

RESPIRATORY SYSTEMS OF INSECT EGG SHELLS¹

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All animals require a relatively extensive surface through which to absorb oxygen from the ambient environment. Because the oxygen molecule is larger than the water molecule, no animal has been able to evolve a membrane that is at once permeable to oxygen and impermeable to water (10). It is for this reason that any relatively dry environment presents the animal with contradictory demands: on the one hand, it must have an extensive surface permeable to oxygen but, on the other hand, it must not lose too much water through such a surface. Arthropods are a group of small animals that have been successful in dealing with these contradictory demands of dry environments. The exposed cuticle is water-proofed, and effectively oxygen-proofed, by a continuous fatty acid layer. At the same time, a very extensive surface is invaginated and forms tracheae that may ramify through the body. The air in the tracheae can be kept saturated and the loss of water can be reduced to manageable proportions because the total cross-sectional area of the spiracles is only a small fraction of the surface area of the tracheae. As a further improvement, a spiracular closing apparatus may be evolved and water loss restricted to periods when the spiracles are open, or the spiracular atrium may have dense layers of cuticular projections that by pressure resistance and frictional drag prevent bulk exchanges of air with the ambient environment and so reduce water loss (9).

Dry environments present insect eggs, no less than other stages, with the contradictory demands already noted. The different types of chorionic respiratory systems that have been evolved in large measure reflect different solutions to the same problem: oxygen needs must be satisfied without losing too much water.

The first very extensive study of the respiratory systems of insect eggs was that of Leuckart (32). This was followed by the important papers by Korschelt (29, 30). Although there have been numerous descriptions of the respiratory systems of single species or small groups of species, few indeed have been accurate. For instance, at the time of writing, I know of no accurate account of the respiratory system of any lepidopterous egg. Reviews of work on the respiratory systems of the eggs of larger groups are almost nonexistent, the papers by Southwood (39) and Cobben (3) being noteworthy exceptions.

¹The survey of the literature pertaining to this review was concluded in April 1968.

KINDS OF RESPIRATORY SYSTEMS

Very many insects have a more or less solid chorion in the sense that, with the light microscope or even with a low-resolution electron microscope, no holes appear to be present. Nevertheless, since oxygen enters and carbon dioxide leaves through the shell, it necessarily follows that the shell must have holes large enough to permit the exchange of these respiratory gases. No high-resolution electron micrographs of such shells appear to have been published. However, both on general grounds and on what is now known about the fine structure of the shell of *Leptohylemyia* (17), it seems that the chorion is made up of fibrils that form a meshwork with interstices large enough to permit the passage of respiratory gases. In *Leptohylemyia* the interstices are about 20 to 25 Å wide. In such apparently solid shells, the interstices of the meshworks are at least an order of magnitude narrower than the mean free path of the respiratory gases (0.1 μ for oxygen at 23°C).

Chorionic respiration when no distinct respiratory system is present is analogous to the cutaneous respiration of other stages when these lack an open tracheal system. The majority of aquatic and semiaquatic eggs that have been examined lack a chorionic respiratory system, and the chorion is everywhere "solid."

A large number of kinds of aquatic and semiaquatic eggs that lack a respiratory system are imbedded in a jelly-like substance, particularly it seems when they are laid in habitats liable to sudden drying, e.g., many Chironomidae. The "jelly" is hygroscopic, and it is often a proteinaceous substance. When the eggs are subjected to some desiccation, the jelly loses water slowly so that if the drying period is not too long the egg is protected from desiccation. A number of eggs that are normally laid above water are also imbedded in a hygroscopic jelly, e.g., *Limnephilus* and some other Trichoptera. The role of the jelly-like substance urgently requires investigation. There can be no doubt that it helps tide the egg over relatively short periods when it would otherwise become too dry. Unless the surface of the jelly alters with drying so that it becomes relatively impermeable to water after a certain period, it would seem that the protection it affords is only temporary; in time equilibrium will be achieved between the moisture content of the jelly and the ambient environment.

It now seems that the majority of terrestrial eggs have meshworks in the chorion that hold a layer of gas. The proportion of aquatic eggs with such meshworks appears to be relatively small. All species that have chorionic meshworks that hold a layer of gas also have aeropyles or holes that extend through much of the shell and effect the continuity of the chorionic layer of gas and the ambient atmosphere. The aeropyles are normally an appreciable fraction of a micron wide to several microns wide, and there is rarely any difficulty in recognizing them with the light microscope. The interstices between the struts of the chorionic meshworks that hold the gas

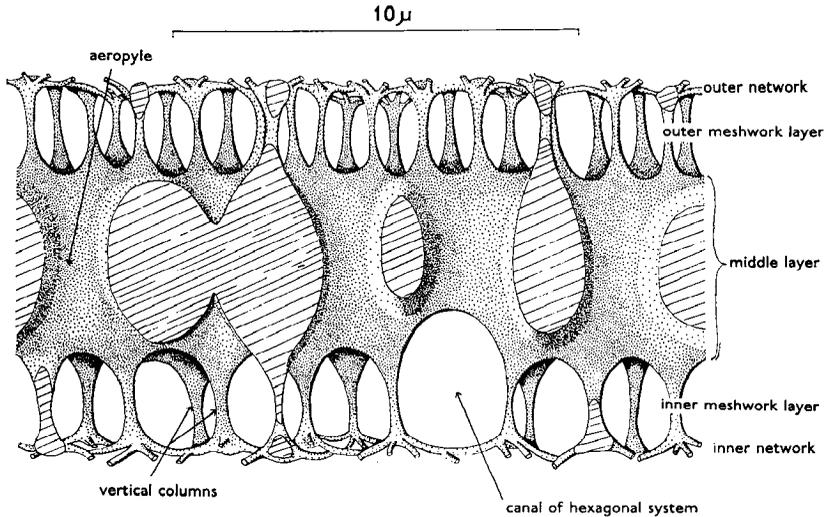


FIG. 1. Diagrammatic view of a section through the egg-shell outside the hatching lines of a muscid fly to show the relation of parts [after Hinton (23)]. In many Muscidae and some other insects, the innermost surface of the chorion is an open network. However, in most insects it is a sheet of chorionin that appears to be solid at all but the very highest resolutions of the electron microscope.

are usually about as wide as, or distinctly wider than, the mean free path of the respiratory gases, as might be expected.

The respiratory system of the egg may become filled with gas while it is still bathed in fluid in the common oviduct, as in the Phasmidae (45) and Diptera-Cyclorrhapha (12, 33, 45), or the intrachorionic spaces may dry out and fill with air after the egg is laid, as in the Acrididae (6), Nepidae (15), and Staphylinidae (34). Gas filling of the intrachorionic spaces while the egg is immersed in a liquid probably involves active absorption of the contained liquid, which would reduce the pressure in the intrachorionic spaces and cause bubbles of gas to be formed. The formation of bubbles would be assisted by any increase in the hydrophobe properties of the chorion, such as might accompany tanning or the addition of lipophylic substances. Gas filling of the intrachorionic spaces while the egg is bathed by a liquid does not appear to differ in principle from gas filling of the tracheal system before hatching or at the apolyses (= moults) of some larval insects.

The pressures of gases in the chorionic respiratory system have not been measured, but the steady-state of a system of this kind may be postulated. In a steady-state in which there is a net inflow of gas, there will be almost no difference in the total pressure between the atmosphere and the

intrachorionic air spaces. The intrachorionic oxygen pressure is maintained below that of the atmosphere. The difference is nearly equalized by an increase in the partial pressure of nitrogen, carbon dioxide, and water vapour. The partial pressure of nitrogen in the intrachorionic air spaces will be maintained slightly above that of the ambient air because of the greater number of collisions with incoming molecules, and there will be no net transference of nitrogen. However, if the number of molecules of carbon dioxide plus water vapour produced equals the number of molecules of oxygen used, there will be no net inflow of gas and the partial pressure of nitrogen within the shell will be the same as that of the ambient air. This, of course, assumes that all gas exchange occurs through the aeropyles.

Two kinds of chorionic respiratory systems may be distinguished: those that do not function as plastrons when the egg is immersed in water and those that do. For the respiratory system to function as a plastron, the total water-air interface across the aeropyles, or across any superficial networks the chorion may have, must be such as to satisfy all or a significant part of the oxygen demands in well-aerated water. The minimum water-air interface per unit weight of tissue that must exist to satisfy a significant amount of the oxygen requirements of the egg is not known (see discussion on p. 362). Although intermediates between eggs with plastrons and those without are not uncommon, in the great majority of instances there is no difficulty about making a distinction, a distinction that has great ecological significance.

In those eggs that do not have a chorionic plastron, the number of aeropyles and the total area of their openings may nevertheless vary greatly. For instance, in *Rhodnius* (Fig. 2) there are about 185 aeropyles and the total area of their openings is about $536 \mu^2$ without allowing for the "spongy" area around each aeropyle. In such eggs the total area of the aeropyle openings per milligram of tissue is usually at least two or three orders of magnitude below that of even an egg with a poorly developed plastron. It is, of course, possible that in some of those eggs that have too few aeropyles to constitute a plastron, the apparently "solid" chorionin may nevertheless be a fine open meshwork that functions as a plastron in water.

Many of the terrestrial eggs in which the total area of the aeropyle openings per milligram of tissue is several orders of magnitude too little for there to be effective plastron breathing, are nevertheless laid in situations where they are often wetted by rain. Many of these are laid on leaves and other places that drain rapidly and so do not accumulate water. Others are exposed to prolonged flooding from time to time, and their particular adaptation to such a contingency appears to be their capacity to survive a great reduction in their metabolic rate: they tolerate a switch from a metabolic rate necessary for growth to one adequate only for maintenance or a little more.

In such eggs as have aeropyles that open into gas containing meshworks in the chorion, it may be supposed that most of the gas exchanges

with the ambient air take place through the aeropyles. However, very little is yet known about the permeability of the chorion, and it may be that some or many eggs depend not only upon oxygen entering through the aeropyles but also upon that diffusing through the areas of chorion without aeropyles. For instance, Tuft (44) has shown that when the aeropyles of *Rhodnius* are blocked with shellac, the egg continues to take up oxygen although only at about a tenth of the normal rate. Unfortunately, this kind of information about the permeability of the chorion is lacking for other eggs.

Among terrestrial eggs that do not have a plastron, the aeropyles sometimes open on the apices of stalks and so open well above the general surface. Such stalked aeropyles may be scattered over the surface, e.g., some Psocoptera and Geometriidae (*Semiothisa*), or they may be arranged in some kind of circle at the anterior end of the egg, as is the general rule in Hemiptera of the superfamilies Pentatomoidea, Coreoidea, Lygaeoidea, Pyrrhocoroidea, and Aradoidea. One selective advantage of elevating the aeropyles above the general surface seems evident: every increase in the height of the aeropyle openings enables the egg to utilize atmospheric oxygen when covered by correspondingly thicker layers of water.

In a few eggs the aeropyles are grouped together and open on the apex, or on both the apex and sides, of long anterior respiratory horns. Eggs of this kind occur in some bugs of the family Miridae (4, 20), e.g., Brycorinae (*Helopeltis*, *Parabrycoropsis Pseudodoniella*) and Dicyphinae (*Dicyphus*, *Macrolophus*). In *Helopeltis schoutedeni*, for instance, the body of the egg is 1.5 mm long. The ventral horn is about 0.7 mm long with 45 aeropyles, and the dorsal horn is about 0.5 mm long and has fewer aeropyles (20). In such eggs as have anterior horns, the horns almost always bear a plastron; eggs with horns but without a plastron are very uncommon.

In the great majority of eggs, the aeropyles are quite distinct from the micropyles. Occasionally, aeropyles have been identified as micropyles, for example, in the Miridae. It has sometimes been said that micropyles are absent in all Hemiptera-Cimicoidea [e.g. (39)], but they have been found in all Miridae examined (8, 20). In very many Hemiptera-Pentatomomorpha the micropyle is a tube extending down the middle of a stalked aeropyle [figures in (39, 45)]. The aeropyle and micropyle may have the same external opening when the aeropyle does not project above the surface, as appears to be the case in the moth *Cerura vinula* (Fig. 5).

Although this review is not concerned with the fine structure of the chorion, it should be noted that the practice of calling an outer layer "exochorion" and an inner layer "endochorion" suggests homologies that do not always exist. Because there is no strict correspondence between these layers in different insects, it is perhaps best merely to speak of the outer and inner layers of the chorion, as has been often suggested (7, 21, 37). There are commonly only two distinct layers in the shell, as in many Diptera, but there are often many more. For instance, in the moth, *Cerura vinula*, there are more than 40 distinct gas-containing layers, 16 of which are shown in

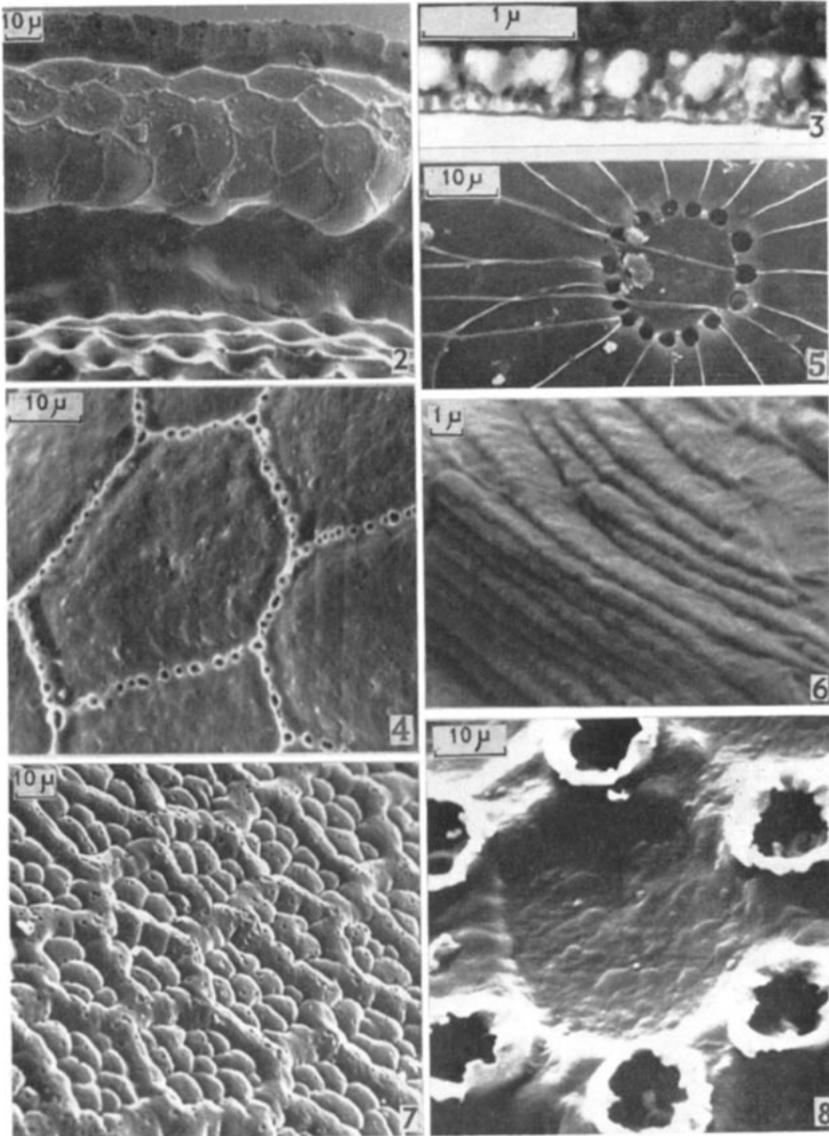


FIG. 2. Stereoscan electron micrograph of the egg shell of *Rhodnius prolixus*. Anterior margin of shell before cap showing a row of aeropyles and a single micropyle in the spermatic groove.

FIG. 3. Transmission electron micrograph of the inner air-containing meshwork of the shell of *Rhodnius prolixus*.

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Figure 6. It may be noted here that attempts by Wigglesworth and his co-workers (45-47) to elucidate chorionic respiratory systems by means of the cobalt sulphide injection method proved to be misleading for a number of reasons (1, 11, 14, 15, 21).

PLASTRON RESPIRATION

Attention has been drawn to the fact that preoccupation with the aquatic adaptations of aquatic insects has resulted in an almost total neglect of the aquatic adaptations of terrestrial insects (13). But whenever it rains heavily, a large number of terrestrial insects are submerged beneath a layer of water. Insect eggs are normally glued to the substrate and necessarily remain submerged until it has stopped raining and the water has evaporated or flowed away. In most climates, therefore, insect eggs are alternately dry and flooded. To be submerged in water for several hours or even days, a period that may, for instance, exceed the incubation period of the egg, is no rare and isolated event but is a normal hazard of the environment. It therefore seems likely that some stages of insects, especially the immobile eggs, are likely to be adapted for respiration in water in a manner no less complex than are many aquatic insects.

When the terrestrial environment is seen as one that is alternately dry and flooded, and that when flooded the water is usually well-aerated, it is possible to predict the kind of respiratory adaptations that might be expected to be found amongst terrestrial insects. For instance, one of the most characteristic respiratory adaptations of insects that live in aquatic environments, that at one moment are flooded by well-aerated water and that at another may be dry, is the possession of a physical gill called a plastron.

The term plastron has been restricted to denote a gill that consists of a gas film of constant volume and an extensive water-air interface. Such films are held in position by a system of hydrofuge structures, and they resist wetting by the hydrostatic pressures to which they are normally subjected in nature. In well-aerated water, a plastron enables an animal to remain im-

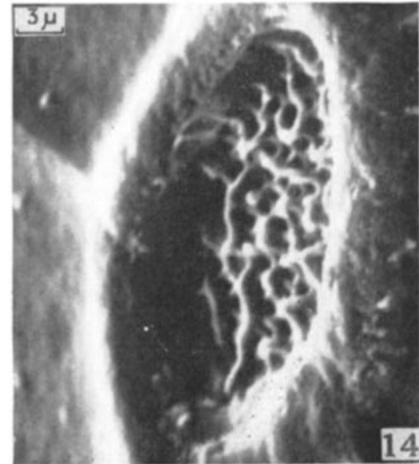
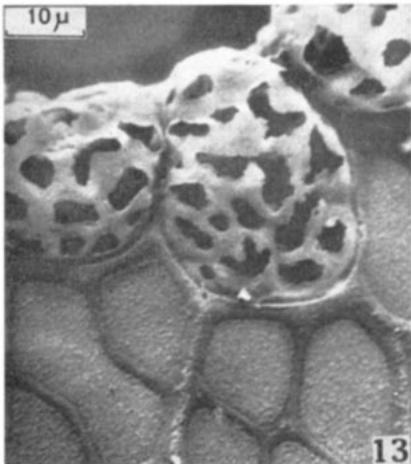
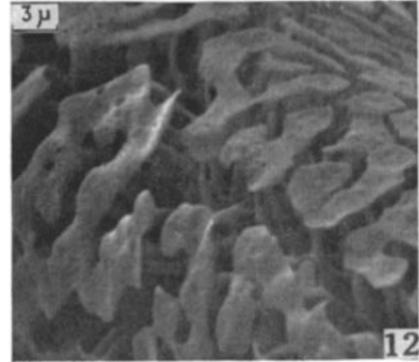
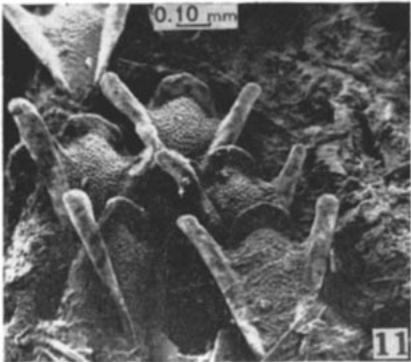
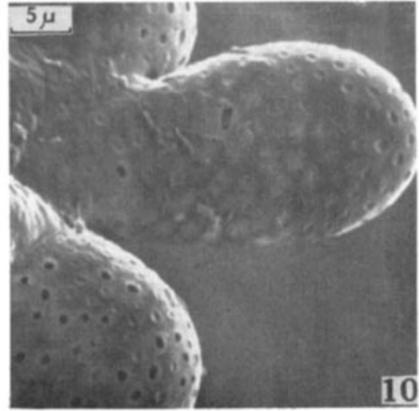
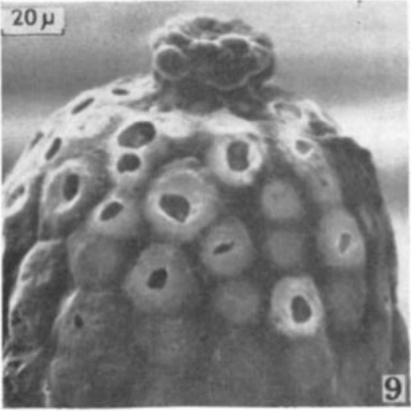
FIG. 4. Stereoscan electron micrograph of the side of the shell of the moth *Phragmatobia fuliginosa*.

FIG. 5. Stereoscan electron micrograph of the anterior end of the shell of the moth *Cerura vinula*.

FIG. 6. Stereoscan electron micrograph of a section through the middle of the shell of *Cerura vinula*.

FIG. 7. Stereoscan electron micrograph of surface of side of shell of *Bombyx mori*.

FIG. 8. Stereoscan electron micrograph of surface of side of shell of *Antheraea pernyi*. There are between 12,000 and 14,000 large aeropyles in the shell.



mersed indefinitely and obtain the oxygen it requires from the ambient water.

The great selective advantage of the plastron method of respiration can only be understood in relation to an environment that is alternately dry and flooded. In water, the plastron provides a relatively enormous water-air interface for the extraction of oxygen dissolved in the ambient water. This enormous surface for the extraction of oxygen is provided without necessarily involving any reduction in the impermeability of the cuticle or chorion. In air, the interstices of the plastron network provide a direct route for the entry of atmospheric oxygen that does not necessarily involve the animal in water loss over a large area because the connection between the plastron and the internal tissues may be very restricted. Thus, the capacity to avoid loss of water when the environment is dry is not necessarily impaired by the provision of a plastron.

The great disadvantage of a plastron is that it becomes an efficient method of extracting oxygen from the tissues should the oxygen pressure of the environment fall below that of the tissues. It is therefore no accident that aquatic eggs and pupae with plastrons are restricted to environments in which the oxygen pressure is maintained at a high level such as in streams, the littoral of large lakes, and intertidal areas. Adult insects with plastrons are generally restricted to the same environments, but there are a few adult beetles, such as *Macrophea* (Chrysomelidae) and some weevils, that live in marshes or ponds in which the oxygen pressure may drop greatly, especially at night. Presumably such insects move to the upper layers of water or climb out when the oxygen pressure of the water falls enough to cause the plastron to work in reverse.

The problems of respiration in well-aerated aquatic environments liable to sudden drying are so similar to those of terrestrial environments liable to sudden flooding by well-aerated water as to suggest that a respiratory adaptation characteristic of the former may be found in the latter. And this is indeed so. A plastron was first reported in the eggs of *Drosophila* and some

Stereoscan electron micrographs.

FIG. 9. Anterior end of shell of the bug *Hydrometra stagnalis*.

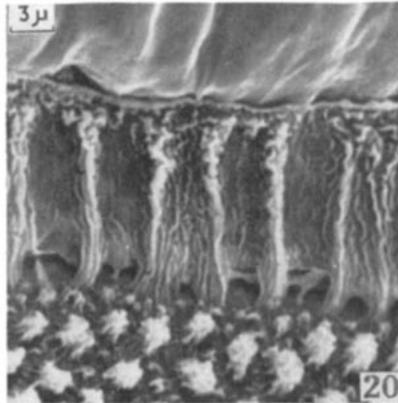
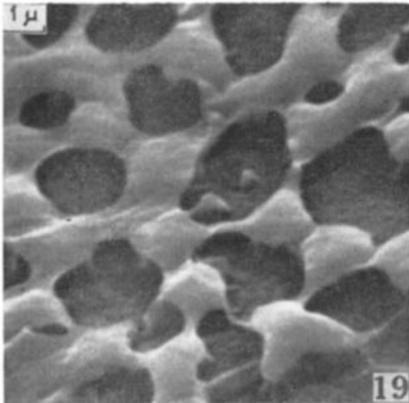
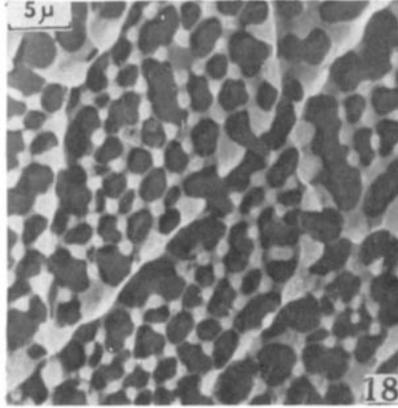
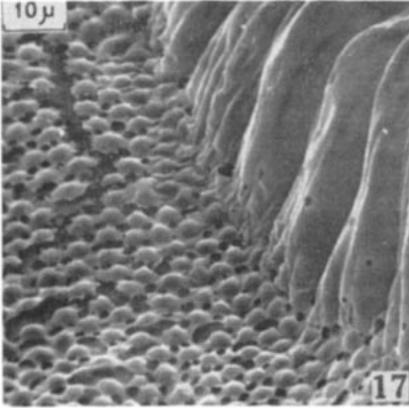
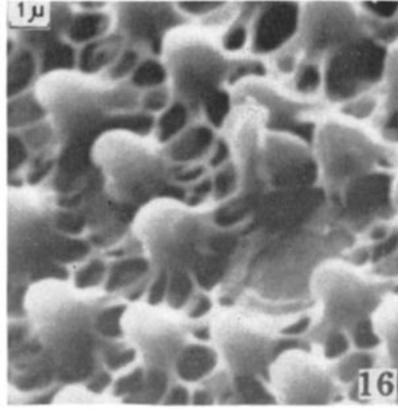
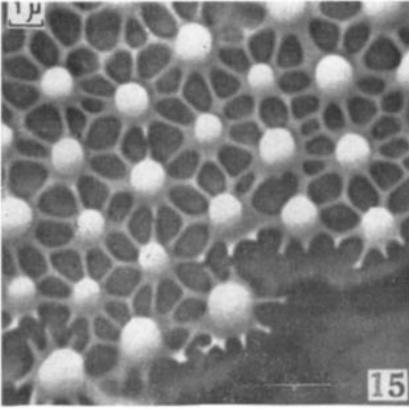
FIG. 10. Respiratory horn of the fly *Mydaea urbana*.

FIG. 11. A fragment from the top of a cow pat showing the eggs of *Scopemu stercorarium*.

FIG. 12. Surface of plastron of respiratory horn of *Scopemu stercorarium*.

FIG. 13. Elevated side by hatching line of the fly *Phaonia variegata* showing the surface of the plastron.

FIG. 14. Plastron crater of side of egg of the Australian bush fly *Musca vetustissima*.



other terrestrial flies in 1959 (11), and it is already quite clear that instances of plastron respiration among terrestrial eggs greatly outnumber instances of plastron respiration among all stages of aquatic insects.

THE KINDS OF PLASTRONS

A natural classification of chorionic plastrons is precluded because of their polyphyletic origin. A number of different classifications of convenience can be made, but at this stage it is probably best merely to speak of those with and those without plastron-bearing horns. Most eggs lack plastron-bearing horns. In these the plastron network may extend over the entire shell, as in most Muscinae (Fig. 1), or it may be confined to a part of the shell. Among the Diptera-Cyclorrhapha, for instance, the plastron is often restricted to the area between the hatching lines, as in many Calliphoridae and Muscidae. The plastron is sometimes present only on one side of the egg, e.g., some bugs of the family Saldidae (4), or the plastron may consist of a few or many discrete islands (or craters) scattered over the surface of the shell, as in *Musca vetustissima* (Fig. 14).

According to the fine structure of the surface of the plastron, two rather different types may be recognized: (*a*) plastrons that clearly consist of an enlargement of the aeropyles, or a great increase in their number, or both; and (*b*) plastrons, such as those of the Muscidae, that consist of a network. The origin of some surface networks by a sufficient approximation of many aeropyles is not difficult to visualize and no doubt often occurs. However, it seems improbable that the plastron network of such insects as the Culicidae (Figs. 15–20) originated in this way. Aeropyles sufficiently numerous to form a plastron may be more or less evenly scattered over the surface or they may be confined to certain restricted areas. Sometimes the aeropyles appear to be formed in the centres of the hexagons that mark the boundaries of the individual follicular cells, as in some Tettigoniidae (Fig. 26), or they may be confined to the boundaries of the hexagons, as in many Lepidoptera (Figs. 4, 8).

The possession of a chorionic plastron poses a special problem in preventing water loss simply because a plastron consists of an extensive sur-

Stereoscan electron micrographs of the plastron of various mosquitoes.

FIG. 15. *Culex pipiens molestus*, middle of shell.

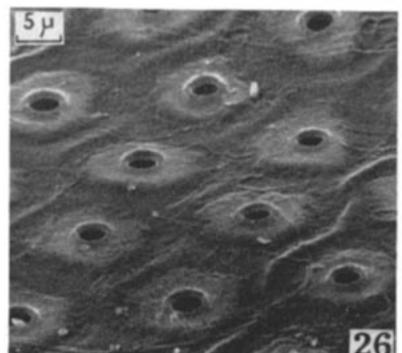
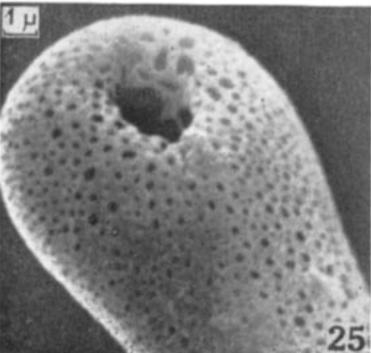
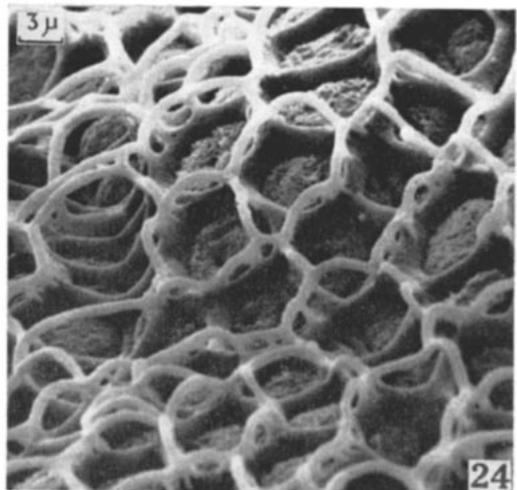
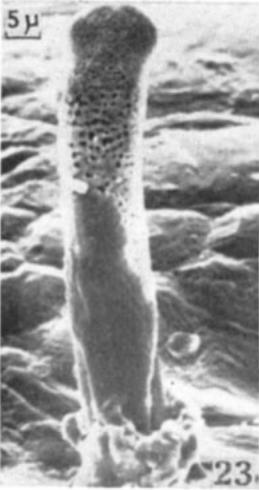
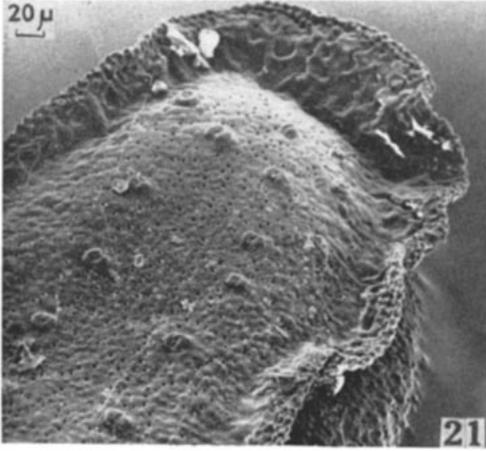
FIG. 16. *Culex pipiens molestus*, middle of shell.

FIG. 17. *Anopheles stephensi*, plastron network near lower margin of float.

FIG. 18. *Anopheles quadrimaculatus*, plastron network of lower surface.

FIG. 19. *Anopheles pharoensis*, lower surface.

FIG. 20. *Anopheles farauti* showing deck tubercles, frill, and float.

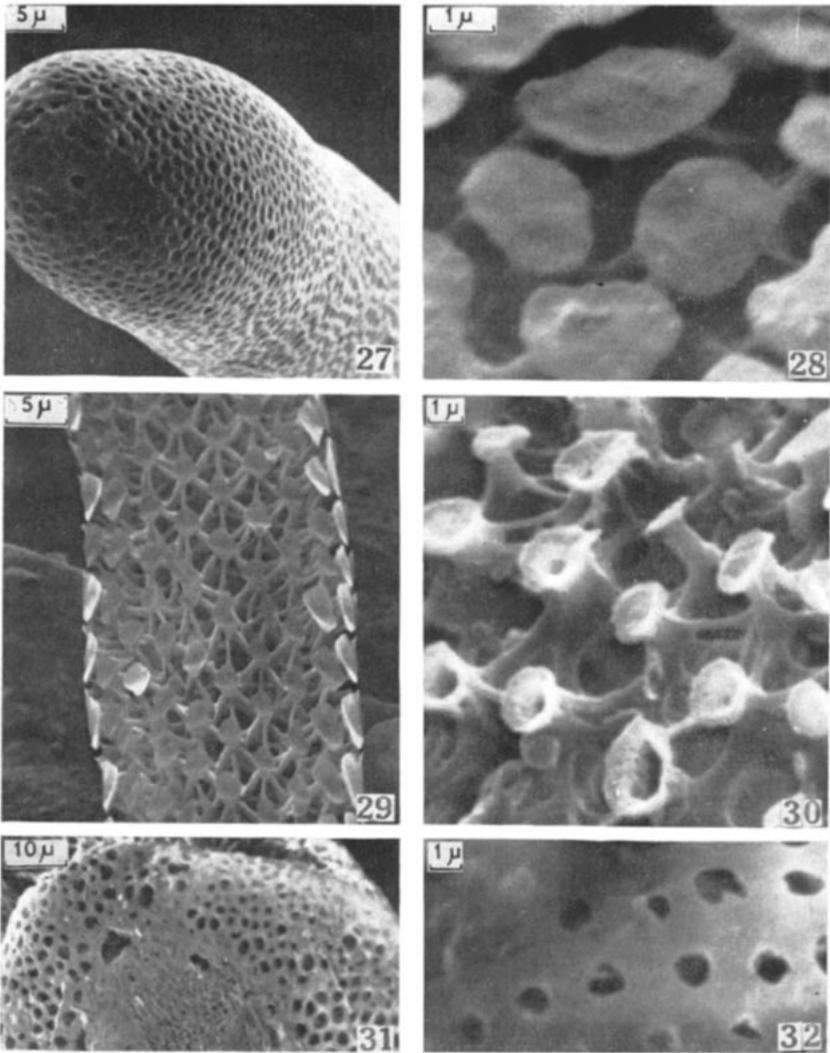


face area open to the outside air. A not uncommon method of solving the problem of having an extensive surface through which oxygen may be absorbed when the egg is in water, but through which little water is lost when the egg is dry, is to evolve a plastron-bearing horn. In eggs with plastron-bearing horns, such as *Drosophila*, no limit is necessarily placed upon the impermeability of the chorion elsewhere. If the chorion of the body of the egg is impermeable, water will be lost only through the cross-sectional areas of the horns, whereas when the eggs are in water a relatively enormous water-air interface is available for extraction of oxygen. When the egg lacks plastron-bearing horns but has a plastron over part or all of the surface, precisely the same effect may be achieved by (a) having only a small area of the innermost chorion permeable to the respiratory gases, or (b) by having only a small area of the subchoral membranes permeable to gases. Neither of these conditions has been conclusively demonstrated in any egg, although it is taking no great risk to predict that at least the first will be. In all Tettigoniidae that I have examined, a plastron is present. The plastron gas is held in a superficial layer often separated from the subchoral membranes by a thick inner layer of chorion. Fine canals extend nearly all of the distance through this thick and apparently solid layer. This type of structure could achieve the same effect as a chorion with respiratory horns: when the egg is exposed to desiccating conditions, water loss could be confined to the sum of the cross-sectional areas of the fine canals of the inner chorion if the rest of the inner chorion were impermeable.

The type of plastron that extends over the whole or over a large part of the surface of the egg, and where the inner surface of the chorion is an open network (Fig. 1), offers little resistance against desiccation. For instance, Larsen (31) has shown that eggs of the flies *Haematobia* and *Lyperosia* fail to hatch when the relative humidity is 83 per cent, and only 5 per cent of the eggs of *Lyperosia* will hatch when the relative humidity is as low as 93 to 94 per cent. On the other hand, eggs with a plastron over the whole surface may be very resistant to desiccation: in the fly *Leptohylemyia coarctata*, for instance, the resistance to desiccation is due to a waxy

Stereoscan electron micrographs of egg-shells.

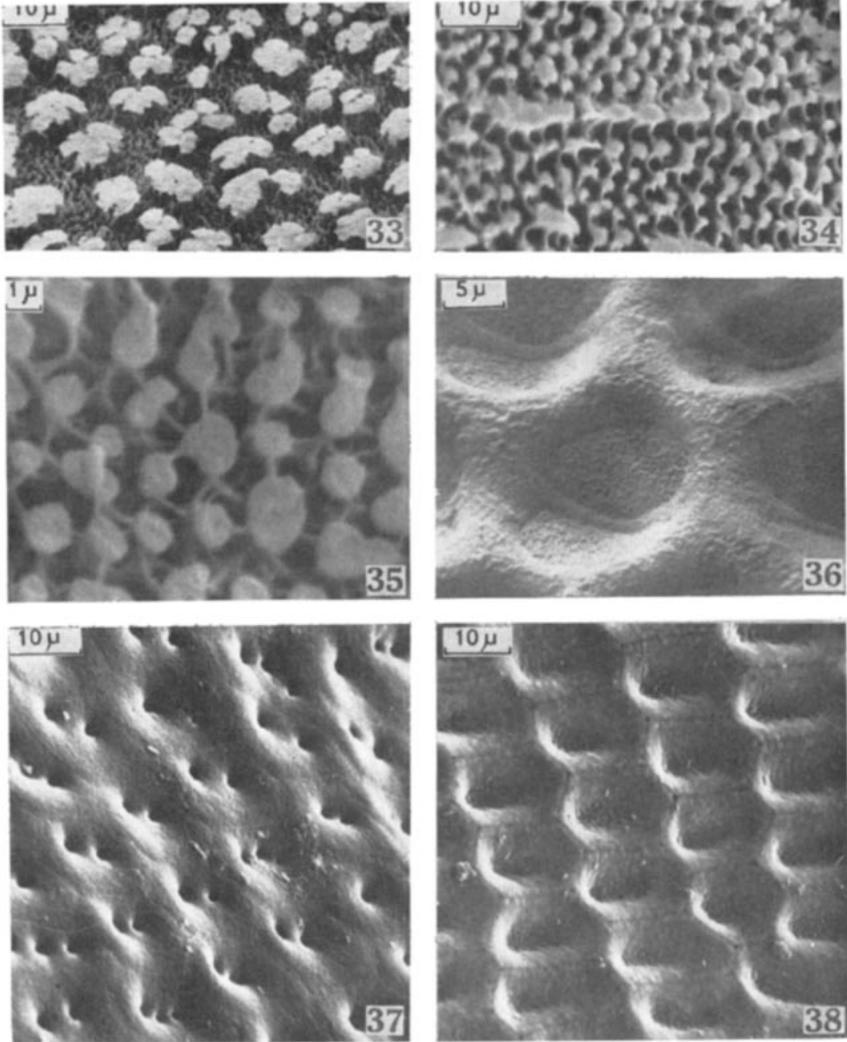
- FIG. 21. Anterior dorsal surface of the staphylinid beetle *Gabrius appendiculatus*.
FIG. 22. Dorsal acropyles of the staphylinid beetle *Philonthus finctarius*.
FIG. 23. Respiratory horn of *Microterys flavus* projecting through the dorsal surface of the host scale insect.
FIG. 24. Side of shell of ovarian egg of *Fannia armata*.
FIG. 25. Apex of the respiratory horn of the mirid bug *Termitophylidea opaca*.
FIG. 26. Surface of side of shell of *Tettigonia viridissima*.



Stereoscan electron micrographs of egg-shells.

- FIG. 27. Apex of posterior horn of *Drosophila (Drosophila) gibberosa*.
FIG. 28. Plastron surface of horn of *Drosophila (Sophophora) melanogaster*.
FIG. 29. Middle of the respiratory horn of the sepsid fly *Saltella scutellaris*.
FIG. 30. Surface of respiratory horn of the cordilurid fly *Clinoceroides glaucescens*.
FIG. 31. Outer apex of horn of the fly *Limnophora riparia*.
FIG. 32. Apex of the respiratory horn of the bug *Nepa cinerea*.

PLATE VI



Stereoscan electron micrographs of the middle area between the hatching lines of various muscoid flies.

- FIG. 33. *Polietes lardarius*.
- FIG. 34. *Musca domestica*.
- FIG. 35. *Egle cinerella*.
- FIG. 36. *Phaonia variegata*.
- FIG. 37. *Myospila meditabunda*.
- FIG. 38. *Stomoxys calcitrans*.

membrane attached to the inner surface of the open network of the shell (17).

Sometimes eggs have a chorionic structure that appears to be a plastron on morphological grounds. However, if these structures are readily flooded by water, there can be no question of plastron respiration. A good example of such an egg is that of the cabbage root fly, *Erioischia brassicae*. In this fly the structure of the chorion is typical of the Muscinae and Anthomyiinae, but the meshworks are readily flooded by water at virtually no excess pressures (27).

If the insect has a "perfect" plastron, its oxygen consumption under water should approach that in air. The physical efficiency of most plastrons of both eggs and other stages is very much less than this. In the methods given in another section (p. 360) for comparing the efficiency of plastrons of different insects, it must be remembered that the efficiencies being compared are purely physical. The plastron of one insect that was, say, only 20 per cent as efficient as that of another, might nevertheless be 100 per cent efficient in the biological sense if it always enabled the insect to survive the hazards to which it was exposed in nature.

INDEPENDENT EVOLUTION OF PLASTRON-BEARING HORNS

In order to establish the independent evolution of a similar structure in two or more groups, it is only necessary to show that the nearest common ancestor of the groups concerned lacked the structure in question. A demonstration that two structures or organs are of independent origin is, of course, also a demonstration that they are not homologous however close and detailed may be their resemblance. Conversely, lack of resemblance between organs or structures of different groups is *of itself* no argument against homology because phyletic continuity may exist between organs that have had a long history in quite different environments and may even have come to subserve quite different functions.

In most of the species known to have plastron-bearing horns, the plastron is confined to the horn or part of the horn. However, in such flies as the Calliphoridae and Muscidae that have plastron-bearing horns, a plastron is also present between the hatching lines. Such flies clearly illustrate the difficulty of classifying chorionic plastrons because it is frequently very difficult to decide whether or not the dilated sides of the median area between the hatching lines are sufficiently produced anteriorly to be called horns. Thus, whether a particular egg is said to have a respiratory horn or not may rest on a decision that is largely subjective or at best purely arbitrary.

Although the respiratory structures of relatively few eggs have been adequately described, enough is now known about the general form of insect eggs to show that eggs with respiratory horns are not common. Their extremely sporadic occurrence not only in the Insecta but also within particular families seems to be sufficient testimony to their independent origin, in the absence of evidence to suggest that the ancestral egg of the Insecta

was provided with horns. Horns bearing a plastron seem to be a primitive feature in only one family of insects, namely, the Nepidae (Hemiptera). It seems very unlikely that any Nepidae will be found without plastron-bearing horns, and already half of all the known genera of the family have been examined (15, 18). It was previously supposed that plastron-bearing horns were a primitive feature of flies of the family Sepsidae (16), but it has recently been found that some Sepsidae have respiratory horns without a plastron.

It is now known (3, 16, 19) that eggs with plastron-bearing horns have been independently evolved in the following groups:

HEMIPTERA

1. Tettigometriidae (*Tettigometra*)
2. Acanaloniidae (*Acanalonia*)
3. Tropiduchidae (some)
4. Nepidae (Fig. 32)
5. Miridae (*Termtophylidca*) (Fig. 25)
6. Miridae (some Cylapinac)

HYMENOPTERA

7. Encyrtidae (some) (Fig. 23)

DIPTERA

8. Dryomyzidae (*Dryomyza*)
9. Sepsidae (many) (Fig. 29)
10. Coelopidae (*Orygma*)
11. Sphaeroceridae (*Coprophila*)
12. Sphaeroceridae (some *Leptocera*)
13. Drosophilidae (some *Drosophila s. lat.*) (Figs. 27, 28)
14. Cordiluridae (some) (Figs. 11, 12)
15. Muscidae (some *Eumusca*)
16. Muscidae (*Myospila*)
17. Muscidae (*Mydea*) (Fig. 10)
18. Muscidae (*Hebecnema*)
19. Muscidae (some *Linnophora*) (Fig. 31)

Many more than 19 instances of the independent origin of plastron-bearing horns will be found. Even among the groups cited above, the number is greater. For instance, the Drosophilidae are cited as a single instance of the independent evolution of such horns, but within the genus *Drosophila* such horns have been evolved on several occasions unless we are to suppose that the common ancestor of recent species had a large number of horns and that differences in number between the species are due to reduction rather than to the acquisition of additional pairs of horns. Horns are certainly not a primitive feature in the Drosophilidae, and they are absent even in a few species of *Drosophila (s. lat.)* e.g., *D. (Phteridosa) flavicola* Sturt, and *D. (Hirtodrosophila) sexvittata* Okada. In the subgenus *Hirtodrosophila* there are species with and those without horns. In a recent study (un-

published) it was found that the fine structure of the plastron of the species of the subgenus *Sophophora* (Fig. 28) was very different from that of the species of the subgenus *Drosophila* (Fig. 27).

The great majority of instances of the independent evolution of chorionic plastrons occur, as might be expected, among species without horns, but no attempt has yet been made to list these. Some idea of the enormous variation that can exist in the structure of the surface of the shell, even among closely related groups, is shown in Figures 33–38.

RESPIRATORY EFFICIENCY OF EGG PLASTRONS

If a plastron is to serve as an efficient respiratory structure it must (*a*) resist wetting at the hydrostatic pressures to which it is subjected in nature; (*b*) resist loss of waterproofing from surface active materials; (*c*) maintain a satisfactory ratio between the rate of oxygen consumption and the area of the plastron; and (*d*) ensure that the drop in oxygen pressure along the plastron be small enough so that the whole of the plastron is effectively used.

Resistance to wetting by hydrostatic pressures and surface active substances.—The resistance of the plastrons of the eggs to wetting by excess pressures has been determined for a number of species of flies (11–14, 17, 24, 26) and bugs of the family Nepidae (15). Wetting of the plastron always occurs before there is a mechanical breakdown of the plastron, as is also true of the plastrons of spiracular gills. It has been said that in adults of the bug *Aphelocheirus* the resistance to the entry of water is greater than the mechanical strength of the hair-pile (40, 41), but recent experiments on this bug show that its plastron conforms to the general rule and is wetted before a breakdown of the hair-pile occurs.

Crisp (5) has given figures for the resistance of the plastrons of the eggs of 14 species of Hemiptera and Diptera. Crisp's figures are based upon calculations from my drawings. In every instance they exceed the figures determined by me experimentally, often by a factor of 3 although by a factor of no less than 13 in *Musca domestica*. Crisp's calculations involve a number of assumptions about the angle of contact. Furthermore, no allowance is made for the time that the pressure is applied, and his equations therefore do not allow for creep. Figures for the resistance of the plastron to wetting by excess pressures have little meaning unless the times that the pressures were applied are also given.

Most eggs with plastrons occur in places where they can be struck by drops of rain. Assuming a raindrop to be spherical, the pressure it exerts on striking a plastron is equivalent to a head of water of about 1000 times its diameter. A very large raindrop of a diameter of 4 mm will thus exert a pressure equivalent to about 31 cm Hg. But this pressure is exerted only for about a millisecond, and it has been shown that plastrons least resistant to wetting will withstand such pressures for about 30 minutes (12).

The resistance of the plastron to wetting by excess pressures varies di-

rectly as the surface tension of the water. Any change in the geometry or the nature of the surface of the plastron network that increases its resistance to wetting by surface-active substances, also increases its resistance to wetting in clean water by excess pressures because wetting at excess pressures always occurs before there is a mechanical breakdown of the plastron network. It therefore follows that selection for greater resistance to wetting by surface-active substances inevitably results in an increase in the resistance to wetting by excess pressures. These facts seem to provide a satisfactory explanation of the paradox that the plastrons of many kinds of terrestrial eggs are more resistant to wetting by excess pressures in clean water than are the plastrons of many wholly aquatic insects (12): under natural conditions many terrestrial eggs are often exposed to concentrations of surface-active substances that rarely if ever occur in the streams in which the aquatic insects live. In many environments the very flooding necessary to produce high pressures will also dilute the surface-active substances and so increase surface tension. However, many eggs, such as those of flies, are often laid in decomposing materials in cracks and crevices. When such niches are flooded there may be no persistent turbulence, and the surface tension of the water immediately around the eggs will be lowered by surface-active substances diffusing out of the decomposing materials in which the eggs were laid.

It has been found (12-14) that dipterous eggs may be placed in two groups according to the resistance of their plastrons to excess pressures: (a) those normally found in dung, especially cow dung, and (b) those normally found in decaying vegetable and animal materials. The first group includes some Cordiluridae (*Scopeuma*) and a number of Muscidae (*Musca*, *Orthellia*, *Polietes*, *Hebecnema*) in which the resistance of the plastron falls off rapidly on exposure to excess pressures of over 30 cm Hg for 30 minutes. The second group includes *Drosophila* and Calliphoridae (*Calliphora*, *Lucilia*) in which the plastron resists excess pressures of 60 to 100 cm Hg for 30 minutes or more.

It would appear that the difference between the two groups of eggs in the resistance of their plastrons to excess pressures may be related to the degree to which surface-active materials reduce the surface tension of water in contact with the two kinds of materials. Most of the material in cow dung consists of lignin and undigested cellulose, and these decompose very slowly. It seems likely that the concentrations of organic acids and other surface-active substances in cow dung do not reach the levels to be found in liquifying flesh or liquifying vegetable material from which most of the fats and proteins have not been removed. The surface tension on temporary pools of rain water on the surface of a cow pat was found to be 50 dynes/cm. Under comparable conditions the surface tension of water standing on decomposing flesh is reduced to 39 or 40 dynes/cm (12). Dilution has a relatively slight effect on surface tension. For instance, when the liquid collected from the surface of a cow pat was diluted with tap water

to half its strength, the surface tension was only increased to 53.5 dynes/cm, and when diluted to a quarter the surface tension was increased to 55.5 dynes/cm. In this connection it is of some interest to note that the Sepsidae, which are the only flies of the first group that will sometimes also oviposit on dead animals, have egg plastrons that are more resistant to excess pressures than those of the species restricted to dung.

Rate of oxygen uptake and area of plastron.—The aeropyles of perhaps most kinds of terrestrial insect eggs are hydrophobe. When the egg is immersed in water, a water-air interface is established across the openings of the aeropyles, and at normal excess pressures water does not flood the respiratory system. The water-air interface across the aeropyles inevitably functions as a plastron. But when only a small number of aeropyles is present, the total water-air interface is small and such plastron respiration as occurs may be of very little, if any, significance. It is only necessary to increase the number or size, or both, of the aeropyles to form a water-air interface of sufficient extent to satisfy the oxygen requirements of the egg by plastron respiration.

One of the factors that necessarily determines the efficiency of a plastron is the area of its water-air interface in relation to the weight of the insect. When this is expressed as units of water-air interface per unit body weight, a comparison can be made between the efficiency of plastrons of insects of quite different weights. The validity of such comparisons rests upon the fact that, in general, the rate of respiration of insects is directly proportional to their total live weight [review by Keister & Buck (28)]. Comparisons between different insects must, of course, be made when they are in strictly comparable phases of development.

In most insects with plastrons, the water-air interface is about 10^5 to $10^6 \mu^2$ per milligram. The insect with a structure clearly evolved for plastron respiration but with the poorest ratio of water-air interface to weight is the pupa of the fly *Eutanyderus wilsoni*, which has $1.5 \times 10^4 \mu^2$ per milligram (25). It may be supposed that an insect egg has a plastron that satisfies a significant part of its oxygen requirements when the water-air interface/weight ratio is 15,000 μ^2 /mg, although selection for plastron respiration as such must occur well before even this ratio is achieved.

The staphylinid beetle *Oxyopus olens* has about 4000 aeropyles confined to an equatorial band (34). When the egg is immersed in water there will be a water-air interface of 3000 to 4000 μ^2 /mg. It was found that the oxygen uptake of the egg was reduced from 1.6 to 1.8 μ l/hour to 0.4 μ l/hour when it was covered by a 2 mm layer of well-aerated water. The egg would recover and develop normally after its respiration had been continuously reduced to 0.4 μ l/hour for 4 days (34). It would appear that the egg of this beetle has a rudimentary plastron sufficient for maintenance but not for growth when it is flooded.

The percentage of the surface area that must be water-air interface for there to be 15,000 μ^2 per milligram has been calculated for spherical eggs

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of different diameters and for prolate spheroids of different shapes using the equation: surface area =

$$2\pi b^2 + 2\pi ab [a^2 / (a^2 - b^2)]^{1/2} \sin^{-1} [(a^2 - b^2) / a^2]^{1/2}$$

where a is the major semiaxis and b is the minor semiaxis. The specific gravity of the tissue is assumed to be 1. Because, in other stages of most plastron-bearing insects, the water-air interface to weight relation is usually about $10^6 \mu^2$ per milligram, the percentage of the surface that must be aeropyle openings to satisfy this condition is also calculated and is shown in brackets in Table I.

The percentage of the surface required to satisfy the conditions indicated in Table I is calculated for the weight of the tissue in the egg. The same area of gas-water interface is required at the outer surface of the shell. However, the shell has a total surface area greater than that of the metabolically active part of the egg by a factor of the square of the ratio of the linear dimensions. The percentage of the shell that must be gas-water interface is therefore smaller by this factor. To correct this, the percentages given in the Table must be multiplied by $(r/R)^2$, where r is the radius of the egg without the shell and R is the radius of the egg including the shell.

It requires relatively little experience to be able to estimate at first sight the approximate percentage of the surface of the egg that is aeropyle openings. For instance, in both *Phragmatobia* (Fig. 4) and *Tettigonia* (Fig. 26) the aeropyle openings occupy about 1 to 2 per cent of the surface, whereas in *Antheraea pernyi* (Fig. 8) they occupy about 12 per cent. In both *Phragmatobia* and *Tettigonia*, plastron respiration is probably significant when the egg is flooded, whereas in *Antheraea* there can hardly be any doubt about its significance. In Table I it may be seen that in a spherical egg of 2 mm diameter, 0.50 per cent of the surface is equivalent to $1.5 \times 10^4 \mu^2/\text{mg}$. However, multiplying by the correction factor $(r/R)^2$, only 0.45 per cent of the surface is required for the same relation. The value for *Antheraea* is therefore about $4 \times 10^5 \mu^2/\text{mg}$. The actual relation of water-gas interface to weight is, however, somewhat better than this because the egg of *Antheraea* is semispherical rather than spherical.

A much more accurate comparison between the efficiency of the plastron of different species can be obtained when the rate of oxygen uptake is known. Values of q/Ai_o for the different species can then be compared, where q is the rate of oxygen uptake under water (ml/sec), A the area of the plastron (cm^2), and i_o the invasion coefficient of oxygen (4.8×10^{-4}). The values of q/Ai_o for three species of blowflies at 15° C were found by R. J. Thompson (unpublished data) to be as follows: *Calliphora erythrocephala*, 0.13; *C. vomitoria*, 0.26; and *Protophormia terrae-novae*, 0.12. These values are, so far, the only ones that have been calculated for insect eggs. The values obtained by Thorpe & Crisp (43) for six species of adult insects range from 0.005 for *Apheliocheirus aestivalis* to 0.12–0.17 for

TABLE I
THE PERCENTAGE OF SURFACE AREA THAT MUST BE WATER-AIR INTERFACE FOR THERE TO BE 15,000 μ^2 INTERFACE PER MILLIGRAM FOR SPHERES OF DIFFERENT DIAMETERS AND PROLATE SPHEROIDS OF DIFFERENT DIAMETERS AND SHAPES. THE PERCENTAGE OF SURFACE AREA REQUIRED FOR 10⁶ μ^2 /MG IS GIVEN IN BRACKETS.

b/a	Diameter in mm										
	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0	2.6	3.0
1.00	0.100 (6.67)	0.150 (10.0)	0.200 (13.3)	0.250 (16.7)	0.300 (20.0)	0.350 (23.3)	0.400 (26.7)	0.450 (30.0)	0.500 (33.3)	0.650 (43.3)	0.750 (50.0)
0.95	0.102 (6.78)	0.153 (10.2)	0.203 (13.5)	0.254 (16.9)	0.305 (20.3)	0.356 (23.7)	0.407 (27.1)	0.458 (30.5)	0.508 (33.9)	0.661 (44.1)	0.763 (50.1)
0.90	0.103 (6.89)	0.155 (10.3)	0.207 (13.8)	0.258 (17.2)	0.310 (20.7)	0.362 (24.1)	0.413 (27.6)	0.465 (31.0)	0.517 (34.4)	0.672 (44.8)	0.775 (51.7)
0.85	0.105 (7.01)	0.158 (10.5)	0.210 (14.0)	0.263 (17.5)	0.315 (21.0)	0.368 (24.5)	0.420 (28.0)	0.473 (31.5)	0.525 (35.0)	0.683 (43.5)	0.788 (52.5)
0.80	0.107 (7.12)	0.160 (10.7)	0.214 (14.2)	0.267 (17.8)	0.320 (21.4)	0.374 (24.9)	0.427 (28.5)	0.481 (32.0)	0.534 (35.6)	0.694 (46.3)	0.801 (53.4)
0.75	0.109 (7.23)	0.163 (10.8)	0.217 (14.5)	0.271 (18.1)	0.326 (21.7)	0.380 (25.3)	0.434 (28.9)	0.488 (32.5)	0.543 (36.2)	0.705 (47.0)	0.814 (54.3)
0.70	0.110 (7.35)	0.165 (11.0)	0.221 (14.7)	0.276 (18.4)	0.331 (22.0)	0.386 (25.7)	0.441 (29.4)	0.496 (33.1)	0.551 (36.7)	0.717 (47.8)	0.827 (55.1)
0.65	0.112 (7.47)	0.168 (11.2)	0.224 (14.9)	0.280 (18.7)	0.336 (22.4)	0.392 (26.1)	0.448 (29.8)	0.504 (33.6)	0.560 (37.3)	0.728 (48.5)	0.840 (56.0)
0.60	0.114 (7.58)	0.171 (11.4)	0.227 (15.2)	0.284 (18.9)	0.341 (22.7)	0.398 (26.5)	0.455 (30.3)	0.512 (34.1)	0.568 (37.9)	0.739 (49.3)	0.853 (56.8)
0.55	0.115 (7.69)	0.173 (11.5)	0.231 (15.4)	0.288 (19.2)	0.346 (23.1)	0.404 (26.9)	0.461 (30.7)	0.519 (34.6)	0.577 (38.4)	0.750 (50.0)	0.865 (57.7)
0.50	0.117 (7.80)	0.176 (11.7)	0.234 (15.6)	0.293 (19.5)	0.351 (23.4)	0.410 (27.3)	0.468 (31.2)	0.527 (35.1)	0.585 (39.0)	0.761 (50.7)	0.878 (58.5)
0.40	0.120 (8.00)	0.180 (12.0)	0.240 (16.0)	0.300 (20.0)	0.360 (24.0)	0.420 (28.0)	0.481 (32.0)	0.541 (36.0)	0.601 (40.0)	0.781 (52.0)	0.901 (60.1)
0.30	0.123 (8.19)	0.184 (12.3)	0.246 (16.4)	0.307 (20.5)	0.369 (24.6)	0.430 (28.7)	0.492 (32.8)	0.553 (36.9)	0.615 (41.0)	0.799 (53.3)	0.922 (61.4)
0.20	0.125 (8.34)	0.188 (12.5)	0.250 (16.7)	0.313 (20.9)	0.376 (25.0)	0.438 (29.2)	0.501 (33.4)	0.563 (37.5)	0.626 (41.8)	0.814 (54.2)	0.939 (62.6)
0.10	0.127 (8.45)	0.190 (12.7)	0.253 (16.8)	0.317 (21.1)	0.380 (25.3)	0.444 (29.7)	0.507 (33.8)	0.570 (38.0)	0.634 (42.1)	0.824 (55.7)	0.951 (64.1)

Hydrophilus piceus. A value of 0.16 was obtained for the pharate adult of *Simulium ornatum*, using the pupal spiracular gill (22). The values of q/Ai_0 will vary according to the stage of development of the egg, and the area of the plastron will become most critical when the oxygen consumption is greatest.

Drop in pressure along the plastron.—It has been shown by Thorpe & Crisp (42) that the function $(i_0x_1^2/Dh)^{1/2}$ ($=nx_1$) determines the shape of the curve of distribution of partial pressures within the plastron (i.e., the efficiency of the plastron as a respiratory structure for a given mean drop in partial pressure between the outside medium and the spiracular atrium), where i_0 is the invasion coefficient of oxygen, x_1 the greatest distance of the plastron network from the tissue, D the diffusion constant of oxygen in the plastron space, and h the thickness of the plastron. The diffusion constant of oxygen within the plastron will be similar to its value in air, $0.18 \text{ ml cm}^{-2} \text{ s}^{-1}$. The values used for D and i_0 when calculating nx_1 should be reduced appropriately to allow for obstructions caused by very dense plastron meshworks. However, errors caused by imprecise assumptions in making these adjustments are reduced in importance because the square root is taken.

In most, if not all, eggs without respiratory horns, the plastron is so close to the tissues that all of the plastron is used effectively. In many of the eggs with respiratory horns the plastron is in the form of a tube. The outer surface of the respiratory horn bears the plastron network across which oxygen diffuses from the ambient water and diffuses along the tube to the meshwork of the inner shell. If the tube is assumed to be of uniform radius of cross-section R , h must be replaced by $R/2$ so that $nx_1 = 2i_0x_1^2/DR)^{1/2}$. From my illustrations of various eggs with respiratory horns in the form of tubes, Crisp (5) has calculated the values for nx_1 . With some corrections these are as follows:

	Length of plastron (mm)	nx_1
<i>Nepidae</i>		
<i>Nepa cinerea</i>	0.6	0.10
<i>Ranatra linearis</i>	4	1.7
<i>Cercotmetus asiaticus</i>	12	2.45
<i>Sepsidae</i>		
<i>Sepsis violacea</i>	4	0.94
<i>Saltella scutellaris</i>	2.3	0.40
<i>Drosophilidae</i>		
<i>Drosophila gibberosa</i> (posterior pair of horns)	0.26	0.01

As the value of nx_1 exceeds 1.0, a progressively smaller proportion of the plastron area is effectively used. The respiratory horns of the genus

Cercotmetus (Nepidae) are 10 to 13 mm long with a plastron over most of their lengths. In insects with such exceptionally long respiratory horns, only part of the plastron is effectively used: the value of nx_1 for *Cercotmetus asiaticus* is 2.45. When the respiratory horn is so long that only part of its plastron is used, the selective advantage of the apical part may lie in its function as a simple respiratory tube that permits the egg to utilize atmospheric oxygen even when it is covered by a considerable depth of water.

UTILIZATION BY LARVA OF CHORIONIC RESPIRATORY SYSTEM

For one stage of an insect to utilize the plastron of the previous stage is a phenomenon that is already known among insect pupae with spiracular gills: the plastron of the pupal gill is always the chief respiratory organ of the young adult before it sheds the pupal cuticle, that is, the pharate adult (25). Whatever the type of chorionic respiratory system, it seems that it is always utilized by the young larva before it hatches. However, in some parasitic wasps of the family Encyrtidae the relation of the larva to the egg-shell is most unusual in that the larva continues to use the chorionic respiratory system after it has hatched.

Two types of eggs are recognized in the Encyrtidae, the stalked and the encyrtiform. The ovarian egg of both types is two-bodied. The contents of the anterior body or bulb are forced into the posterior body or bulb during oviposition. The tube that connects the two bulbs, together with part of the anterior body, is left as a slender stalk projecting above the surface of the host. In the genera that have the encyrtiform type of egg, e.g., *Oöencyrtus*, *Microterys*, and *Leptomastix*, a narrow-to-wide strip of the chorion of the posterior body contains a film of air supported between vertical columns or meshworks precisely as in the chorion of many Diptera, Hemiptera, and other insects. The air-containing part of the chorion was called the aeroscopic plate by Silvestri (38), and it has since been known by that name. The air film in the aeroscopic plate is continuous with that contained in the meshwork of the horn projecting above the surface of the host (Fig. 23).

Previous views of the function of the horn and aeroscopic plate have been summarised by Maple (35, 36), Clausen (2), and Zinna (48). More recently, it has been shown that there is a fundamental difference between the part of the aeroscopic plate external to the host, i.e., the meshwork on the horn, and that inside the host in the main body of the shell (16). The outer surface of the horn external to the host has an open meshwork. The outer surface of the aeroscopic plate within the host consists of an unbroken sheet of chorionin, but the inner surface of the aeroscopic plate consists of an open meshwork. Because of this structure the aeroscopic plate cannot be, as has been suggested (40), a plastron mechanism for extracting oxygen from the host's blood.

When it rains or when the host is otherwise submerged in water, the air is not displaced in the meshwork of the horn, which thus functions as a plastron (16). In the Encyrtidae that have eggs with plastron-bearing

horns, the first three larval instars are metapneustic. The posterior spiracles of the larva are closely applied to the inner surface of the aeroscopic plate of the egg shell. It would seem that a circle of branched structures around each spiracle engages the open meshwork of the aeroscopic plate so that the continuity is effected between the air in the aeroscopic plate and that in the tracheal system of the larva.

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