respiratory organs. Most aquatic molluscs, however, possess gills or ctenidia, the history of which, like that of the organs just considered, shows how close a relationship exists between respiration and ciliary feeding. Respiratory surfaces must be kept clean, and a flow of water maintained over them; needs that are often met in animals by the secretion of mucus, and by the development of cilia to maintain movement over the surface. Clearly this is precisely the situation that also best lends itself to the collection and transport of food particles, but unfortunately we often lack the evidence to determine whether or not events have followed this course. In the molluscs, however, we have a group of animals in which the close interlocking of respiratory and nutritional requirements is particularly well shown, and in which there is evidence that enables us to trace something of the history of the organs concerned.

As already noted, we can regard the body of a mollusc as composed of two components: a ventral portion (the head and foot), in which the activity is predominantly muscular, and a dorsal portion (the visceral hump), in which ciliary action and mucus secretion predominate (Fig. 11–8). The surface of the visceral hump extends into an overhanging fold, the mantle, which secretes the shell, and which encloses between itself and the visceral hump a space called the mantle cavity. This cavity is the centre of external respiration, for protected within it are the gills or ctenidia. It has been generally assumed that, in the primitive state, there were two of these, but some doubt now attaches to this since the discovery of *Neopilina*, with its five pairs of ctenidia (Fig. 11–9). However, even if the earliest molluscs did have serially repeated ctenidia (and we cannot be sure that this was so), these organs must have been reduced to a single pair at a very early stage of molluscan history. Their condition at that stage was the basis for the later history of the respiratory organs in the group, and we can develop our analysis from that point.

The structure of the early molluscan ctenidium, which can be deduced from its condition in primitive archaeogastropod prosobranchs, may be thought of as consisting of a longitudinal axis from which triangular filaments were given off alternately on its two sides (cf. Fig. 11–8). Essentially it was a hollow outgrowth of the body, supplied with branchial muscles, nerves, and blood vessels; the blood travelled up and down the axis in a dorsal (afferent) and ventral (efferent) vessel, and flowed from one to the other of these through the filaments. If we assume that only two ctenidia were present, oxygenated blood would have flowed from them into a single pair of auricles, and so into the ventricle for general distribution (Fig. 11–8A). The condition in *Neopilina* could then have been derived from this by secondary increase in number (Fig. 11–8B).

The functional relationships of this system, so simple in principle, are subtly adapted in present-day molluscs to ensure the maximum efficiency of respiratory exchange. The protection of the filaments within the mantle cavity makes ventilation the more essential, and this is secured by lateral cilia on the face of each filament. These cilia, which draw the respiratory stream of water into the mantle cavity, lie near the efferent limb of the circulation. Here they create a current of water that is directed upwards and inwards, in the opposite direction to the flow of the blood. This arrangement therefore involves counterflow; its effect is to increase the efficiency of gaseous exchange between the blood and the water. The gill filaments must be supported against the flow of water, and chitinous supporting rods provide for this. Further, the surface of the filaments needs to be kept clear of foreign material which

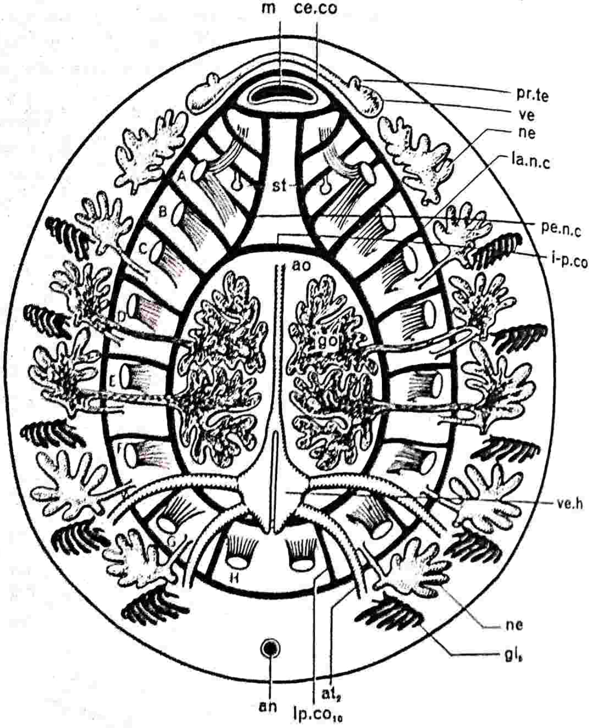
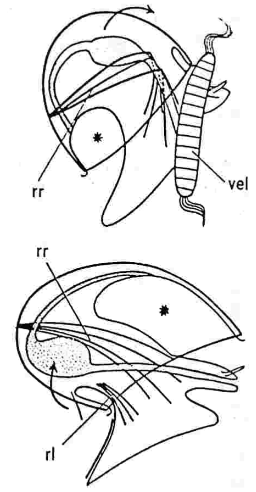


Fig. 11-9. Diagram of the relations between the 'segmented' organ systems in *Neopilina*. The gill nerves, the gill vessels, and many smaller muscles are also repeated, but are not included in the drawing. *A–H*, foot retractor muscles; *an*, anus; *ao*, aorta; at_2, 2nd atrium (auricle) of heart; *ce.co*, cerebral commissure; gi_5, 5th gill; *i-p.co*, interpedal commissure; *la.n.c*, lateral nerve cord; $lp.co_{10}$, 10th latero-pedal connective; *m*, mouth; *ne*, excretory organs; *pe.n.c*, pedal nerve cord; *pr.te*, preoral tentacle; *st*, statocyst; *ve*, velum; *ve.h*, ventricle of heart. From Lemche and Wingstrand, 1959. *Galathea Rep.*, vol. 3, 9–71. Danish Science Press, Copenhagen.

will tend to settle on them from the water, and in adaptation to this requirement there are frontal and abfrontal cilia situated on the afferent and efferent edges of the filaments (cf. Fig. 11–10, p. 268). These sweep material towards the central axis, where it is removed by a ciliary current along the afferent surface.

As Yonge points out, these arrangements will not in themselves ensure the protection of the ctenidia from sediment, particularly as these organs increase in size, for the ciliary currents may prove too weak to remove heavy deposits of material. It is probably because of this that two other paired structures, the osphradia and the hypobranchial glands, are present in the primitive mantle cavity; these structures, with the ctenidia, form a functionally associated system which can be called the pallial complex. The osphriada, which are universally present in the mantle cavities of aquatic gastropods, irrespective of their habitat or the nature of their food, are receptors, consisting of raised areas of epithelia that are rich in mucus, and in ciliated and sensory cells. They test the quality of the incoming water, perhaps by chemical sensitivity, for they are extremely large in carnivores such as *Buccinum*. Perhaps they also estimate through mechanoreception the amount of sediment entering the mantle cavity. The hypobranchial glands (Fig. 11–8), present in the gastropods and in some bivalves, are folds of mucus-secreting epithelium lying on the roof of the mantle cavity. They vary in size and complexity, apparently in relation to the amount of sediment that is likely to enter the mantle cavity in the particular habitat favoured by the species; their function seems to be to aid the removal of the sediment by consolidating it into larger masses. Their absence from cephalopods is thought to be correlated with the exceptionally powerful currents in those animals, which remove the need for such consolidation.

Fig. 11-10. The process of torsion in a prosobranch veliger larva, showing the position of the asymmetrically developed shell muscle. Asterisk indicates position of the mantle cavity. *rl*, left retractor muscles; *rr*, right retractor muscles; *vel*, velum. From Morton and Yonge, 1964. *op. cit.*



Not surprisingly, the highly organized respiratory systems of the pallial cavity reflect a great deal of adaptive evolution in relation to changes in the habits and organization of the members of this highly diversified phylum. This is already apparent in the primitive chitons. In these animals the number of gills is secondarily increased in correlation with the forward extension of the mantle cavity, and the osphradia lie posteriorly, where the outgoing current of water leaves. Within the gastropods the respiratory process has been profoundly affected by two characteristic features of the group. The first of these is the asymmetrical coiling of the visceral mass, which is an adaptation to secure a more compact arrangement of the internal organs. The second is torsion, a process that takes place early in development (Sec. 19–2), quite independently of coiling, and which brings the mantle cavity of the veliger larva from its primitively posterior position round to the anterior end (Fig. 11–10).

The significance of torsion for the respiratory process is that the visceral and pallial organs are rotated through 180°, so that the mantle cavity is now in more sensitive touch with its surroundings. Additional advantages are that the forward movement of the animal will now reinforce the incurrent stream instead of opposing it, while the gills receive water direct from in front of the animal, and the osphradium is in the anterior position that is suitable for a major receptor organ. On the other hand, a serious problem arises in disposing of the excurrent water stream with its contained faeces. It would be unsatisfactory for these to be discharged anteriorly into the path of the animal, and so, as a primitive solution to this problem, openings are formed in the shell to direct this stream away from the incurrent one. *Haliotis* is an example of this.

More advanced solutions to the problem are influenced by the fact that asymmetrical coiling produces on one side of the mantle cavity a compression that favours reduction of the corresponding part of the pallial complex. Thus the right ctenidium and its associated auricle are lost, the original two rows of gill filaments of the ctenidium are reduced to one, and the axis of the ctenidium now becomes attached along its whole length to the wall of the mantle cavity. With the water current entering on the left side of the head and leaving on the right side, close to where the rectal opening has moved, an efficient respiratory circulation is ensured for most of the prosobranchs, without the need to have openings in the shell. Only the Order Archaeogastropoda retain the primitve symmetry of paired gills and auricles, together with the shell perforations. The Subclass Opisthobranchia shows varying degrees of detorsion, accompanied by reduction of the shell and mantle, until in the Order Nudibranchia a secondary symmetry is achieved with loss of the shell, mantle cavity and ctenidium. Respiration now takes place through the body surface, or through secondarily developed gills.

Many prosobranchs, particularly in the tropics, have become terrestrial, and have converted their mantle cavity into a lung for aerial respiration, its vascularized epithelium forming the respiratory surface. A similar adaptation is found in the Subclass Pulmonata, which probably evolved from prosobranchs. The pulmonate lung usually retains its anterior position, but it has only a single external opening, the pneumostome, which can be opened and closed. Because of this change of function, the hypobranchial gland is lost, as would be expected from what we have said above regarding its supposed role in the removal of small particles, while the osphradium is usually outside the mantle cavity. The respiratory surface is now the lining of that cavity, and, as in other types of lung, its area is greatly increased by ridges that are richly supplied with blood vessels. These ridges are said to increase the respiratory surface of air-breathing snails by as much as two or three times.

We are accustomed to regard lungs as being organs that require ventilation if they are to function satisfactorily, and this is obviously true of vertebrates. Probably because of this, it has been thought that the pulmonate lung also requires ventilation, but Krogh showed that this was not necessarily so. In slugs (*Arion*) of about 10 g weight, with a pneumostome of 4–6 mm diameter, and with a respiratory surface of 6–7 cm², a pressure difference of only 2 mm will ensure diffusion of atmospheric oxygen to the wall of the mantle cavity; even larger animals could therefore be satisfactorily supplied in this way. This conclusion applies, of course, to animals with a relatively low metabolic rate; ventilation of the lungs certainly becomes necessary with increasing oxygen consumption, and with increase in size of the body.

In any case, ventilation movements do occur in *Helix*, and have been demonstrated by recording pressure changes in the lung (Fig. 11–11). When the pneumostome is open, as it may be when the animal is crawling slowly, the pressure remains unchanged and respiration depends upon diffusion. When the penumostome is closed the pressure begins to rise, reaching a maximum in 4–5 sec, and then falling again. These pressure changes, which are brought about by muscular movements of the floor of the lung, result in air movement and hence redistribution of oxygen within the lung cavity; at maximal pressure, they probably facilitate the passage of oxygen into the blood stream.

The pulmonate lung is by no means purely a terrestrial respiratory organ, nor is it restricted to aerial respiration. We shall deal elsewhere with some of the factors that operate as animals of different phyla move to and fro between water and air in the course of their evolutionary history. It will be sufficient here to note some examples of the varied respiratory potentialities of this organ. The siphonariid limpets are marine pulmonates that are completely aquatic in habit; the mantle cavity is filled with water, and has developed secondary pallial gills, formed by folding of the wall of the cavity. Many other examples, showing different degrees of adaptation to aquatic or amphibious habits, are provided by the fresh-water pulmonates. Thus *Lymnaea truncatula* has its lung filled with air; this animal, living an essentially aerial life in marshy habitats, plays a role of no small economic importance in

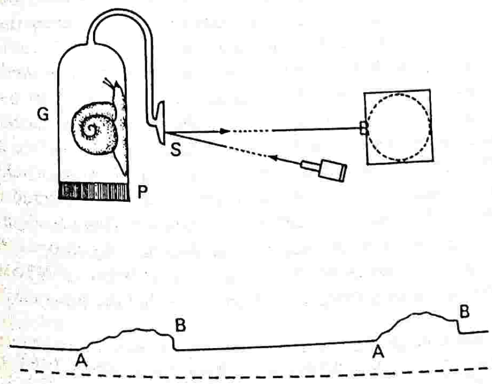


Fig. 11-11. *Above*, measurement of respiratory movements in *Helix*. The snail is closed in a vessel (G) connected to a Marey tambour (S). A small mirror on the tambour reflects a beam of light on a photokymograph. Pressure changes inside the vessel will be recorded through movements of the mirror. *Below*, modifications of the lung in *H. pomatia* during normal respiration. At A the pneumostome is closed; at B it is opened. From Ghiretti, 1966. In *Physiology of the Mollusca*, vol. 2. (Wilbur and Yonge, eds.). Academic Press, New York.

providing an intermediate host for the sheep liver fluke, *Fasciola hepatica*. At the other extreme is *L. abyssicola*, which lives in deep water without coming to the surface, while *L. stagnalis* is intermediate in habit, living in water, but returning to the surface to refill its lung with air.

Planorbis corneus resembles *Lymnaea stagnalis* in this respect, but is able to handle the situation differently because it possesses dissolved haemoglobin in its blood; a good example of the ecological implications of the presence or absence of the pigment. *Planorbis* has a secondary gill, and probably respires through its body surface as well, but it relies largely upon its air-filled lung, functioning in conjunction with the vascular haemoglobin. This pigment, because of its high oxygen affinity, makes the animal better able than *Lymnaea* to take up oxygen from its pulmonary cavity at lower concentrations during the later stage of the dive, for *Lymnaea* can only take it up into simple solution. As a result, *Planorbis* can exploit its oxygen store more effectively (Table 11–2), can dive deeper and for longer periods, and can feed by browsing upon the bottom deposits. The dives of *Lymnaea* are more restricted, and, in correlation with this, it feeds on submerged vegetation near the surface. Nevertheless, the ecological significance of vascular haemoglobins in molluscs is not always so clear, as is apparent in their absence from many species that live in conditions of oxygen shortage. Individuals of *Glycymeris nummaria*, for example, even though they may be living in the same environment, range widely in their content of haemoglobin, some of them lacking it altogether.

Probably, then, the haemoglobin of *Planorbis* functions mainly to facilitate the uptake of oxygen from the pulmonary store, and there is little evidence that the pigment itself serves any storage function. A puzzling feature is the reversed Bohr effect which is found at high carbon dioxide tensions, as it is in some haemocyanin-containing snails. The physiological significance of this is not clear, but it may perhaps facilitate the transport of oxygen from the lung to the tissues when the animal is withdrawn into its shell and the carbon dioxide tension rises.

It is to be expected that oxygen lack will be one factor in stimulating the return of these animals to the surface of the water, but another factor is the hydrostatic property of the lung. If the cavity of a fresh-water pulmonate is artificially filled with oxygen instead of air, the animal will return to the surface before it has exhausted the supply; it is driven by the reduction in the volume of the gas enclosed in the lung.

The most complex of all molluscan ctenidia are those found in the Bivalvia, where they are involved in the elaborately specialized ciliary feeding mechanisms of this group. In our earlier discussion we saw that the respiratory functioning of the ctenidium demands the presence on it of mucus glands and ciliated tracts that serve to keep its delicate surface clean from detritus, so that molluscs may be said to have been pre-adapted for ciliary feeding. We have observed that certain gastropods have taken advantage of this to become ciliary feeders, but it is clearly the bivalves that have most fully exploited the situation.

Table 11–2 Percentage of oxygen in pulmonary air (with standard errors) at beginning and end of dive. Number of samples in brackets. From Jones, 1961. *Comp. Biochem. Physiol.*, 4, 1–29.

Venue	Initial		Final	
	Planorbis	*Lymnaea*	*Planorbis*	*Lymnaea*
Aquarium (18)	15.2 ± 0.51	19.0 ± 0.12	7.9 ± 0.84	10.2 ± 0.53
Ditch (6)	16.2 ± 0.99	18.2 ± 0.48	4.2 ± 1.47	8.8 ± 0.81

Yonge has outlined a course of events that could have led to the elaboration of the gills of the most advanced bivalves. The first step, according to his analysis, was the overgrowth of the body by the mantle lobes, for this led to the anterior and ventral extension of the mantle cavity, and to the forward movement of the ctenidia. This movement brought them into functional association with the mouth, through the intermediation of the labial palps. Initially, while the ctenidia were primarily respiratory, they were horizontally disposed, but later the filaments bent downwards to form a V-shaped pattern. The outer filaments became fused with the mantle, and the inner ones to their partners on the other ctenidium or to the visceral mass; thus the mantle cavity became subdivided into inhalent and exhalent chambers. The filaments then became elaborated into an increasingly complex sieve by the development of interlamellar junctions, and of ciliary and tissue junctions (Sec. 10–2).

The increasing ciliation which would have accompanied these structural advances probably increased the intake of sediment with the respiratory stream, and the development of latero-frontal cilia would serve to counteract this by preventing the passage of particles between the filaments. In correlation with this the abfrontal cilia, still present in *Nucula*, would have been lost. It is obvious that all of these advances, serving primarily to improve respiratory exchange by increasing the flow of water and by elaborating the surface of the gills, would also have improved the collection of suspended food material. Indeed, the two functions were presumably elaborated side by side in this group, together also with the specialization of the sorting and transport mechanisms. At quite the opposite extreme is the situation in the anomalous and highly specialized septibranchs, where a muscular pumping organ is formed by a septum, which is perforated by ciliated pores, and which probably evolved from the fusion of modified ctenidia.

The close interrelationship between respiration and ciliary feeding, upon which we have already commented, is shown particularly clearly in studies of bivalves. Oxygen utilization can be determined by comparing the oxygen content of samples of water taken from the incurrent and the excurrent siphons. Because of technical difficulties (e.g. there is a gradient of oxygen within the exhalent current) the results are only approximate, but they certainly show a very low rate of utilization (Table 11–3). This is surprising, considering the very high rates of ventilation that are made possible in these animals by the specialized structure of the ctenidia. Galtsoff found that ventilation rates in the oyster (*Crassostrea virginica*) might be as high as 3.9 l hr^{-1} at 25°C; other procedures, based on the rate of clearance of suspensions in the water in which the animals are placed, have yielded results of the same order for *Mytilus*. The energy expended by these animals in their filtering activities must presumably be justified by the food obtained, rather than by the oxygen.

In contrast to this, there is a much higher level of oxygen utilization in gastropods and cephalopods (Table 11–3). The active life of Cephalopoda, in particular, presents a remarkable contrast with that of the sedentary forms that we have just considered (Fig. 11–12). In this class the ctenidia are contained within a mantle cavity that has become elongated in a dorso-ventral direction, and that is usually itself involved in the respiratory movements. A primitive form of the respiratory

Table 11–3 Percentage of available oxygen utilized by various molluscs. Data from various authors. From Ghiretti, 1966. *Physiology of Mollusca* (K. M. Wilbur and C. M. Yonge, eds.), vol. 2, 175–208. Academic Press, New York.

	%
Bivalvia	
Mya arenaria	3–10
Cardium tuberculatum	6–10
Solen siliqua	7–12
Gastropoda	
Haliotis tuberculatus	48–70
Doris tuberculata	64–69
Cephalopoda	
Octopus vulgaris	50–80

mechanism is found in the Tetrabranchia, represented by *Nautilus*, where the presence of two pairs of ctenidia, instead of the single pair that is so generally characteristic of molluscs, has been regarded as a secondary specialization. We have seen that this may also be true of the five pairs in *Neopilina*.

In respiration the important functional characteristic of cephalopods is the production of the respiratory current by muscular action. *Nautilus* creates this ventilation by pulsations of the funnel, which is formed, as we have seen, from two halves of the foot that are not yet fused at this primitive stage of evolution. In the Coleoidea fusion is complete, and the current correspondingly more vigorous; it is now brought about by contractions of the mantle wall as well as of the muscles of the foot and head, this being made possible by the reduction of the shell and its overgrowth by the body. Cilia are thus no longer a necessary part of the respiratory mechanism, and they are absent from the gill surface, which is greatly increased in area by primary and secondary folding of the filaments.

We have seen that the cephalopods are beautifully designed for rapid locomotion by jet propulsion. Execution of this is directly and economically linked with the respiratory mechanism. As with all such active animals, there is a demand for the most efficient possible oxygen supply; the elaborate folding of the gill surface is one contribution to this, while the presence of a respiratory pigment is another. Significantly, of all the animals that possess haemocyanin, cephalopods have the blood with the highest oxygen-carrying capacity. Yet this is not as great as capacity of the blood in many animals with haemoglobin. Representative values for the latter are 21 volumes of oxygen per 100 volumes of blood in man, 5.5–7.8% for the dogfish *Mustelus*, and 8.4% to 9.7% for *Arenicola*. Corresponding values for the haemocyanin-containing blood of molluscs are 3.1% to 4.5% for *Octopus vulgaris*, 3.8% to 4.5% for *Loligo pealei*, and 1.15% to 2.2% for *Helix pomatia*. The environment of cephalopods is rich in oxygen, and in adaptation to this the blood of *Loligo* has a low oxygen affinity, and is saturated only at relatively high oxygen tensions. There is a typical and large Bohr effect, which facilitates the release of oxygen to the active tissues. While, therefore, these animals are very sensitive to oxygen lack, under normal conditions they can achieve the very high level of activity which is so characteristic of them.

The efficiency of their respiratory mechanism is further increased by a capillary circulation in the gills, contrasting markedly with the haemocoelic type of system found in other molluscan groups. Associated with this are branchial hearts at the bases of the gills. Thus the whole system is organized for maximum efficiency of respiration within the limits of the molluscan plan of structure. The complex of respiratory, locomotor, and circulatory mechanisms in cephalopods provides an instructive example of the way in which the parts of highly specialized animals can become closely integrated, so that each contributes to the successful functioning of the others.

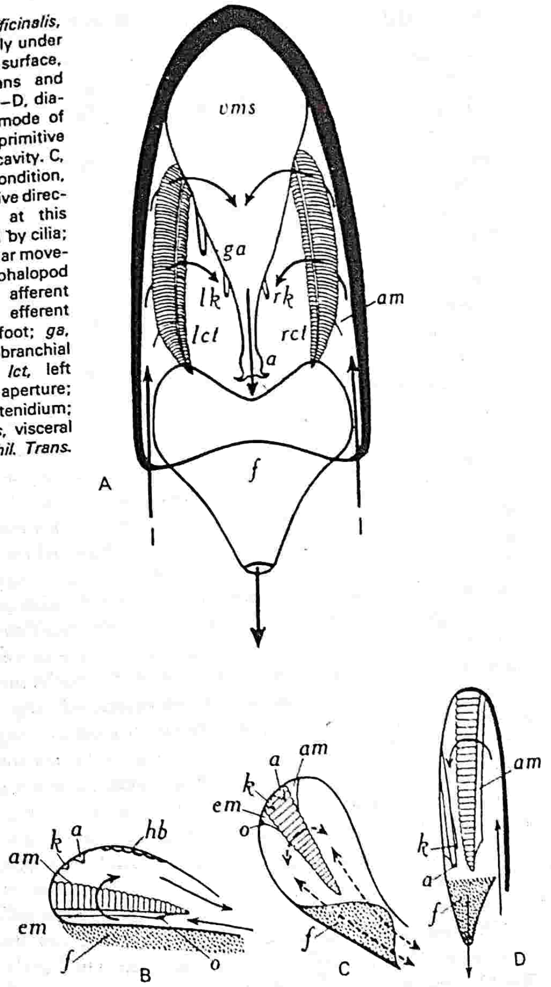


Fig. 11-12. A, *Sepia officinalis*, mantle cavity of topographically under (morphologically posterior) surface, showing disposition of organs and course of respiratory current. B–D, diagrams illustrating postulated mode of evolution of mantle cavity. B, primitive mollusc with posterior mantle cavity. C, postulated intermediate condition, broken arrows indicate alternative directions of respiratory current at this stage (i.e. as in B if produced by cilia; as in D if produced by muscular movement of pedal flaps). D, cephalopod mantle cavity. *a*, anus; *am*, afferent membrane of ctenidium; *em*, efferent membrane of ctenidium; *f*, foot; *ga*, genital aperture; *hb*, hypobranchial gland; *k*, kidney aperture; *lct*, left ctenidium; *lk*, left kidney aperture; *o*, osphradium. *rct*, right ctenidium; *rk*, right kidney aperture; *vms*, visceral mass. From Yonge, 1947. *Phil. Trans. R. Soc. B*, 232, 443–518.

11–5 GILLS AND TRACHEAE IN ARTHROPODS

The organization of the respiratory mechanism of the Arthropoda reflects the evolutionary history of the group, which, as we have already shown, began in the sea and continued later in fresh water and on the land. The most primitive method of respiratory exchange is found in the smaller aquatic crustaceans, such as early larvae, adult copepods, and most ostracods and cirripedes. These animals, like many worms, respire through their general body surface. It is reasonable to assume that the thin-walled and foliaceous appendages of the branchiopods, like the parapodia of polychaetes, facilitate gaseous exchange, and that they have, therefore, a respiratory function additional to their use in feeding. The maintenance of the filter-feeding current would, of course, serve also for ventilation. In fact, it may well be that in these animals, as in the bivalves, the feeding mechanism was a specialization of a more primitive respiratory one, but we cannot be sure of this.

The larger crustaceans develop specialized outgrowths that are regarded as gills, although there is often a lack of physiological evidence for their respiratory function. Structures of this type are particularly well developed in the Malacostraca, where they take the form of foliaceous outgrowths of the coxae of the thoracic limbs. These outgrowths, which are termed podobranchs, may be supplemented, particularly in the decapods, by similar outgrowths arising from the arthrodial membrane at the base of the limb (arthrobranchs), or from the body wall (pleurobranchs). In their simplest form such gills may be only hollow, flattened outgrowths, but they become much more complex, with a central axis and various types of lateral branch. They are well vascularized, with an afferent and efferent circulation, but they do not develop either capillaries or branchial hearts such as are found in the cephalopods. Ventilation is maintained by the rhythmic beating of one or more appendages; primitively a number of these are concerned, as in *Anaspides*, but in the decapods this function is restricted to the scaphognathite of the second maxilla.

Another example of the use of limbs in respiration is probably to be seen in the Trilobita (Fig. 11–13), although here we are restricted to inferences drawn from their fossil remains. We have seen that these animals show a uniformity of structure in their biramous limbs, apart from the differentiation of the antennules. Of the two rami, the inner one supposedly functioned as a walking leg, since it bore a terminal claw. The outer ramus, with its fringe of broad filaments, presumably had some respiratory function.

A third example of the respiratory use of the limb occurs in *Limulus* (Fig. 7–12, p. 191). Five pairs of swimming paddles exist on the opisthosoma of this animal, each of these limbs consisting of a slender internal ramus and a broad external one. The latter bears a peculiar type of gill formed of as many as 200 delicate branchial leaves, for which reason it is called a gill book. Ventilation of the gill book is readily provided by the locomotor actions of the limbs. For much of its time the animal is shovelling its way through sand and mud, and the moulding of the ventral surface of the body into a trough probably provides some protection for the delicate gill books. The overhanging genital operculum, regarded as the fused limbs of the first opisthosomatic segment, provides a further safeguard.

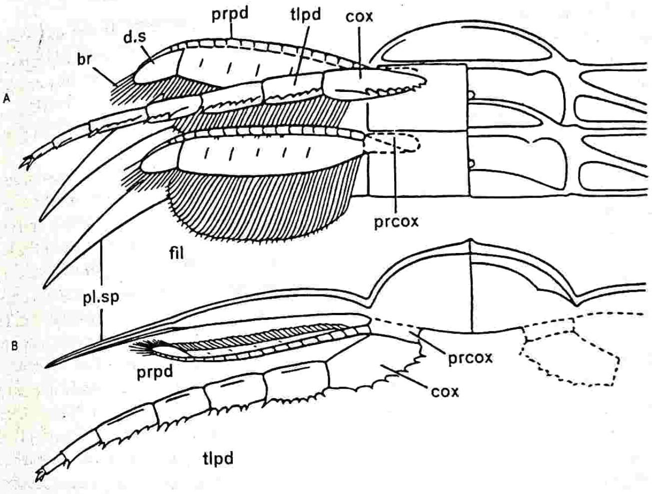


Fig. 11-13. Reconstructions of the appendages of the trilobite *Olenoides* (*Neolenus*) *serratus* Rominger, 100 mm, Middle Cambrian. After Størmer. *br*, bristle; *cox*, coxa; *d.s*, distal segment of pre-epipodite; *fil*, filaments; *pl.sp*, pleural spine; *prcox*, precoxa; *prpd*, pre-epipodite; *tlpd*, telopodite. From Tiegs and Manton, 1958. *op. cit.* Used by courtesy of the Cambridge Philosophical Society.

We have seen that few crustaceans have achieved any success in the invasion of land (Sec. 7–3). Some malacostracans, however, have surmounted the difficulties, examples being found among the anomuran decapods, and also among the true crabs. Here the solution of the respiratory problem has been the development of vascularized folds of the wall of the branchial chamber; a development that is not greatly different in principle from the possession of pleurobranchs. These adaptations may be called lungs. Another solution is found in the Porcellionidae and Armadillidiidae, terrestrial isopods in which the respiratory endopodite of each pleopod is protected by an operculum formed by the exopodite, which also contains branched tubules (pseudotracheae, p. 383, opening to the outside by a narrow aperture. This is a simple illustration of the possibility of distributing gases through tissues by tubular ingrowths of the body surface. The principle has been widely exploited in the arthropods, where it has presumably been encouraged by the development of the hard cuticle; it provides one of the clearest indications of the widespread convergent evolution that has marked the history of the group.

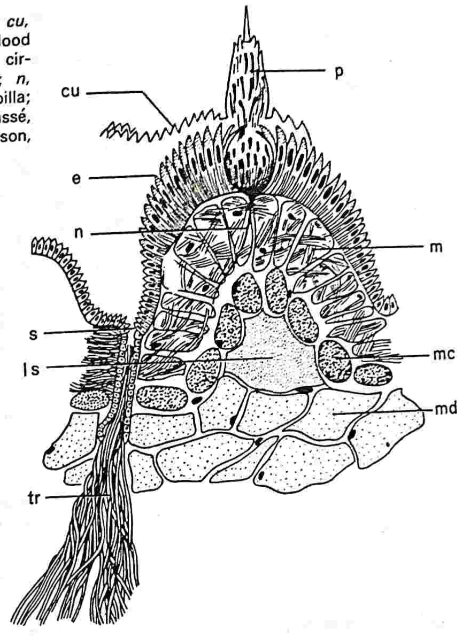
It is convincingly demonstrated, for example, in the chelicerates, which, since they include the aquatic *Limulus*, must have developed their terrestrial adaptations independently of other arthropods (Sec. 7–2). The line of evolution seems likely to have passed through the scorpions, which are known from the Upper Silurian. These animals bear some resemblance to the eurypterids, an extinct group of aquatic chelicerates that were more generalized in structure than the highly specialized *Limulus*. Unfortunately the respiratory organs of the eurypterids are not satisfactorily known, but we may assume that they were of the same type as the gill books of *Limulus*, and that the aerial respiratory organs of scorpions were evolved from them. These are invaginated organs that are called lung books, because they consist of closely apposed leaflets, which are set, like the pages of a book, within a pit that opens to the outside through a narrow aperture. No special provision is made for ventilation, so that gaseous exchange must depend upon diffusion.

Limulus can survive for several days out of water; it has been suggested, therefore, that primitive chelicerates had a similar capacity, and that lung books evolved as a consequence of this. It may be, for example, that the limbs were closely applied to the ventral body surface, that the gill books became enclosed by fusion of the limbs with the body wall, and that the gill lamellae in their turn fused with the wall of the chamber. Four pairs of lung books exist in scorpions, which have remained conservative in their respiratory equipment, but other arachnids are more specialized. Thus some spiders have two pairs of lung books, some have only one pair, and in one family there are none at all. This reduction is doubtless correlated with the tendency for lung books to be replaced in these animals by tracheae, which resemble in principle those of insects and other groups to be mentioned below, but which have clearly been developed quite independently. In the spiders they may perhaps have evolved as diverticula of the missing lung books. Tracheae are also found in other arachnids: the Solifugae, the Phalangidae, and some of the Acarina. In these groups there is no evidence for a primitive lung-book phase, and it is at least possible that they may have developed tracheal respiration independently of the spiders.

We have already seen that *Peripatus*, the myriapods, and the insects may constitute a natural group of terrestrial arthropods, the product of an invasion of the land that was achieved quite independently of the arachnid line. All of these forms have developed tracheal respiration, but their tracheae are not uniform in structure, and we cannot assume that they necessarily had a common evolutionary origin. They could, in theory, be independent expressions of a common genetic potentiality in these several groups. We have no means of judging this, and the dangers of speculation are shown by the fact that the tracheae of the Solifugae show detailed resemblances to those of insects, despite their undoubted independent origin. In *Peripatus* (Fig. 11–14) the tracheae are delicate tubules, passing inwards to the organs, and arising in tufts from pits of the body surface. Each pit opens by a spiracle, the spiracles being scattered irregularly instead of showing the segmental arrangement seen in insects. A fact of great physiological and ecological importance for the Onychophora is that they are unable to close the spiracles. Because of this they cannot resist desiccation, a feature that is correlated with their occupation of sheltered and damp habitats. In the myriapods the tracheae are more complex in structure, and are commonly supported, as they are in insects, by a spiral thickening. In centipedes they usually branch and anastomose; in millipedes they may branch but anastomoses do not develop.

The operation of tracheae has been best studied in insects, where they achieve an efficiency in operation that makes a major contribution to the diversity of specialization and high level of activity that these animals attain. Tracheae have, however, the one major disadvantage that transport of gases by diffusion is suited only to small organisms. Thus they are one of the features of insect organization (the exoskeleton is another) that severely limit the size of these animals; a limitation for which the rest of the animal kingdom should be thankful.

Fig. 11-14. T.S. *Peripatus trinitatis*. *cu*, cuticle, detached; *e*. epidermis; *ls*, blood lacuna; *m*, subepithelial muscles; *mc*, circular muscles; *md*, diagonal muscles; *n*, nerve of sensory papilla; *p*, sensory papilla; *s*, stigma; *tr*, bundle of tracheae. From Grassé, 1949. *Traité de Zoologie*, vol. 6. Masson, Paris.



Tracheae are ectodermal structures, formed by invagination, or ingrowth, from the surface. As a result they are lined with cuticle, called the intima, which is thickened to form delicate ridges arranged either as a continuous spiral or as separate rings. These thickenings, the taenidia, serve to maintain an open lumen throughout the tracheal system, and thereby ensure the passage of gases. Communication with the outside is by means of openings called spiracles, referred to above; they may be regarded as the sites of the original invagination. Typically these are found in the thorax and abdomen (Fig. 11–15), situated on the pleura, but there is much variation in detail, and distinctions can be made in the insects between holopneustic, hemipneustic, and apneustic systems. The first of these, with eight pairs of spiracles on the abdomen and two on the thorax, is the most primitive, and is particularly characteristic of adult stages. Hemipneustic systems, in which one or more of the pairs of spiracles are closed, are particularly characteristic of those larvae in which respiratory exchange has become localized at one end of the body; this is usually an adaptation for life in a fluid or semi-fluid medium. In apneustic systems all of the spiracles are closed, so that respiratory exchange must now occur either through the body surface, or through outgrowths of it that are called gills. This mode of functioning is particularly characteristic of endoparasites and of fully aquatic insects.

The essential feature of the fully developed tracheal system of insects is that it transports oxygen to the tissues by tracheal tubes that branch to supply all parts of the body, and form extremely fine terminations called tracheoles. These terminations

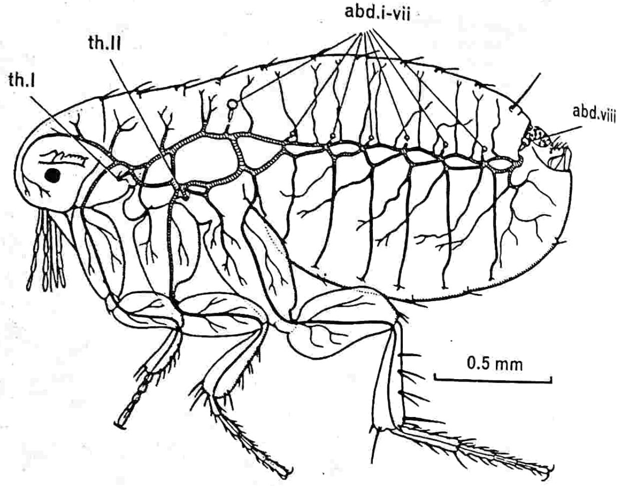


Fig. 11-15. Tracheal system of *Xenopsylla cheopsis. th.I, th.II,* thoracic spiracles; *abd. i–viii,* abdominal spiracles. From Wigglesworth, 1947. *The Principles of Insect Physiology* (3rd ed.). Methuen, London.

possess thin walls that are permeable to water, and that are provided, like the tracheae, with taenidia so delicate that they can only be seen by electron microscopy. Because of the minute size of the tracheoles they enter into so close a relationship with the tissue that they surround the cells and end blindly within them. Moreover, the degree of their development and branching can be adaptively adjusted to meet fluctuations in the oxygen demands of particular tissues.

It is difficult sometimes to make a clear-cut distinction between pulmonary and tracheal respiration. As Krogh points out, the tracheae of spiders may function essentially as lungs, for they do not convey oxygen to the tissue, but merely aerate the blood in the adjacent ventral sinus. Even in insects there is a blood stream which must necessarily play some part in gas transport; the tracheoles may sometimes be found suspended in the blood, and presumably provide a source of oxygen that it can then transport. Moreover, tracheae are sometimes expanded to form thin-walled air sacs. These may sometimes serve as hydrostatic organs, but they are probably of particular importance in increasing the capacity of the respiratory system as a whole, so that the respiratory movements result in the exchange of a correspondingly greater volume of air. There is an analogy here with the function of the air sacs of birds, and a further analogy is implied in a suggestion that the air sacs of insects may aid flight by reducing specific gravity. A similar function has been suggested in birds, for in these animals the air sacs penetrate extensively into the bony skeleton.

As with other types of respiratory system, the mode of functioning of tracheae is closely governed by the physical properties of air and water. We have seen that air is a more favourable medium for respiratory exchanges than in water, and that this is

particularly apparent in connection with the diffusion of oxygen, which is very much more rapid in air than in water. Krogh's calculations showed that in a large *Cossus* (goat moth) larva, 60 mm long and weighing 3.4 g, the tracheae had an average length of 6 mm, with a cross-sectional area of 6.7 mm^2. In these circumstances diffusion is ample for supplying the necessary oxygen; it requires a pressure difference of only 11 mm, so that the animal need not expend any energy at all upon ventilation movements. The same is probably true of very many tracheate arthropods, including the Onychophora, the arachnids, the myriapods, and a large number of the smaller insects, together with larvae and pupae. The efficiency of tracheal respiration, given the small size of insects (see also p. 296) is well brought out by some calculations of Alexander. These show that a larva with the same oxygen consumption as a goat moth larva (0.3 cm^3/g hr), and with the same proportion of its body occupied by tracheae, could in theory reach a radius of 0.9 cm, whereas an earthworm-like animal, relying upon a circulatory system for distributing its oxygen, could only reach 0.3 cm.

Two factors that modify this situation are size and activity. Many insects are smaller than the larva mentioned, and are in an even more favourable position, but conditions deteriorate with increased size, as Krogh showed. If, for example, the linear dimensions increase by a factor of 10, giving tracheae 6 cm long and 6.7 cm^2 in cross-section, the rate of diffusion could be increased by a factor of 10, but the animal would be 1,000 times heavier, and its metabolism at least 100 times greater. Diffusion would now be totally inadequate for meeting its needs, and this is why tracheal respiration limits the size of arthropods. Conditions are at their most difficult in insects. The expenditure of energy during flight is formidably high, amounting to 100 cm^3/cn^3 tissue hr, and transport of oxygen by diffusion is thought to become inadequate when the body weight reaches 0.1 g. Respiratory movements are now needed to ensure an adequate supply of oxygen, and so these are seen in bees, for example, which weigh 100 mg. It is, of course, the flight muscles which are mainly consuming the oxygen, and they have a specialized tracheal supply, with a main trunk running throughout the muscle, and giving off lateral branches which continue to divide. Even so, Alexander shows that the greatest diameter that a flight muscle could achieve, while still maintaining this rate of oxygen consumption, is 0.5 cm. This is, indeed, the limit normally found. But there is a tropical water bug, *Lethocerus*, which reaches a length of 11 cm, being one of the largest of known insects. This has a further adaptation in its wing, in that air is pumped through the larger of the branch tracheae as well as through the main trunk, whereas in other insects it is only pumped through the latter.

A special difficulty arises in species in which the legs are unduly long relative to the size of the body; reliance upon diffusion over such distances may result in the oxygen concentration in the tracheae of these limbs falling to very low levels. It is doubtless in adaptation to this that harvestmen (Order Opiliones), with exceptionally long legs, have spiracles on their tibiae.

With tracheae, as with lungs, there is bound to be some loss of water vapour through the respiratory membranes; this constitutes a serious drawback in the tracheal system, particularly as terrestrial animals must achieve maximum economy in the use of water. Since the general body surface is impermeable, the spiracles become the main site of water loss. Primitively this loss was doubtless accepted, as it still is today in *Peripatus*, but the extraordinarily successful exploitation of aerial

Since oxygen diffuses much more rapidly through air than through water, the effect of this will be to improve the supply of oxygen to the cells. This result is analogous to the opening-up of the capillaries in the active muscles of the vertebrate body.

It remains to add that the possession of such a highly specialized respiratory system has not prevented insects from returning to an aquatic life, any more than the possession of lungs has prevented mammals from doing the same. Various devices are adopted for this purpose. Some larvae obtain air from aquatic plants but a more common practice is to return to the surface to breathe through the spiracles. In this case, hydrophobe structures or secretions must be present around the spiracular openings to prevent flooding of the tracheae. This procedure may be supplemented by carrying down under the water a temporary reservoir of air on the body surface. This reservoir, which serves a hydrostatic function as well as being an oxygen store, may be retained beneath the wings, as in *Dytiscus*, or among hydrofuge hairs, as in *Notonecta*.

Another device is the use of spiracular gills, mainly confined to the pupae of certain flies and beetles, in which they must have been independently evolved on many occasions. These structures, which are modifications of the spiracle, or body wall, or both, usually bear a device called a plastron. This is an air store held in place by a complex system of hydrofuge structures, which may consist of hydrofuge hairs, or be formed of much more elaborate systems of tubercles, struts, and arches (Fig. 11-18). The air–water interface of this structure is very large, facilitating gaseous exchange without any increase in the permeability of the cuticle. The plastron can be regarded as a 'physical gill', depending for its operation on the air store being maintained at constant volume. Give this condition, and provided that the ambient water is well aerated, oxygen diffuses continuosly from the water into the plastron, replacing what has entered the tracheae; the animal can thus remain submerged for a long time. If, however, the oxygen tension in the water is low, the animal suffers because oxygen will diffuse out from it, through the plastron, into the water. If the animal is exposed to air, the plastron no longer functions, except in so far as it can provide channels for gaseous diffusion, but it does restrict water loss through the spiracles. These properties have important ecological implications. Plastron respiration is usually restricted to insects living in well-aerated water, subject to frequent changes in water level, with consequent periodical exposure to dry conditions.

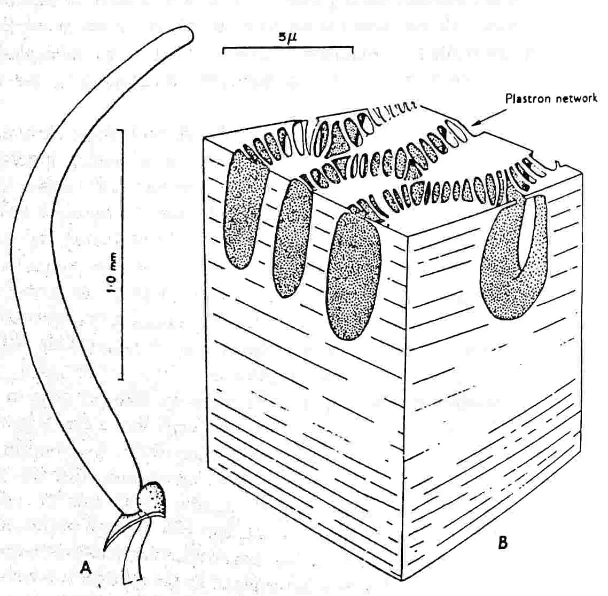


Fig. 11-18. Spiracular gill of *Eutanyderus wilsoni*. A, lateral view of right spiracular gill, which is formed by an outgrowth of the body wall adjoining the first pair of spiracles. B, diagram of the structure of the wall of the spiracular gill showing the plastron. Vertical pillars distributed over the surface of the gill are connected by horizontal struts. The interstices between the struts provide the air–water interface. From Hinton, 1968. *Adv. Ins. Physiol.*, 5, 65–162.

Finally, many aquatic insects have become fully aquatic by developing tracheal gills, which make it possible to obtain oxygen by diffusion from the surrounding water. The essential feature of these is the presence of many fine tracheae immediately below the cuticle, ventilation being sometimes provided by the movements of the animal, and sometimes by movements of the gills themselves. Krogh pointed out in this connection a curious analogy between the respiratory system of the nymph of the dragonfly *Aeschna* and that of the cephalopods. The former has tracheal gills that lie in the rectum, and that are ventilated by muscular movements that also provide for the locomotion of the animal. In principle, this is the same combination of respiratory movement and locomotion that has been developed with such success in the operation of the cephalopod pedal siphon.