

Bourne, B.Sc., of University College, has prepared from actual specimens the drawings of this part in the male and female Nautilus reproduced in fig. 88, and has restored the parts to their natural form when expanded. The drawings show very strikingly the difference between male and female. In the female (lower figure), we observe in the centre of the disc the buccal cone *c* carrying the beak-like pair of jaws which project from the finely papillate buccal membrane. Three tentaculiferous lobes of the fore-foot are in immediate contact with this buccal cone; they are the right and left (*c, c*) inner lobes, as we propose to call them, and the inferior inner lobe (*d*),—called inferior because it really lies ventralwards of the mouth. This inner inferior lobe is clearly a double one, representing a right and left inner inferior lobe fused into one. A lamellated organ on its surface, probably olfactory in function (*n*), marks the separation of the constituent halves of this double lobe. Each half carries a group of fourteen tentacles. The right and the left inner lobes (*c, c*) each carry twelve tentacles. Ex-

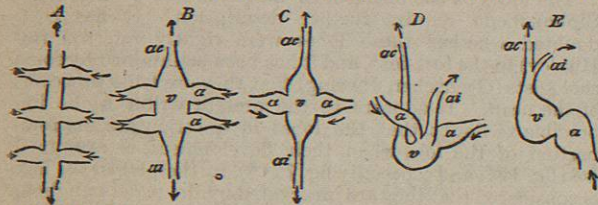


FIG. 105.—Diagram to show the relations of the heart in the Mollusca (from Gegenbaur). A. Part of the dorsal vascular trunk and transverse trunks of a worm. B. Ventricle and auricles of Nautilus. C. Of a Lamellibranch, of Chiton, or of Loligo. D. Of Octopus. E. Of a Gastropod. *a*, auricle; *v*, ventricle; *ac*, arteria cephalica (aorta); *ai*, arteria abdominalis. The arrows show the direction of the blood-current.

ternal to these three lobes the muscular substance of the mouth-embracing foot is raised into a wide ring, which becomes especially thick and large in the dorsal region where it is notably modified in form, offering a concavity into which the coil of the shell is received, and furnishing a protective roof to the retracted mass of tentacles. This part of the external annular lobe of the fore-foot is called the "hood" (figs. 90, 91, *m*). The median antero-posterior line traversing this hood exactly corresponds to the line of concrescence of the two halves of the fore-foot, which primitively grew forward one on each side of the head, and finally fused together along this line in front of the mouth. The tentacles carried by the great annular lobe are nineteen on each side, thirty-eight in all. They are somewhat larger than the tentacles carried on the three inner lobes. The dorsalmost pair of tentacles (marked *g* in fig. 88) are the only ones which actually belong to that part of the disc which forms the great dorsal hood *m*. The hood is, in fact, to a large extent formed by the enlarged sheaths of these two tentacles. In the Ammonites (fossil Tetrabranchiata allied to Nautilus) the dorsal surface of the hood secreted a shelly plate in two pieces, known to paleontologists as Trigonellites and Aptychus. Possibly, however, this double plate was carried on the surface of the bilobed nidamental gland with the form and sculpturing of which, in Nautilus, it closely agrees. All the tentacles of the circum-oral disc are set in remarkable tubular sheaths, into which they can be drawn. The sheaths of some of those belonging to the external or annular lobe are seen in fig. 91, marked *n*. The sheaths are muscular as well as the tentacles, and are simply tubes from the base of which the solid tentacle grows. The functional significance of this sheathing arrangement is as obscure as its morphological origin. With reference to the latter, it appears highly probable that the tubular sheath represents the cup of a sucker such as is found on the fore-foot of the

Dibranchiata. In any case, it seems to the writer impossible to doubt that each tentacle, and its sheath on a lobe of the circum-oral disc of Nautilus, corresponds to a sucker on such a lobe of a Dibranchiata. Keferstein follows Owen in strongly opposing this identification, and in regarding such tentacle as the equivalent of a whole lobe or arm of a Decapod or Octopod Dibranch. We find in the details of these structures, especially in the facts concerning the hectocotylus and spadix, the most conclusive reasons for dissenting from Owen's view. We have so far enumerated in the female Nautilus ninety tentacles. Four more remain which have a very peculiar position, and almost lead to the suggestion that the eye itself is a modified tentacle. These remaining tentacles are placed one above (before) and one below (behind) each eye, and bring up the total to ninety-four (fig. 91, *v, v*). They must be considered as also belonging to the fore-foot which thus surrounds the eye.

In the adult male Nautilus we find the following important differences in the tentaculiferous disc as compared with the female (see upper drawing in fig. 88). The inner inferior lobe is rudimentary, and carries no tentacles. It is represented by three groups of lamellae (*d*), which are not fully exposed in the drawing. The right and left inner lobes are subdivided each into two portions. The right shows a larger portion carrying eight tentacles, and smaller detached groups (*q*) of four tentacles, of which three have their sheaths united whilst one stands alone. These four tentacles may be called the "anti-spadix." The left inner lobe shows a similar larger portion carrying eight tentacles, and a curious conical body in front of it corresponding to the anti-spadix. This is the "spadix" of Van der Hoeven (36). It carries no tentacles, but is terminated by imbricated lamellae. These lamellae appear to represent the four tentacles of the anti-spadix of the right internal lobe, and are generally regarded as corresponding to that modification of the sucker-bearing arms of male Dibranchiate Siphonopods to which the name "hectocotylus" is applied. The spadix is in fact the hectocotylized portion of the fore-foot of the male Nautilus. The hectocotylized arm or lobe of male Dibranchiata is connected with the process of copulation, and in the male Nautilus the spadix has probably a similar significance, though it is not possible to suggest how it acts in this relation. It is important to observe that the modification of the fore-foot in the male as compared with the female Nautilus is not confined to the existence of the spadix. The anti-spadix and the reduction of the inner inferior lobe are also male peculiarities. The external annular lobe in the male does not differ from that of the female; it carries nineteen tentacles on each side. The four ophthalmic tentacles are also present. Thus in the male Nautilus we find altogether sixty-two tentacles, the thirty-two additional tentacles of the female being represented by lamelliform structures.

If we now compare the fore-foot of the Dibranchiata with that of Nautilus, we find in the first place a more simple arrangement of its lobes, which are either four or five pairs of tapering processes (called "arms") arranged in a series around the buccal cone, and a substitution of suckers for tentacles on the surface of these lobes (figs. 92, 95, 96). The most dorsally-placed pair of arms, corresponding to the two sides of the hood of Nautilus, are in reality the most anterior (see fig. 75, (6)), and are termed the first pair. In the Octopoda there are four pairs of these arms (figs. 94, 95), in the Decapoda five pairs, of which the fourth is greatly elongated (figs. 92, 93). In Sepia and other Decapoda (not all) each of these long arms is withdrawn into a pouch beside the head, and is only ejected for the purpose of prehension. The figures referred to show some of the variations in form which these arms may assume. In the

Octopoda they are not unfrequently connected by a web, and form an efficient swimming bell. The suckers are placed on the ad-oral surface of the arms, and may be in one, two, or four rows, and very numerous. In place of suckers in some genera we find on certain arms or parts of the arms horny hooks; in other cases a hook rises from the centre of each sucker. The hooks on the long arms of Onychoteuthis are drawn in fig. 97. The fore-foot, with its apparatus of suckers and hooks, is in the Dibranchiata essentially a prehensile apparatus, though the whole series of arms in the Octopoda serve as swimming organs, and in many (e.g., the Common Octopus or Poulp) the sucker-bearing surface is used as a crawling organ.

In the males of the Dibranchiata one of the arms is more or less modified in connexion with the reproductive function, and is called the "hectocotylized arm." This name is derived from the condition assumed by the arm in those cases in which its modification is carried out to the greatest extent. These cases are those of the Octopods *Argonauta argo* and *Parasira catenulata* (fig. 96). In the males of these the third arm (on the left side in *Argonauta*, on the right side in *Parasira*) is found before the breeding season to be represented by a globular sac of integument. This sac bursts, and from it issues an arm larger than its neighbours, having a small sac at its extremity in *Parasira* (fig. 96, *x*), from which subsequently a long filament issues. Before copulation the male charges this arm with the spermatophores or packets of spermatozoa removed from its generative orifice beneath the mantle-skirt, and during coitus the arm becomes detached and is left adhering to the female by means of its suckers. A new arm is formed at the cicatrix before the next breeding season. The female, being much larger than the male, swims away with the detached arm lodged beneath her mantle-skirt. There, in a way which is not understood, the fertilization of the eggs is effected. Specimens of the female *Parasira* with the detached arm adherent were examined by Cuvier, who mistook the arm for a parasitic worm and gave to it the name Hectocotylus. Accordingly, the correspondingly modified arms of other Siphonopoda are said to be hectocotylized. Steenstrup has determined the hectocotylized condition of one or other of the arms in a number of male Dibranchs as follows:—in all, excepting *Argonauta* and *Parasira*, the modification of the arm is slight, consisting in a small enlargement of part or the whole of the arm, and the obliteration of some of its suckers, as shown in fig. 95, A, B; in *Octopus* and *Eledone* the third right arm is hectocotylized; in *Rossia* the first left arm is hectocotylized along its whole length, and the first right arm also in the middle only; in *Sepioida* only the first left arm along its whole length; in *Sepia* it is the fourth left arm which is modified, and at its base only; in *Sepioteuthis*, the same at its apex; in *Loligo*, the same also at its apex; in *Lololus*, the same along its whole length; in *Ommastrephes*, *Onychoteuthis*, and *Loligopsis* no hectocotylized arm has hitherto been observed.

In the females of several Dibranchs (*Sepia*, &c.) the packets of spermatozoa or spermatophores received from the male have been observed adhering to the smaller arms. How they are passed in this case by the female to the ova in order to fertilize them is unknown.

**Musculature, Fins, and Cartilaginous Skeleton.**—Without entering into a detailed account of the musculature of Nautilus, we may point out that the great muscular masses of the fore-foot and of the mid-foot (siphon) are ultimately traceable to a large transverse mass of muscular tissue, the ends of which are visible through the integument on the right and left surfaces of the body dorsal of the free flap of the mantle-skirt (fig. 89, *l, l*, and fig. 91, *k*). These muscular arms have a certain adhesion to the shell,

and serve both to hold the animal in its shell and as the fixed supports for the various movements of the tentaculiferous lobes and the siphon. They are to be identified with the ring-like area of adhesion by which the foot-muscle of the Limpet is attached to the shell of that animal (see fig. 27). In the Dibranchs a similar origin of the muscular masses of the fore-foot and mid-foot from the sides of the shell—modified, as this is, in position and relations—can be traced.

In Nautilus there are no fin-like expansions of the integument, whereas such occur in the Decapod Dibranchs along the sides of the visceral hump (figs. 92, 93). As an exception among Octopoda lateral fins occur in *Pinnocotopus* (fig. 94, A), and in *Cirrhoteuthis* (fig. 94, D). In the Pteropodous division of the Cephalopoda such fin-like expansions of the dorsal integument do not occur, which is to be connected with the fact that another region, the mid-foot, which in Siphonopods is converted into a siphon, is in them expanded as a pair of fins.

In Nautilus there is a curious plate-like expansion of integument in the mid-dorsal region just behind the hood, lying between that structure and the portion of mantle-skirt which is reflected over the shell. This is shown in fig. 90, *b*. If we trace out the margin of this plate we find that it becomes continuous on each side with the sides of the siphon or mid-foot. In *Sepia* and other Decapods (not in Octopods) a closely similar plate exists in an exactly corresponding position (see *b* in figs. 110, 111). In *Sepia* a cartilaginous development occurs here immediately below the integument forming the so-called "nuchal plate," drawn in fig. 116, D. The morphological significance of this nuchal lamella, as seen both in Nautilus and in *Sepia*, is not obvious. Cartilage having the structure shown in fig. 117 occurs in various regions of the body of Siphonopoda. In all Glossophorous Mollusca the lingual apparatus is supported by internal skeletal pieces, having the character of cartilage; but in the Siphonopodous Cephalopoda such cartilage has a wider range.

In Nautilus a large H-shaped piece of cartilage is found forming the axis of the mid-foot or siphon (fig. 116, A, B). Its hinder part extends up into the head and supports the peri-oesophageal nerve-mass (*x*), whilst its two anterior rami extend into the tongue-like siphon. In *Sepia*, and Dibranchs generally, the cartilage takes a different form, as shown in fig. 116, C. The processes of this cartilage cannot be identified in any way with those of the capitopodal cartilage of Nautilus. The lower larger portion of this cartilage in *Sepia* is called the cephalic cartilage, and forms a complete ring round the oesophagus; it completely invests also the ganglionic nerve-collar, so that all the nerves from the latter have to pass through foramina in the cartilage. The outer angles of this cartilage spread out on each side so as to form a cup-like receptacle for the eyes. The two processes springing right and left from this large cartilage in the median line (fig. 116, C) are the "pre-orbital cartilages;" in front of these, again, there is seen a piece like an inverted T, which forms a support to the base of the "arms" of the fore-foot, and is the "basibrachial" cartilage. The Decapod Dibranchs have, further, the "nuchal cartilage" already mentioned, and in *Sepia*, a thin plate-like "sub-ostreaal" or (so-called) dorsal cartilage, the anterior end of which rests on and fits into the concave nuchal cartilage. In Octopoda there is no nuchal cartilage, but two band-like "dorsal cartilages." In Decapods there are also two cartilaginous sockets on the sides of the funnel—"siphon-hinge cartilages"—into which fleshy knobs of the mantle-skirt are loosely fitted. In *Sepia*, along the whole base-line of each lateral fin of the mantle (fig. 92), is a "basipterygial cartilage." It is worthy of remark that we have, thus developed, in Dibranch Siphonopods a more



complete internal cartilaginous skeleton than is to be found in some of the lower Vertebrates. There are other instances of cartilaginous endo-skeleton in groups other than the Vertebrata. Thus in some capito-branchiate Chastopods cartilage forms a skeletal support for the gill-plumes, whilst in the Arachnids (*Mygale*, *Scorpio*) and in *Limulus* a large internal cartilaginous plate—the ento-sternite—is developed as a support for a large series of muscles.

**Alimentary Tract.**—The buccal cone of *Nautilus* is terminated by a villous margin (buccal membrane) surrounding the pair of beak-like jaws. These are very strong and dense in *Nautilus*, being calcified. Fossilized beaks of *Tetrabranchiata* are known under the name of *Rhyncholites*. In *Dibranchs* the beaks are horny, but similar in shape to those of *Nautilus*. They resemble in general those of a parrot, the lower beak being the larger, and overlapping the upper or dorsal beak. The lingual ribbon and odontophoral apparatus has the structure which is typical for the Glosso-phorous Mollusca. In fig. 107, A is represented a single row of teeth from the lingual ribbon of *Nautilus*, and in fig. 107, B, C, of other Siphonopoda.

In *Nautilus* a long and wide crop or dilated oesophagus (*cr*, fig. 110) passes from the muscular buccal mass, and at the apex of the visceral hump passes into a highly muscular stomach, resembling the gizzard of a bird (*gizz*, fig. 110). A nearly straight intestine passes from the muscular stomach to the anus, near which it develops a small caecum. In other Siphonopods the oesophagus is usually narrower (fig. 106, *oe*), and the muscular stomach more capacious (fig. 106, *v*), whilst a very important feature in the alimentary tract is formed by the caecum. In all but *Nautilus* the caecum lies near the stomach, and may be very capacious—much larger than the stomach in *Loligo vulgaris*—or elongated into a spiral coil, as in fig. 106, *e*. The simple



FIG. 106.—Alimentary canal of *Loligo sagittata* (from Gegenbaur). The buccal mass is omitted. *oe*, oesophagus; *s*, the stomach opened longitudinally; *x*, probe passed through the pylorus; *c*, commencement of the caecum; *sp*, its spiral portion; *i*, intestine; *a*, ink-bag; *b*, its opening into the rectum.

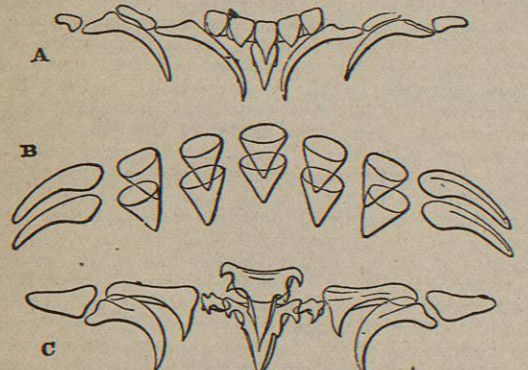


FIG. 107.—Lingual dentition of Siphonopoda. A, A single row of lingual teeth of *Nautilus pompilius* (after Kieferstein). B, Two rows of lingual teeth of *Sepia officinalis* (after Troschel). C, Lingual teeth of *Eledone cirrhosa* (after Löwen).

U-shaped flexure of the alimentary tract as seen in fig. 106, and in fig. 110, is the only important one which it exhibits in the Cephalopoda,—the Pteropoda (except the *Limacinida*) agreeing with the Siphonopoda in this sim-

ilarity in consequence of their visceral hump being untwisted. The acini of the large liver of *Nautilus* are compacted into a solid reddish-brown mass by a firm membrane, as also is the case in the *Dibranchiata*. The liver has four paired lobes in *Nautilus*, which open by two bile-ducts into the alimentary canal at the commencement of the intestine. The bile-ducts unite before entering the intestine. In *Dibranchiata* the two large lobes of the liver are placed antero-dorsally (beneath the shell in *Decapoda*), and the bile-ducts open into the caecum. Upon the bile-ducts in *Dibranchiata* are developed yellowish glandular diverticula, which are known as "pancreas," though neither physiologically nor morphologically is there any ground for considering either the so-called liver or the so-called pancreas as strictly equivalent to the glands so denominated in the Vertebrata. In *Nautilus* the equivalents of the pancreatic diverticula of the *Dibranchs* can be traced upon the relatively shorter bile-ducts.

Salivary Glands are not developed in *Nautilus* unless a pair of glandular masses lying on the buccal cavity are to be considered as such. In the *Dibranchs*, on the contrary, one (*Sepia*, *Loligo*) or two pairs of large salivary glands are present, an anterior and a posterior (*Octopus*, *Eledone*, *Onychoteuthis*). Each pair of salivary glands has its paired ducts united to form a single duct, which runs forward from the glands and opens into the buccal cavity

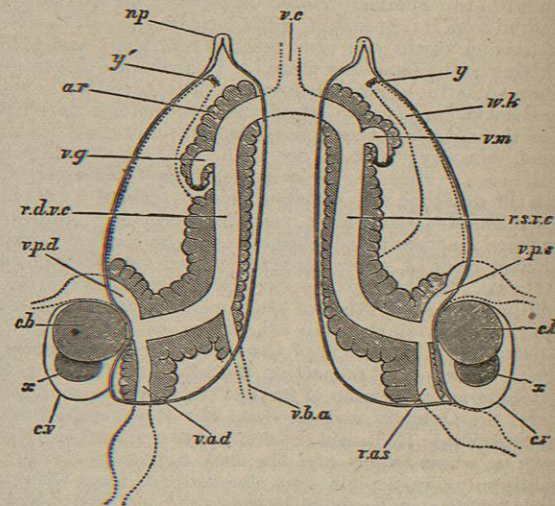


FIG. 108.—Diagram of the nephridial sacs, and the veins which run through them, in *Sepia officinalis* (after Vigilius). The nephridial sacs are supposed to have their upper walls removed. *v.c.*, vena cava; *r.d.v.c.*, right descending branch of the same; *r.s.v.c.*, left descending branch of the same; *v.a.a.*, vein from the ink-bag; *v.m.*, mesenteric vein; *v.g.*, genital vein; *v.a.d.*, right abdominal vein; *v.a.s.*, left abdominal vein; *v.p.d.*, right pallial vein; *v.p.s.*, left pallial vein; *c.b.*, branchial heart; *x*, appendage of the same; *c.s.*, capsule of the branchial heart; *ap*, external aperture of the right nephridial sac; *s*, reno-pericardial orifice placing the left renal sac or nephridium in communication with the visco-pericardial sac, the course of which below the nephridial sac is indicated by dotted lines; *y*, the similar orifice of the right side; *a.r.*, glandular renal outgrowths; *v.k.*, visco-pericardial sac (dotted outline).

near the radula. The anterior pair of glands when present lie in the head near the buccal mass, the posterior pair lie much farther back beneath the liver, at the sides of the oesophagus. It is the posterior pair which alone are present in *Sepia* and *Loligo*. The ink-bag is to be considered as an appendage of the rectum. It is not developed in *Nautilus*, nor in the Pteropoda; in all *Dibranchiata* (even in the fossil *Belemnites*) it is present (fig. 106, *a*; fig. 103, *t*), and has been observed to develop as a diverticulum of the rectum, with spirally plaited walls which very early secrete a black pigment. The spiral plaitings of the walls diminish

in relative size as the volume of the sac increases. Its outer surface acquires a metallic iridescence similar to that of the integuments of many fishes. The opening of the ink-sac is in the adult sometimes distinct from but near to

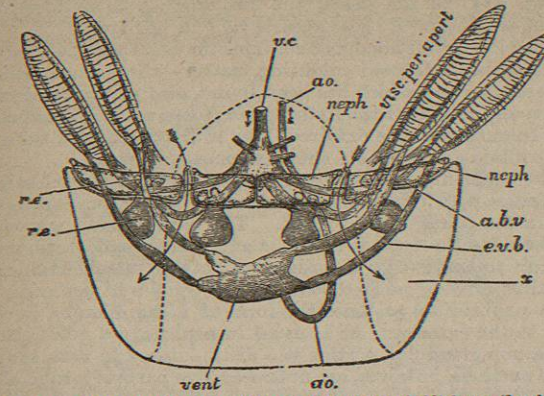


FIG. 109.—Diagram to show the relations of the four nephridial sacs, the visco-pericardial sac, and the heart and large vessels in *Nautilus* (drawn by A. G. Bourne). *neph*, *neph*, on the right side point to the two nephridia of that side (the two of the opposite side are not lettered).—each is seen to have an independent aperture; *x* is the visco-pericardial sac, the dotted line indicating its backward extension; *visc.per.apert* marks an arrow introduced into the right aperture of the visco-pericardial sac; *r.a.*, *r.e.*, point to the glandular enlarged walls of the afferent branchial vessels,—two small glandular bodies of the kind are seen to project into each nephridial sac, whilst a larger body of the same kind depends from each of the four branchial afferent vessels into the visco-pericardial sac; *v.c.*, vena cava; *vent*, ventricle of the heart; *ao.*, cephalic aorta (the small abdominal aorta not drawn); *a.b.v.*, afferent branchial vessel; *e.v.b.*, efferent branchial vessel.

the anus (*Sepia*); in other cases it opens into the rectum near the anus. The ink-bag of *Dibranch Siphonopoda* is possibly to be identified with the adrectal (purpuriparous) gland of some *Gastropoda*.

**Calom, Blood-vascular System, and Excretory Organs.**—*Nautilus* and the other Siphonopoda conform to the

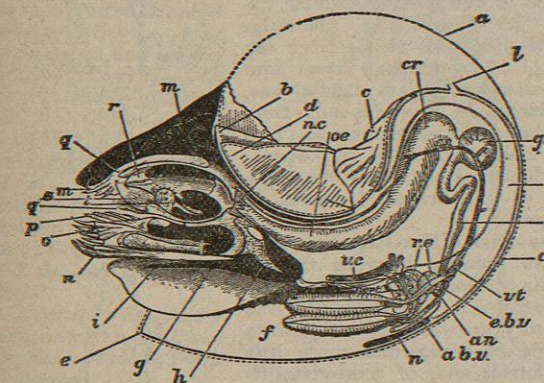


FIG. 110.—Diagram representing a vertical approximately median antero-posterior section of *Nautilus pompilius* (from a drawing by A. G. Bourne). The parts which are quite black are the cut muscular surfaces of the foot and buccal mass. *a*, the shell; *b*, the nuchal plate identical with the nuchal cartilage of *Sepia* (see fig. 90, *b*); *c*, the integument covering the visceral hump; *d*, the mantle flap or skirt in the dorsal region where it rests against the coil of the shell; *e*, the inferior margin of the mantle-skirt resting on the lip of the shell represented by the dotted line; *f*, the pallial chamber with two of the four gills; *g*, the vertically cut median portion of the mid-foot (siphon); *h*, the capito-pedal cartilage (see fig. 110); *i*, the valve of the siphon; *j*, the siphonular pedicle (cut short); *m*, the hood or dorsal enlargement of the annular lobe of the fore-foot; *n*, tentacles of the annular lobe; *o*, tentacles of the inner inferior lobe; *q*, buccal membrane; *r*, upper jaw or beak; *s*, lower jaw or beak; *t*, lingual ribbon; *z*, the visco-pericardial sac; *a.e.*, nerve-collar; *oe*, oesophagus; *cr*, crop; *gizz*, gizzard; *int*, intestine; *an*, anus; *nd*, nidamental gland; *apert*, aperture of a nephridial sac; *r.s.*, renal glandular masses on the walls of the afferent branchial veins (see fig. 109); *a.b.v.*, afferent branchial vessel; *e.v.b.*, efferent branchial vessel; *vt*, ventricle of the heart.

general Molluscan characters in regard to these organs. Whilst the general body-cavity or coelom forms a lacunar

blood-system or series of narrow spaces, connected with the trunks of a well-developed vascular system, that part of the original coelom surrounding the heart and known as the Molluscan pericardium becomes shut off from this general blood-lymph system, and communicates, directly in *Nautilus*, in the rest through the nephridia, with the exterior. In the Siphonopoda this specialized pericardial cavity is particularly large, and has been recognized as distinct from the blood-carrying spaces, even by anatomists who have not considered the pericardial space of other Mollusca to be thus isolated. The enlarged pericardium, which may even take the form of a pair of sacs, has been variously named, but is best known as the visco-pericardial sac or chamber. In *Nautilus* this sac occupies the whole of the postero-dorsal surface and a part of the antero-dorsal (see fig. 110, *x*), investing the genital and other viscera which lie below it, and having the ventricle of the heart suspended in it. Certain membranes forming incomplete septa, and a curious muscular band—the pallio-cardiac band—traverse the sac. The four branchial afferent veins, which in traversing the walls of the four nephridial sacs give off, as it were, glandular diverticula into those sacs, also give off at the same points four much larger glandular

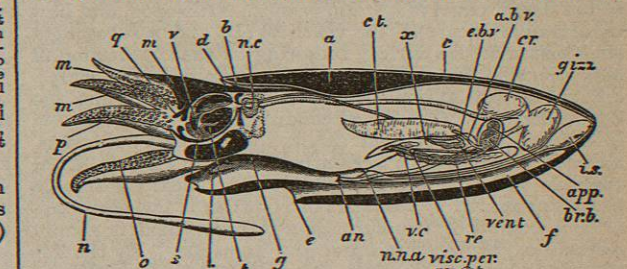


FIG. 111.—Diagram representing a vertical approximately median antero-posterior section of *Sepia officinalis* (from a drawing by A. G. Bourne). The lettering corresponds with that of fig. 110, with which this drawing is intended to be compared. *a*, shell (here enclosed by a growth of the mantle); *b*, the nuchal plate (here a cartilage); *c*, the reference line should be continued through the black area representing the shell to the outline below it; the integument covering the visceral hump; *d*, the reflected portion of the mantle-skirt forming the sac which encloses the shell; *e*, the inferior margin of the mantle-skirt (mouth of the pallial chamber); *f*, the pallial chamber; *g*, the vertically cut median portion of the mid-foot (siphon); *h*, the valve of the siphon; *m*, the two upper lobes of the fore-foot; *n*, the long prehensile arms of the same; *o*, the fifth or lowermost lobe of the fore-foot; *p*, the third lobe of the fore-foot; *q*, the buccal membrane; *r*, the upper jaw or beak; *s*, the lower jaw or beak; *t*, the lingual ribbon; *z*, the visco-pericardial sac; *a.e.*, the nerve-collar; *cr*, the crop; *gizz*, the gizzard; *int*, intestine; *an*, the anus; *c.l.*, the left ctenidium or gill-plume; *vent*, ventricle of the heart; *a.b.v.*, afferent branchial vessel; *e.v.b.*, efferent branchial vessel; *r.s.*, renal glandular mass; *n.a.a.*, left nephridial aperture; *visc.per.apert*, visco-pericardial aperture (see fig. 108); *br.b.*, branchial heart; *app.*, appendage of the same; *i.s.*, ink-bag.

masses, which hang freely into the visco-pericardial chamber (fig. 109, *r.e.*). In *Nautilus* the visco-pericardial sac opens to the exterior directly by a pair of apertures, one placed close to the right and one close to the left posterior nephridial aperture (fig. 101, *visc.per.*). This direct opening of the pericardial sac to the exterior is an exception to what occurs in all other Molluscs. In all other Molluscs the pericardial sac opens into the nephridia, and through them or the one nephridium to the exterior. In *Nautilus* there is no opening from the visco-pericardial sac into the nephridia. Therefore the external pore of the visco-pericardial sac may possibly be regarded as a shifting of the reno-pericardial orifice from the actual wall of the nephridial sac to a position alongside of its orifice. Parallel cases of such shifting are seen in the varying position of the orifice of the ink-bag in *Dibranchiata*, and in the orifice of the genital ducts of Mollusca, which in some few cases (e.g., *Spondylus*) open into the nephridia, whilst in other cases they open close by the side of the nephridia on the surface of the body. The visco-pericardial sac of the



Dibranchs is very large also, and extends into the dorsal region. It varies in shape—that is to say, in the extensions of its area right and left between the various viscera—in different genera, but in the Decapods is largest. In an extension of this chamber is placed the ovary of *Sepia*, whilst the ventricle of the heart and the branchial hearts and their appendages also lie in it. It is probable that water is drawn into this chamber through the nephridia, since sand and other foreign matters are found in it. In all it opens into the pair of nephridial sacs by an orifice on the wall of each, not far from the external orifice (fig. 108, *y, y'*). There does not seem any room for doubting that each orifice corresponds to the reno-pericardial orifice which we have seen in the Gastropoda, and shall find again in the Lamellibranchia. The single tube-like nephridium and the pericardium of the Pteropoda also communicate by an aperture.

The circulatory organs, blood-vessels, and blood of Nautilus do not differ greatly from those of Gastropoda. The ventricle of the heart is a four-cornered body, receiving a dilated branchial efferent vessel (auricle) at each corner (fig. 109). It gives off a cephalic aorta anteriorly, and a smaller abdominal aorta posteriorly. The diagram, fig. 105, serves to show how this simple form of heart is related to the dorsal vessel of a worm or of an Arthropod, and how by a simple flexure of the ventricle (D) and a subsequent suppression of one auricle, following on the suppression of one branchia, one may obtain the form of heart characteristic of the Anisopleurous Gastropoda (excepting the Zygobranchia). The flexed condition of the heart is seen in *Octopus*, and is to some extent approached by *Nautilus*, the median vessels not presenting that perfect parallelism which is shown in the figure (B). The most remarkable feature presented by the heart of *Nautilus* is the possession of four instead of two auricles, a feature which is simply related to the metamerism of the branchia. By the left side of the heart of *Nautilus*, attached to it by a membrane, and hanging loosely in the visco-pericardial chamber, is the pyriform sac of Owen. This has recently been shown to be the rudimentary left oviduct or sperm-duct, as the case may be (Lankester and Bourne, 37), the functional right ovi-sac and its duct being attached by a membrane to the opposite side of the heart.

The cephalic and abdominal aortæ of *Nautilus* appear, after running to the anterior and posterior extremes of the animal respectively, to open into sinus-like spaces surrounding the viscera, muscular masses, &c. These spaces are not large, but confined and shallow. Capillaries are stated to occur in the integument. In the Dibranchs the arterial system is very much more complete; it appears in some cases to end in irregular lacunæ or sinuses, in other cases in true capillaries which lead on into veins. An investigation of these capillaries in the light of modern histological knowledge is much needed. From the sinuses and capillaries the veins take origin, collecting into a large median trunk (the vena cava), which in the Dibranchs as well as in *Nautilus* has a ventral (postero-ventral) position, and runs parallel to the long axis of the animal. In *Nautilus* this vena cava gives off at the level of the gills four branchial advehent veins (fig. 109, *v.c.*), which pass into the four gills without dilating. In the Dibranchs at a similar position the vena cava gives off a right and a left branchial advehent vein (fig. 108, *r.s.v.c, r.d.v.c.*), each of which, traversing the wall of the corresponding nephridial sac and receiving additional factors (fig. 108, *v.g, v.p.d, v.a.d, v.b.a.*), dilates at the base of the corresponding branchial plume, forming there a pulsating sac—the branchial heart (fig. 104, *x*; and fig. 108, *c.b.*). Attached to each branchial heart is a curious glandular body, which may possibly be related to the larger masses (*r.e* in fig. 109) which depend into the visco-pericardial cavity from the branchial advehent veins

of *Nautilus*. From the dilated branchial heart the branchial advehent vessel proceeds, running up the ad-pallial face of the gill-plume (*vi, v.c'*, fig. 104). From each gill-plume the blood passes by the branchial efferent vessels (*v'*, fig. 104) to the heart, the two auricles being formed by the dilatation of these vessels (*v, v* in fig. 104).

The blood of Siphonopoda contains the usual amœboid corpuscles, and a diffused colouring matter—the hæmocyarin of Fredericque—which has been found also in the blood of *Helix*, and in that of the Arthropods *Homarus* and *Limulus*. It is colourless in the oxidized, blue in the deoxidized state, and contains copper as a chemical constituent.

The nephridial sacs and renal glandular tissue are closely connected with the branchial advehent vessels in *Nautilus* and in the other Siphonopoda. The arrangement is such as to render the typical relations and form of a nephridium difficult to trace. In accordance with the metamerism of *Nautilus* already noticed, there are two pairs of nephridia. Each nephridium assumes the form of a sac opening by a pore to the exterior. As is usual in nephridia, a glandular and a non-glandular portion are distinguished in each sac; these portions, however, are not successive parts of a tube, as happens in other cases, but they are localized areas of the wall of the sac. The glandular renal tissue is, in fact, confined to a tract extending along that part of the sac's wall which immediately invests the great branchial advehent vein. The vein in this region gives off directly from its wall a complete herbage of little venules, which branch and anastomose with one another, and are clothed by the glandular epithelium of the nephridial sac. The secretion is accumulated in the sac and passed by its aperture to the exterior. Probably the nitrogenous excretory product is very rapidly discharged; in *Nautilus* a pink-coloured powder is found accumulated in the nephridial sacs, consisting of calcium phosphate. The presence of this phosphatic calculus by no means proves that such was the sole excretion of the renal glandular tissue. In *Nautilus* a glandular growth like that rising from the wall of the branchial vessel into its corresponding nephridial sac, but larger in size, depends from each branchial advehent vessel into the visco-pericardial sac,—probably identical with the "appendage" of the branchial hearts of Dibranchs.

The chief difference, other than that of number between the nephridia of the Dibranchs and those of *Nautilus*, is the absence of the accessory growths depending into the visco-pericardial space just mentioned, and, of more importance, the presence in the former of a pore leading from the nephridial sac into the visco-pericardial sac (*y, y'* in fig. 108). The external orifices of the nephridia are also more prominent in Dibranchs than in *Nautilus*, being raised on papillæ (*rep* in fig. 108; *r* in fig. 103). In *Sepia*, according to Vigelius (38), the two nephridia give off each a diverticulum dorsalwards, which unites with its fellows and forms a great median renal chamber, lying between the ventral portions

of the nephridia and the visco-pericardial chamber. In *Loligo* the fusion

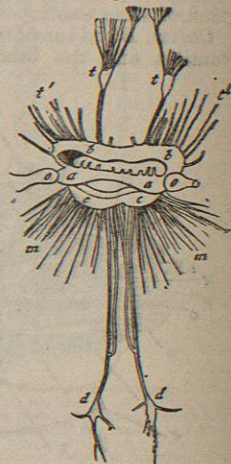


FIG. 112.—Nervous system of *Nautilus pompilius* (from Gegenbaur, after Owen). *t*, tentacles; *f*, nerves to the tentacles of the outer or annular lobe; *b*, pedal ganglion; *c*, cerebral ganglion; *e*, pleuro-visceral ganglion; *d*, genital ganglion placed on the course of the large visceral nerve, just before it gives off its branchial and its osphradial branches; *m*, nerves from the pleural ganglion to the mantle-skirt.

of the nephridia and the visco-pericardial chamber. In *Loligo* the fusion

of the two nephridia to form one sac is still more obvious, since the ventral portions are united. In *Octopus* the nephridia are quite separate.

Tegumental pores have not been described in *Nautilus*, but exist in Dibranchiata, and have been (probably erroneously, but further investigation is needed) supposed to introduce water into the vascular system. A pair of

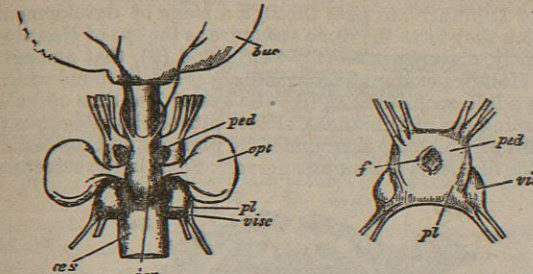


Fig. 113.

FIGS. 113, 114.—Nerve-centres of *Octopus*. Figure 113 gives a view from the dorsal aspect, figure 114 one from the ventral aspect. *buc*, the buccal mass; *ped*, pedal ganglion; *opt*, optic ganglion; *cer*, cerebral ganglion; *pl*, pleural ganglion; *visc*, visceral ganglion; *es*, oesophagus; *f*, foramen in the nerve-mass formed by pedal, pleural, and visceral ganglion-pairs, traversed by a blood-vessel.

such pores leading into sub-tegumental spaces of considerable area, the nature of which is imperfectly known, exist on the back of the head in *Philonexis*, *Tremoctopus*, and *Argonauta*. At the base of the arms and mouth four such pores are found in *Histioteuthis* and *Ommastrephes*, six in *Sepia*, *Loligo*, *Onychoteuthis*. Lastly, a pair of such pores are found in the Decapoda at the base of the long arms, leading into an extensive sub-tegumental pouch on each side of the head into which the long arms can be, and usually are, withdrawn. In *Sepia*, *Sepiolo*, and *Rosalia* the whole arm is coiled up in these sacs; in *Loligo* only a part of it is so; in *Histioteuthis*, *Ommastrephes*, and *Onychoteuthis*, the sacs are quite small and do not admit the arms.

**Nervous System.**—*Nautilus*, like the other Cephalopoda (e.g., *Pneumodermon*, fig. 87; *Octopus*, fig. 113), exhibits a great concentration of the typical Molluscan ganglia, as shown in fig. 112. The ganglia take on a band-like form, and are but little differentiated from their commissures and connectives,—an archaic condition reminding us of *Chiton*. The special optic outgrowth of the cerebral ganglion, the optic ganglion (fig. 112, *o*), is characteristic of the big-eyed Siphonopoda. The cerebral ganglion-pair (*a*) lying above the oesophagus

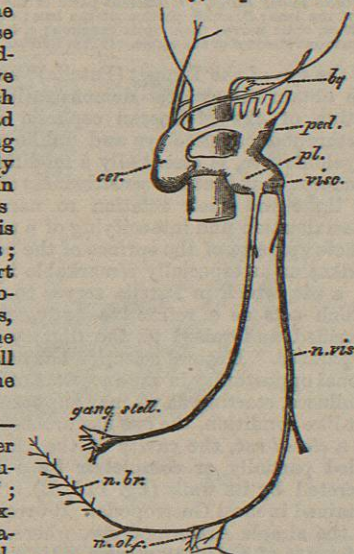


FIG. 114.—Lateral view of the nervous centres and nerves of *Octopus vulgaris* (from a drawing by A. G. Bourne). *by*, buccal ganglion; *ped*, pedal ganglion; *pl*, pleural ganglion; *visc*, visceral region of the pleuro-visceral ganglion; *gang. stell.*, the right stellate ganglion of the mantle connected by a nerve to the pleural portion; *n. visc.*, the right visceral nerve; *n. olf.*, its (probably) olfactory branches; *n. br.*, its branchial branches.

is connected with two sub-oesophageal ganglion-pairs of band-like form. The anterior of these is the pedal *b, b*, and supplies the fore-foot with nerves *t, t*, as also the mid-foot (siphon). The hinder band is the visceral and pleural pair fused (compare fig. 112 with fig. 87, and especially with the typical Euthyneurous nervous system of *Limnaeus*, fig. 22); from its pleural portion nerves pass to the mantle; from its visceral portion nerves to the branchia and genital ganglion (*d* in fig. 112), and in immediate connexion with the latter is a nerve to the osphradium or olfactory papilla. No buccal ganglia have been observed in *Nautilus*, nor has an enteric nervous system been described in this animal, though both attain a special development in the Dibranchiata. The figures (114 and 115) representing the nerve-centres of *Octopus* serve to exhibit the disposition of these parts in the Dibranchiata. The ganglia are more distinctly swollen than in *Nautilus*. In *Octopus* an infra-buccal ganglion-pair are present corresponding to the buccal ganglion-pair of Gastropoda. In Decapoda a supra-buccal ganglion-pair connected with these are also developed. Instead of the numerous radiating pallial nerves of *Nautilus*, we have in the Dibranchiata on each side (right and left) a large pleural nerve passing from the pleural portion of the pleuro-visceral ganglion to the mantle, where it enlarges to form the stellate ganglion. From each stellate ganglion nerves radiate to supply the powerful muscles of the mantle-skirt. The nerves from the visceral portion of the pleuro-visceral ganglion have the same course as in *Nautilus*, but no osphradial papilla is present. An enteric nervous system is richly developed in the Dibranchiata, connected with the somatic nervous centres through the buccal ganglia, as in the Arthropoda through the stomato-gastric ganglia, and anastomosing with deep branches of the visceral nerves of the visco-pericardial ganglion-pair. It has been especially described by Hancock (39) in *Ommastrephes*. Upon the stomach it forms a single large and readily-detected gastric ganglion. It is questionable as to how far this and the "caval ganglion" formed in some Decapoda by branches of the visceral nerves which accompany the vena cava are to be considered as the equivalents of the "abdominal ganglion," which in a typical Gastropod nervous system lies in the middle of the visceral nerve-loop or commissure, having the right and left visceral ganglia on either side of it, separated by a greater or less length of visceral nerve-cord (see figs. 20, 21, 22). There can be little doubt that the enteric nervous system is much more developed in the Dibranchiata than in other Mollusca, and that it effects a fusion with the typical "visceral" cords more extensive than obtains even in Gastropoda, where such a fusion no doubt must also be admitted.

**Special Sense-Organs.**—*Nautilus* possesses a pair of osphradial papillæ (fig. 101, *olf*) corresponding in position and innervation to Spengel's organ placed at the base of the ctenidia (branchia) in all classes of Mollusca. This organ has not been detected in other Siphonopoda. In Pteropoda it is well developed as a single ciliated pit, although the ctenidia are in that group aborted (fig. 87, *Osp.*). *Nautilus* possesses other olfactory organs in the region of the head. Just below the eye is a small triangular process (not seen in our figures), having the structure of a shortened and highly-modified tentacle and sheath. By Valenciennes, who is followed by Keferstein, this is regarded as an olfactory organ. The large nerve which runs to this organ originates from the point of juncture of the pedal with the optic ganglion. The lamelliform organ upon the inner inferior tentacular lobe of *Nautilus* is possibly also olfactory in function. In Dibranchs behind the eye is a pit or open canal supplied by a nerve corresponding in origin to the olfactory nerve of *Nautilus* above mentioned.