BRANCH A.—Glossophora.	BRANCH B.—Lipocephala (=Acephala, *Cuvier*).
Class 1.—GASTROPODA.	Class 1.—LAMELLIBRANCHIA (Syn. Conchifera).
Br. a.—Isopleura.	*Examples*—Oyster, Mussel, Clam, Cockle.
Examples — Chiton, Neomenia.	
Br. b.—Anisopleura.	
Examples—Limpet, Whelk, Snail, Slug.	
Class 2.—SCAPHOPODA.	
Example—Tooth-shell.	
Class 3.—CEPHALOPODA.	
Br. a.—Pteropoda.	
Examples—Hyalæa, Pneumodermon.	
Br. b.—Siphonopoda.	
Examples—Nautilus, Cuttles, Poulp.	

General Characters of the Mollusca.—The forms comprised in the above groups, whilst exhibiting an extreme range of variety in shape, as may be seen on comparing an Oyster, a Cuttle-fish, and a Sea-slug such as Doris; whilst adapted, some to life on dry land, others to the depths of the sea, others to rushing streams; whilst capable, some of swimming, others of burrowing, crawling, or jumping, some, on the other hand, fixed and immobile; some amongst the most formidable of carnivores, others feeding on vegetable mud, or on the minutest of microscopic organisms—yet all agree in possessing in common a very considerable number of structural details which are not possessed in common by any other animals.

The structural features which the Mollusca do possess in common with other animals belonging to other great phyla of the animal kingdom are those characteristic of the Cœlomata, one of the two great grades (the other and lower being that of the Cœlentera) into which the higher animals, or Enterozoa as distinguished from the Protozoa, are divided (13). The Enterozoa all commence their individual existence as a single cell or plastid, which multiplies itself by transverse division. Unlike the cells of the Protozoa, these embryonic cells of the Enterozoa do not remain each like its neighbour and capable of independent life, but proceed to arrange themselves in two layers, taking the form of a sac. The cavity of the two-cell-layered sac or Diblastula thus formed is the primitive gut or ARCH-ENTERON. In the Cœlentera, whatever subsequent changes of shape the little sac may undergo as it grows up to be Polyp or Jelly-fish, the original arch-enteron remains as the one cavity pervading all regions of the body. In the Cœlomata the arch-enteron becomes in the course of development divided into two totally distinct cavities shut off from one another—an axial cavity, the MET-ENTERON, which retains the function of a digestive gut; and a peri-axial cavity, the CŒLOM or body-cavity, which is essentially the blood-space, and receives the nutritive products of digestion and the waste products of tissue-change by osmosis. The Mollusca agree in being Cœlomate with the phyla Vertebrata, Platyhelmia (Flat-worms), Echinoderma, Appendiculata (Insects, Ringed-worms, &c.), and others,—in fact, with all the Enterozoa except the Sponges, Corals, Polyps, and Medusæ.

In common with all other Cœlomata, the Mollusca are at one period of life possessed of a PROSTOMIUM or region in front of the mouth, which is the essential portion of the "head," and is connected with the property of forward locomotion in a definite direction and the steady carriage of the body (as opposed to rotation of the body on its long axis). As a result, the Cœlomata, and with them the Mollusca, present (in the first instance) the general condition of body known as BILATERAL SYMMETRY; the dorsal is differentiated from the ventral surface, whilst a right and a left side similar to, or rather the complements of, one another are permanently established. In common with all other Cœlomata, the Mollusca have the mouth and first part of the alimentary canal which leads into the met-enteron formed by a special invagination of the outer layer of the primitive body-wall, not to be confounded with that which often, but not always, accompanies the antecedent formation of the arch-enteron; this invagination is termed the STOMODÆUM. Similarly, an anal aperture is formed in connexion with a special invagination which meets the hinder part of the met-enteron, and is termed the PROCTODÆUM.

In common with many (if not all) Cœlomata, the Mollusca are provided with at least one pair of tube-like organs, which open each by one end into the cœlom or body cavity, and by the other end to the exterior, usually in the neighbourhood of the anus. These are the NEPHRIDIA.

Like all other Cœlomata, the Mollusca are also provided with special groups of cells forming usually paired or median growths upon the walls of the cœlomic cavity, the cells being specially possessed of reproductive power, and differentiated as egg-cells and sperm-cells. These are the GONADS. As in other Cœlomata, the cells of the gonads may escape to the exterior in one of two ways—either through the nephridia, or, on the other hand, by special apertures.

As in all other Cœlomata, the cells, which build up respectively the primary outer layer of the body, the lining layer of the met-enteron, and the lining layer of the cœlom, are multiplied and differentiated in a variety of ways in the course of growth from the early embryonic condition. TISSUES are formed by the adhesion of a number of similarly modified cells in definite tracts. As in all Cœlomata, there is a considerable variety of tissues characterized by, and differentiated in relation to, particular physiological activities of the organism. Not only the Cœlomata but also many Cœlentera show, in addition to the EPITHELIA (the name given to tissue which bounds a free surface, whether it be that of the outer body-wall, of the gut, or of a blood-space), also deeper lying tissues, of which the first to appear is MUSCULAR tissue, and the second NERVOUS tissue.

The epithelia are active in throwing off their constituent cells (blood-corpuscles from the wall of the cœlom), or in producing secretions (glands of body-wall and of gut), or in forming horny or calcareous plates, spines, and processes, known as CUTICULAR PRODUCTS (shells and bristles of the body-wall, teeth of the tongue, gizzard, &c.).

In the Mollusca, as in all other Cœlomata, in correspondence with the primary bilateral symmetry and in relation to the special mechanical conditions of the prostomium, the nervous tissue which is in Cœlentera, and even in Flat-worms, diffused over the whole body in networks, tends to concentrate in paired lateral tracts, having a special enlargement in the prostomium. The earlier plexiform arrangement is retained in the nervous tissue of the walls of the alimentary canal of many Cœlomata, whilst a concentration to form large nerve-masses (GANGLIA), to which numerous afferent and efferent fibres are attached, affects the nervous tissue of the body-wall.

In all Cœlomata, including Mollusca, muscular tissue is developed in two chief layers, one subjacent to the deric or outer epithelium (SOMATIC MUSCULATURE), and a second surrounding the alimentary canal (SPLANCHNIC MUSCULATURE). Thus, primarily, in Cœlomata the body has the character of two muscular sacs or tubes, placed one within the other and separated from one another by the cœlomic space. The somatic musculature is the more copious and develops

very generally an outer circular layer (*i.e.*, a layer in which the muscular fibres run in a direction transverse to the long axis of the body) and a deeper longitudinal layer; to these oblique and radiating fibres may be added. The splanchnic musculature, though more delicate, exhibits a circular layer nearer the enteric epithelium, and a longitudinal layer nearer the cœlomic surface.

In Cœlomata and in many Cœlentera there are found distributed between the tracts of muscular tissue, bounding them and giving strength and consistency also to the walls of the body, of the alimentary canal, of the cœlom, and of the various organs and tissue-masses (such as nerve-centres, gonads, &c.) connected with these, tracts of tissue the function of which is skeletal. The SKELETAL TISSUE of Mollusca, in common with that of other Cœlomata, exhibits a wide range of minute structure, and is of differing density in various parts; it may be fibrous, membranous, or cartilaginous. The Mollusca, in common with the other Cœlomata, exhibit a remarkable kind of association between the various forms of skeletal tissue and the epithelium which lines the cœlomic cavity. The cœlomic cavity contains a liquid which is albuminous in chemical composition (BLOOD-LYMPH or HÆMOLYMPH), and into this liquid cells are shed from the cœlomic epithelium. They float therein and are known as BLOOD CORPUSCLES or LYMPH CORPUSCLES. The cœlomic space with its contained hæmolymph is not usually in Cœlomata, and is not in Mollusca, a simple even-walled cavity, but is broken up into numerous passages and recesses by the outgrowths, both of the alimentary canal and of its own walls. By the adhesion of its opposite walls, and by an irregularity in the process of increase of its area during growth, the cœlom becomes to a very large extent a spongy system of intercommunicating LACUNÆ or irregular spaces, filled with the cœlomic fluid. At the same time, the cœlomic space has a tendency to push its way in the form of narrow canals and sinuses between the layers of skeletal tissue, and thus to permeate together with the skeletal tissue in the form of a spongy, or it may be a tubular, network all the apparently solid portions of the animal body. This association of the nutritive and skeletal functions is accompanied by a complete identity of the tissues concerned in these functions. Not only is there complete gradation from one variety of skeletal tissue to another (*e.g.*, from membranous to fibrous, and from fibrous to cartilaginous) even in respect of the form of the cells and their intercellular substance, but the cœlomic epithelium, and consequently the hæmolymph with its floating corpuscles derived from that epithelium, is brought into the same continuity. The skeletal and blood-containing and -producing tissues in fact form one widely-varying but continuous whole, which may be called the SKELETO-TROPHIC SYSTEM OF TISSUES.

In many Cœlomata not only do the skeletal tissues allow the cœlomic space with its fluid and corpuscles to penetrate between their layers, but a special mode of extension of that space is found, which consists in the hollowing out of the solid substance of elongated cells having the form of fibres, which thus become tubular, and, admitting the nutritive fluid, serve as channels for its distribution. These are "capillary vessels," and it has yet to be shown that such are formed in the Mollusca. Larger vessels, however, concerned in guiding the movement of the cœlomic fluid in special directions are very usually developed in the Mollusca, as in other Cœlomata, by the growth of skeletal tissue around what are at first ill-defined extensions of the cœlomic space. In this way a portion of the cœlomic space becomes converted into vessels, whilst a large part remains with irregular walls extending in every direction between the skeletal tissues and freely communicating with the system of vessels. As in many other Cœlomata, muscular tissue grows around the largest vessel formed from the primitive cœlom, which thus becomes a contractile organ for propelling the blood-lymph fluid. This "HEART" has in Mollusca, as in most other Cœlomata in which it is developed, a dorsal position. A communication of the blood-lymph space with the exterior by means of a pore situated in the foot or elsewhere has been very generally asserted to be characteristic of Mollusca. It has been maintained that water is introduced by such a pore into the blood, or admitted into a special series of water-vessels. It has also been asserted that the blood-fluid is expelled by the Mollusca from these same pores. Recent investigation (14) has, however, made it probable that the pores are the pores of secreting glands, and do not lead into the vascular system. There is, it therefore appears, no admission or expulsion of water through such pores in connexion with the blood, although in some other Cœlomata it is established that water is taken into the cœlomic space through a pore (Echinoderms), whilst in some others there is no doubt that the cœlomic hæmolymph is occasionally discharged in quantity through pores of definite size and character (Earthworm, &c.).

We have thus seen that the Mollusca possess, in common with the other Cœlomata,—1, a body composed of a vast *number of cells* or plastids, arranged so as to form a sac-like *body-wall*, and within that a second sac, the *met-enteron*, the wall of which is separated from the first by a *cœlom* or blood-lymph space; 2, a *stomodæum* and a *proctodæum*; 3, a *prostomium*, together with a differentiated *dorsal* and *ventral* surface, and consequently *right* and *left sides*, *i.e.*, bilateral symmetry; 4, a pair of *nephridia*; 5, *gonads* developed on the wall of the cœlom; 6, *deric* epithelium (producing horny and calcareous deposits on its surface), *enteric* epithelium, and *cœlomic* epithelium; 7, laterally paired masses of *nerve-tissue*, especially large in the prostomial region (nerve-centres or *ganglia*); 8, *muscular tissue*, forming a *somatic* tunic and a *splanchnic* tunic; 9, *skeleto-trophic tissues*, consisting of membranous, fibrous, and cartilaginous *supporting tissues*, and of *blood-vessels* and the walls of *blood-spaces*, the *cœlomic epithelium*, and the liquid tissue known as *hæmolymph* (commonly blood).

Schematic Mollusc.—Starting from this basis of structural features common to them and the rest of the Cœlomata, we may now point out what are the peculiar developments of structure which characterize the Mollusca and lead to the inference that they are members of one peculiar branch or phylum of the animal pedigree. In attempting thus to set forth the dominating structural attributes of a great group of organisms it is not possible to make use of arbitrary definitions. Of Mollusca, as of other great phyla, it is not possible categorically to enunciate a series of structural peculiarities which will be found to be true in reference to every member of the group. We have to remember that the process of adaptation in the course of long ages of development has removed in some cases one, in other cases another, of the original features characteristic of the ancestors from which the whole group may be supposed to have taken origin, and that it is possible (and actually is realized in fact) that some organisms may have lost all the *primary* characteristics of Molluscan organization, and yet be beyond all doubt definitely stamped as Mollusca by the retention of some *secondary* characteristic which is so peculiar as to prove their relationship with other Mollusca. An example in point is found in the curious fish-like form Phyllirhoë (fig. 58), which has none of the primary characteristics of a Mollusc, and yet is indisputably proved to belong to the Molluscan phylum by possessing the peculiar and elaborate lingual apparatus present in one branch of the phylum, the Glossophora.

In order to exhibit concisely the peculiarities of organization which characterize the Mollusca, we find it most convenient to construct a schematic Mollusc, which shall possess in an unexaggerated form the various structural arrangements which are more or less specialized, exaggerated, or even suppressed in particular members of the group. Such a schematic Mollusc is not to be regarded as an archetype, in the sense which has been attributed to that word, nor as the embodiment of an idea present to a creating mind, nor even as an epitome of developmental laws. Were knowledge sufficient, we should wish to make this schematic

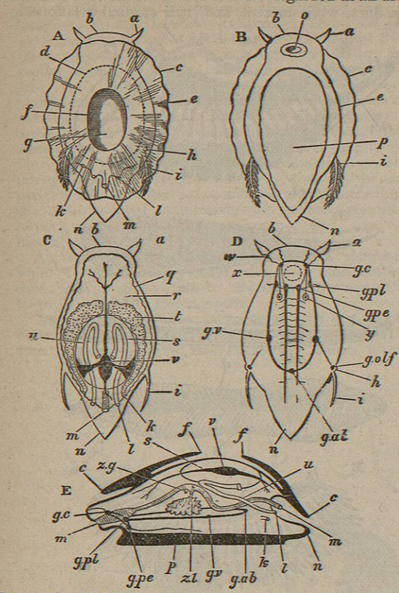

FIG. 1.—Schematic Mollusc. A. Dorsal aspect. B. Ventral aspect. C. The heart, pericardium, gonads, and nephridia shown in position. D. The nervous system; the reader is requested to note that the cord passing backwards from *g.pe* lies beneath, and does not in any way unite with the cord which passes from *g.ab* to *g.pl*. E. Diagram in which the body-wall is represented as cut in the median antero-posterior plane, so as to show organs in position,—the shell-sac is seen in section, but the shell is omitted.

Letters in all the figures as follows:—*a*, cephalic tentacle; *b*, head; *c*, edge of the mantle-skirt or limbus pallialis; *d*, dotted line indicating the line of origin of the free mantle-skirt from the sides of the visceral hump; *e*, outline of the foot seen through the mantle-skirt in A, which is supposed to be transparent, allowing the position of this and of the various parts *h*, *i*, *k*, *l*, *m*, to be seen through its substance; *f*, edge of the shell-follicle; *g*, the shell; *h*, the osphradium, paired (Spengel's olfactory organ); *i*, the ctenidium, paired (gill-plume); *k*, aperture of the gonad, paired; *l*, aperture of one of the two nephridia: *m*, anus; *n*, posterior region of the foot reaching farther back than the mass of viscera (dorsal hump) which it carries; *o*, mouth; *p*, plantar surface of the foot; *q*, cut edge of the body-wall of the dorsal region; *r*, cœlomic space (blood-lymph space or body-cavity), mostly occupied by liver, but to some extent retained as blood-channels and lacunæ; *s*, pericardial cavity; *t*, gonad (ovary or spermary), paired; *u*, nephridium, paired; *v*, ventricle of the heart receiving the right and the left auricles at its sides, and sending off anteriorly a large vessel, posteriorly a small one; *w*, the cephalic eye, paired; *x*, dotted ring to show the position occupied by the œsophagus in relation to the nerve ganglia and cords; *y*, the otocyst, paired; *z.l*, the digestive gland (so-called "liver") of the left side; *z.g*, duct of the digestive gland of the right side; *g.c*, cerebral ganglion united by the cerebral commissure to its fellow; *g.pl*, pleural ganglion united by the cerebro-pleural connective to the cerebral ganglion, and by the pleuro-pedal connective to the pedal ganglion; *g.pe*, the pedal ganglion united to its fellow by the pedal commissure—the two sending off posteriorly the long ladder-like pair of pedal nerves; *g.v*, the visceral ganglion (of the left side) united by the visceral loop or commissure to the similar ganglion on the right side, and by the viscero-pleural connective to the pleural ganglion; *g.ab*, abdominal ganglion developed on the course of the visceral loop; *g.olf*, olfactory ganglion placed near the osphradium on a nerve taking its origin from the visceral ganglion.

Mollusc the representation of the actual Molluscan ancestor from which the various living forms have sprung. To definitely claim for our schematic form any such significance in the present state of knowledge would be premature, but it may be taken as more or less coinciding with what we are justified, under present conditions, in picturing to ourselves as the original Mollusc or archi-Mollusc (more correctly Archimalakion). After describing this schematic form, we shall proceed to show how far it is realized or justified in each class and order of Mollusca successively.

The schematic Mollusc (fig. 1, A to E) is oblong in shape, bilaterally symmetrical, with strongly differentiated dorsal and ventral surface, and has a well-marked HEAD, consisting of the prostomium (*b*) and the region immediately behind the mouth. Upon the head we place a pair of short CEPHALIC TENTACLES (*a*). The *mouth* is placed in the median line anteriorly, and is overhung by the prostomium (B, *o*); the *anus* is placed in the median line posteriorly, well raised on the dorsal surface (A, *m*). The apertures of a pair of NEPHRIDIA are seen in the neighbourhood of the anus right and left (A, *l*). Near the nephridial apertures, and in front of them, right and left, are the pair of apertures (*k*) appropriate to the ducts of the GONADS (generative pores).

The most permanent and distinctive Molluscan organ is the FOOT (Podium). This is formed by an excessive development of the somatic musculature along the ventral surface, distinctly ceasing at the region of the head, below which it suddenly projects as a powerful muscular mass (B, *p*; E, *p*). It may be compared, and is probably genetically identical, with the muscular ventral surface of the Planarians and with the suckers of Trematoda, but is more extensively developed than are those corresponding structures. The muscular tissue of the foot, and of all other parts of the body of all Mollusca, is cellular and unstriated, as distinguished from the composite muscular fibre (consisting of cell-fusions instead of separable cells) which occurs in Arthropoda and in Vertebrata, and which has the further distinction of being composed of alternating bands of substance of differing refractive power (hence "striated"). The appearance of cross striation seen in the muscular cells of some Molluscs (odontophore of Haliotis, Patella, &c.) requires further investigation. It is by no means altogether the same thing as the marking characteristic of striated muscular fibre.

Contrasting with the ventral foot is the thin-walled dorsal region of the body, which may be termed the anti-podial region. This thin-walled region is formed by soft viscera covered in by the comparatively delicate and non-muscular body-wall (fig. 1, E). As the ventral foot is clearly separate from the projecting head, so is this dorsal region, and it is conveniently spoken of as the VISCERAL HUMP or "dome" (cupola). Protecting the visceral dome is a SHELL (conchylium) consisting of a horny basis impregnated with carbonate of lime,[1] and secreted by the deric epithelium of this region of the body (*g*). The shell in our schematic Mollusc is single, cap-shaped, and symmetrical. It does not lie entirely naked upon the surface of the visceral dome, but is embedded all round its margin, to a large extent in the body-wall. In fact, the integument of the visceral dome forms an open flattened sac in which the shell lies. This is the PRIMARY SHELL-SAC, or FOLLICLE (A and E, *f*). The wall of the body projects all round the visceral dome in the form of a flap or skirt, so as to overhang and conceal to some extent the head and the sides of the foot. This skirt, really an out-

[1] As to the minute structure of the shell in various classes, see Carpenter's article "Shell" in the *Cyclop. of Anat. and Physiol.* The limits of our space do not permit us to deal with this or other histological topics.

growth of the dorsal body-wall, is called the MANTLE-FLAP (limbus pallialis), or more shortly the MANTLE or PALLIUM (*c*). The space between the overhanging mantle-flap and the sides and neck of the animal which it overhangs is called the SUB-PALLIAL SPACE or CHAMBER. Posteriorly in this space are placed the anus and the pair of nephridial apertures (see fig. 1, E).

The development of the mantle-skirt and its sub-pallial space appears to have a causal relation, in the way of protection, to a pair of processes of the body-wall which spring, one on the right and one on the left, from the sides of the body, nearer the anus than the mouth, and are concealed by the mantle-flap to some extent (A, B, *t*). These processes have an axis in which are two blood-vessels, and are beset with two rows of flattened filaments, like the teeth of a comb in double series. These are the CTENIDIA or gill-combs. Usually, as will be seen in the sequel, they play the part of gills, but since in many Molluscs (Lamellibranchs) their function is not mainly respiratory, and since also other completely-formed gills are developed as special organs in some Molluscs to the exclusion of these processes, it is well not to speak of them simply as "gills" or "branchiæ," but to give them a non-physiological name such as that here proposed. Near the base of the stem of each ctenidium is a patch of the epithelium of the body-wall, peculiarly modified and supplied with a special nerve and ganglion. This is Spengel's olfactory organ, which tests the respiratory fluid, and is persistent in its position and nerve-supply throughout the group Mollusca. We propose to call it the OSPHRADIUM.

Passing now to the internal organs, our schematic Mollusc is found to possess an ALIMENTARY CANAL, which passes from mouth to anus in the middle line, leaving between it and the muscular body-wall a more or less spongy, in parts a spacious, CŒLOM. The *stomodæum* is large and muscular, the *proctodæum* short; the bulk of the alimentary canal is therefore developed from the met-enteron or remnant of the arch-enteron after the cœlom has been pinched off from it. A paired outgrowth of the met-enteron forms the glandular diverticulum known as the digestive gland or (commonly) liver (E, *zg*, *zl*).

Dorsally to the alimentary tract the cœlom is spacious. The space (C, E, *s*) is termed the PERICARDIUM, since it is traversed by a vessel running fore and aft in the median line, which has contractile muscular walls and serves as a heart to propel the cœlomic blood-fluid. This pericardial space, although apparently derived from the original cœlom, is not in communication with the other spaces and blood-vessels derived from the cœlom; it never (or perhaps in a very few instances) contains in the adult the Molluscan blood or hæmolymph, and is always in free communication with the exterior through the tubes called *nephridia* (renal organs). The HEART receives symmetrically on each side, right and left a dilated vessel bringing aerated blood from the ctenidia. These dilated vessels are termed the *auricles of the heart*, whilst the median portion itself, at the point where these vessels join it, is termed the *ventricle of the heart* (C, *v*). The vessel passing fore and aft from the ventricle gives off a few trunks which open into spaces of the cœlom, the so-called lacunæ; these are excavated in every direction between the viscera and the various bundles of fibrous and muscular tissue, and may assume more or less the character of tube-like vessels with definite walls. Right and left opening into the pericardial cœlom is a coiled tube, the farther extremity of which opens to the exterior by the side of the anus. These two tubes (C, *u*) are the symmetrically disposed NEPHRIDIA (renal organs).

The GONADS (ovaries or spermaries) are placed in the mid-dorsal region of the cœlom (C, *t*), and have their own apertures in the immediate neighbourhood of those of the nephridia. The apertures are paired right and left, and so are the ducts into which they lead; but at present we have no ground for determining whether the gonad itself was primarily in Molluscs a paired organ or a median organ, nor have we any well-founded conception as to the nature of the ducts when present, and their original relationship

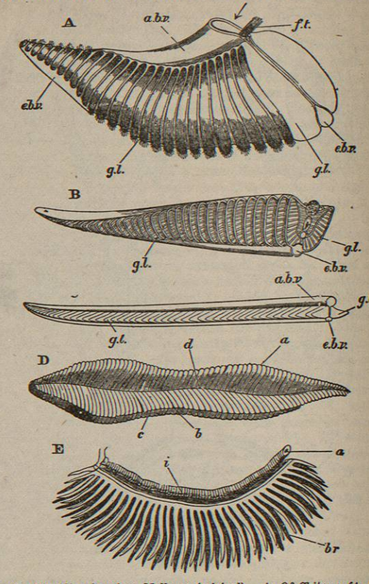

FIG. 2.—Ctenidia of various Molluscs (original). A. Of Chiton; *f.t.*, fibrous tissue; *a.b.v.*, afferent blood-vessel; *e.b.v.*, efferent blood-vessel; *g.l.*, laterally paired lamellæ. B. Of Sepia; letters as in A. C. Of Fissurella; letters as in A. D. Of Nucula; *d*, position of axis with blood-vessels; *a*, inner; *b* and *c*, outer row of lamellæ. E. Of Paludina; *i*, intestine running parallel with the axis of the ctenidium and ending in the anus *a*; *br*, rows of elongate processes corresponding to the two series of lamellæ of the upper figures.

to the gonads. The genital ducts of some organisms are modified nephridia, but the nature of those of Mollusca, of Arthropoda, of Echinoderma, of Nematoidea, and of some Vertebrata has yet to be elucidated.

The disposition of the nerve-centres is highly characteristic. There are four long cords composed of both nerve-fibres and nerve-cells which are disposed in pairs, two right and left of the pedal area or foot, two more dorsally and tending to a deeper position than that occupied by the pedal cords, so as to lie freely within the cœlomic space unattached to the body-wall. These are respectively the PEDAL NERVE-CORDS and the VISCERAL NERVE-CORDS. The latter meet and join one another posteriorly. A right and left (D, *g.v*), and a median abdominal (*g.ab*) ganglion are placed on these cords, and from them are given off the osphradial nerves which have special ganglia (*g.olf*). In the region of the prostomium the pedal nerve-cords are enlarged behind the mouth, forming the *pedal ganglia* (*g.pe*), and are united by nerve-fibres to one another. From this spot they are continued forward into the prostomium, where they enlarge to form the right and left *cerebral ganglia* (*g.c*), which are united to one another by nerve-fibres in front of

the mouth, just as the pedal ganglia are behind it. The right and left pedal ganglia are joined by transverse cords to the right and left visceral cords respectively, the point of union being marked on either side by a swelling (*g.pl*) known as the pleural ganglion. The visceral nerve-cord can also be traced up on each side beyond the pleural ganglion to the cerebral ganglion. Thus we have a nearly complete double nerve-ring formed around the œsophagus by the two pairs of nerve-cords which are in this region drawn, as it were, towards each other and away from their lateral position both behind and before the stomodæal invagination. Whilst the swollen parts of the nerve-tracts are termed *ganglia*, the connecting cords are conveniently distinguished either as *connectives* or as *commissures*. Commissures connect two ganglia of the same pair We have a cerebral commissure, a pedal commissure and a visceral commissure. Connectives connect ganglia of dissimilar pairs, and we speak accordingly of the cerebro-pedal connective, the cerebro-pleural connective, the pleuro-pedal connective, and the viscero-pleural connective.

An ENTERIC NERVOUS SYSTEM forming a plexus on the walls of the alimentary canal exists, but does not exhibit cords and ganglia visible to the naked eye except in the large Dibranchiate Cephalopods.

Our schematic Mollusc is provided with certain ORGANS OF SPECIAL SENSE. Tactile organs occur on the head in the form of short CEPHALIC TENTACLES (*a*). Deeply placed are

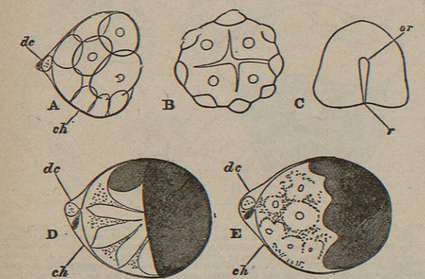

FIG. 3.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *dc*, directive corpuscles (praesemina outcast cells); *ch*, egg-envelope or chorion; *or*, oral end of the blastopore; *r*, anal end of the blastopore. A. Formation of the Diblastula by the invagination of larger cells into the area of smaller cells (optical section). B. View of the same specimen from the surface of invagination; the smaller cells are seen at the periphery; by division they will multiply and extend themselves over the four larger cells. C. Fully-formed Diblastula, surface view to show the elongated form of the orifice of invagination or blastopore; its middle portion closes up and coincides with the region of the foot; the extremity, *or*, coincides with the mouth and stomodæum, the opposite extremity, *r*, with the anus. D. Optical section of an embryo a little older than A. E. Surface view of the same embryo.

a pair of closed vesicles containing each a calcareous concretion and acting as auditory organs; these are known as OCTOCYSTS (D, *y*). They are situated behind the mouth in the foremost portion of the foot. At the base of each cephalic tentacle is a pigmented eye-spot—the CEPHALIC EYE (D, *ve*). The OSPHRADIUM (*h*), or peculiar patch of olfactory epithelium at the base of the ctenidium, has already been mentioned.

To the scheme thus exhibited of the possible organization of the ancestral Mollusc we shall now add a sketch of the mode in which this form of body and series of internal organs are developed from the egg.

The egg-cell of Mollusca is either free from food material—a simple protoplasmic corpuscle—or charged with food material to a greater or less extent. Those cases which appear to be most typical—that is to say, which adhere to a

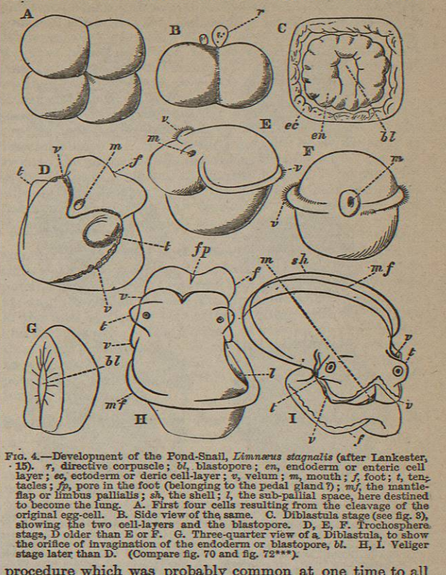

FIG. 4.—Development of the Pond-Snail, *Limnæus stagnalis* (after Lankester, 15). *r*, directive corpuscle; *bl*, blastopore; *en*, endoderm or enteric cell layer; *ec*, ectoderm or deric cell-layer; *v*, velum; *m*, mouth; *f*, foot; *t*, tentacles; *fp*, pore in the foot (belonging to the pedal gland ?); *mf*, the mantle-flap or limbus pallialis; *sh*, the shell; *l*, the sub-pallial space, here destined to become the lung. A. First four cells resulting from the cleavage of the original egg-cell. B. Side view of the same. C. Diblastula stage (see fig. 3), showing the two cell-layers and the blastopore. D, E, F. Trochosphere stage, D older than E or F. G. Three-quarter view of a Diblastula, to show the orifice of invagination of the endoderm or blastopore, *bl*. H, I. Veliger stage later than D. (Compare fig. 70 and fig. 72***).

procedure which was probably common at one time to all then existing Mollusca, and which has been departed from

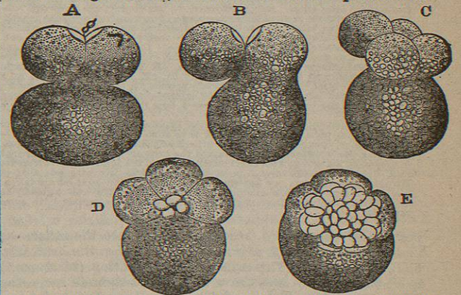

FIG. 5.—Early stages of division of the fertilized egg-cell in *Nassa mutabilis* (from Balfour, after Bobretzky). A. The egg-cell has divided into two spheres, of which the lower contains more food-material, whilst the upper is again incompletely divided into two smaller spheres. Resting on the dividing upper sphere are the eight-shaped "directive corpuscles," better called "praesemina outcast cells or apoblasts," since they are the result of a cell-division which affects the egg-cell before it is impregnated, and are mere refuse, destined to disappear. B. One of the two smaller spheres is reunited to the larger sphere. C. The single small sphere has divided into two, and the reunited mass has divided into two, of which one is oblong and practically double, as in B. D. Each of the four segment-cells gives rise by division to a small pellucid cell. E. The cap of small cells has increased in number by repeated formation of pellucid cells in the same way, and by division of those first formed. The cap will spread over and enclose the four segment-cells, as in fig. 3, A, B.

only in later and special lines of descent—show approxi-