2 | Polyphyletic Evolution of Respiratory Systems of Eggshells, with a Discussion of Structure and Density-independent and Density-dependent Selective Pressures

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INTRODUCTION

The scanning electron microscope has made it possible to study the geometry of insect structures, particularly hard structures, at a magnification and resolution not possible before. In recent years an extensive survey has been made of the respiratory systems of insect eggshells with the aid of the scanning electron microscope. The terrestrial eggs of perhaps the majority of insects have mesh-works in the chorion or shell that hold a layer of gas. Many aquatic eggs also have such meshworks but the percentage of aquatic eggs with distinct respiratory systems of this kind seems to be smaller. The species that have meshworks that hold a layer of gas in the inner part of the chorion also have aeropyles or holes that extend between the gas space and the outer layers of the shell and so effect the continuity of the chorionic layer of gas and the ambient atmosphere. Most aeropyles are easily recognized with the light microscope because they are one or more microns wide. The interstices between the struts of the chorionic mesh-works that hold the gas layer are usually, as might be expected, wider than the mean free path of the respiratory gases, which is 0.1 μm for oxygen at 23 C°.

A very large number of terrestrial eggs, and a smaller number of aquatic ones, have the kind of permanent or unshrinkable physical gill called a plastron. The term plastron has been restricted to describe 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 at the hydrostatic pressures to which they are normally subjected in nature. An egg with a plastron can remain immersed indefinitely and obtain the oxygen it requires from the ambient water provided that the water is well-aerated. The selective advantage of the plastron method of respiration can only be under-

stood in relation to an environment that is alternately dry and flooded. 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 much of the surface of the shell. When the egg is dry, the interstices of the plastron network provide a direct route for the entry of atmospheric oxygen that does not necessarily involve the egg in water loss over a large area because the connection between the plastron and the tissues of the egg, or the pharate larva, may be very restricted. The capacity to avoid loss of water when the environment is dry is therefore not necessarily impaired by the provision of a plastron. For instance, in eggs with respiratory horns, such as those of many species of *Drosophila* (Fig. 1a, b and c) the plastron network of the surface of the horns provides a very large respiratory area when the egg is flooded, but when
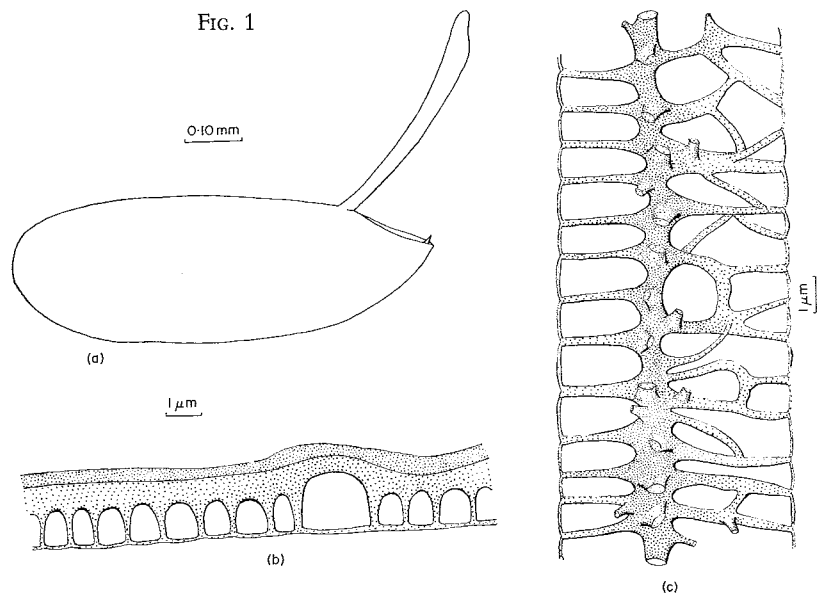
FIG. 1

Fig. 1 (a, b, c). Egg of *Drosophila melanogaster* Meig. (a) Right side of egg. (b) Optical section of chorion showing the inner air spaces. (c) Optical section of dilated part of respiratory horn about 60 μm from its apex.

the egg is dry water is lost only through the cross sectional area at the base of the horn provided of course that the outer layer of the main body of the shell is impermeable. The general principles of plastron respiration have recently been discussed at length (Hinton, 1968, 1969) and do not require elaboration here.

Scanning electron microscope studies of the respiratory systems of a large number of eggs have revealed the fact that respiratory systems almost identical in fine structure have been independently evolved an enormous number of times. In this paper some of the principles of classification are considered in relation to polyphyletic origins. Because the functional significance of a high percentage of the structures of the shell can be determined, it has become possible to distinguish sharply between two kinds of selective pressures, those arising from the density-independent part of the environment and those arising from the density-dependent part of the environment. In the concluding section the significance of these two types of selective pressures is discussed.

POLYPHYLETIC EVOLUTION OF EGG PLASTRONS

In order to establish the independent evolution of similar organs or structures in two or more groups it is only necessary to show that such organs or structures are absent in the common ancestor of the groups concerned, that is, the organs or structures in question have no phyletic continuity. To demonstrate that two organs or structures are of independent origin is also to demonstrate 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 or structures that have had a long history in quite different environments and may even have come to subserve quite dissimilar functions.

A natural classification of the different kinds of egg plastrons, that is, one that would reflect the phylogenetic relationships of the groups, is precluded on principle because of the polyphyletic origin of the plastrons. Egg plastrons have been placed in three groups (Hinton, 1961), but so many intermediates have been found that for the present it is probably best merely to speak of those with and without plastron-bearing horns. The vast majority of eggs that utilize plastron respiration lack plastron-bearing horns. In those lacking horns the plastron network may extend over the entire shell, as in most Muscinae, or it may be confined to a part of the shell. In the Diptera–Cyclorrhapha the plastron is often restricted to the area between the hatching lines, as in the eggs of many of the more specialized flies. The plastron is sometimes present only on one side of the eggshell, as in bugs of the family Saldidae (Cobben, 1968). Sometimes the plastron may consist of a few or many discrete islands or craters scattered over the surface of the shell, as in *Musca vetustissima* and *M. sorbens* (Plate III, Figs 1, 2).

I have recently (Hinton, 1969) drawn attention to the fact that according to the fine structure of the surface of the plastron two rather different types may
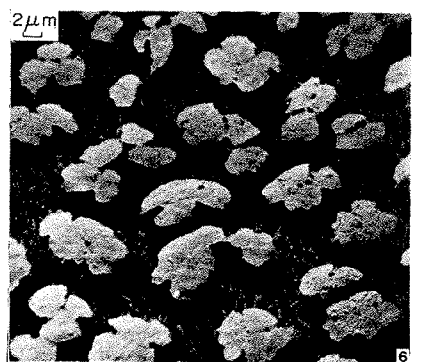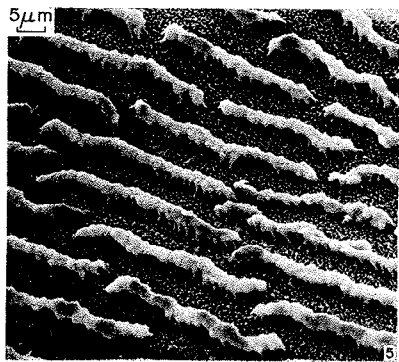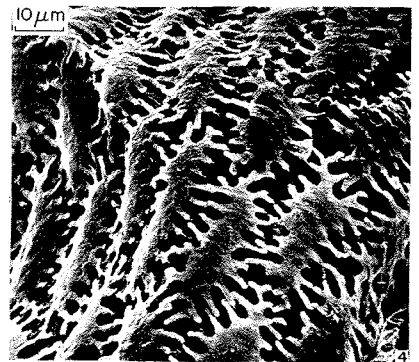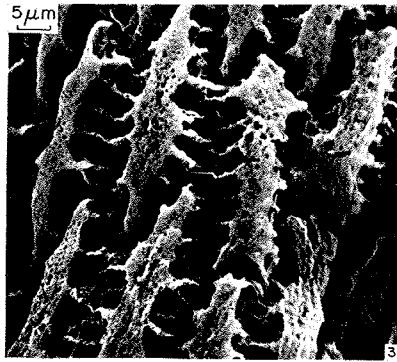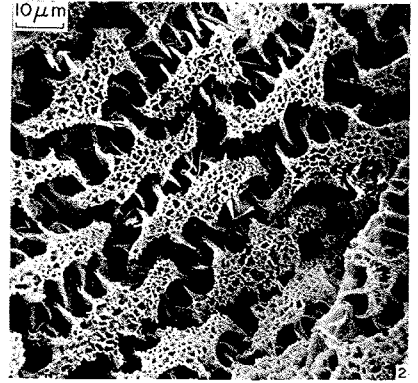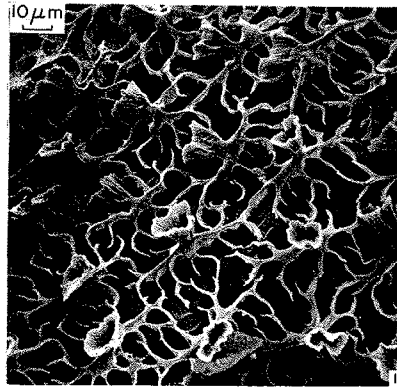
be recognized: (1) plastrons that clearly consist of an enlargement of the aeropyles (Plate IV, Fig. 3), or a great increase in their number, or both (Plate V, Figs 1, 2); and (2) plastrons such as those of the Muscidae that consist of a network (Plate II, Figs 1, 2). The origin of some surface networks by a sufficient approximation of many aeropyles is not difficult to visualize and no doubt often occurs. But it seems improbable that the plastron network of *Anopheles* eggs or those of *Chrysopa* (Plate II, Fig. 6) 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 hexagons that mark the boundaries of individual follicular cells, as in many long-horned grass-hoppers (Tettigoniidae). In many insects, on the other hand, the aeropyles tend to be confined to the boundaries of the hexagons, as they are in the eggs of many different kinds of moths (Plate IV, Figs 1, 2; Plate V, Figs 5, 6).

Egg plastrons have been evolved independently an enormous number of times, particularly within the orders Lepidoptera and Diptera. The great majority of instances of the independent origin of chorionic plastrons are to be found among eggs without respiratory horns, but as yet no attempt has been made to list these. Eggs with plastron-bearing horns are relatively rare (Figs 2 a–g), but, as I have recently shown (Hinton, 1969), there are no less than 19 groups in which such horns have been independently evolved, as follows:

HEMIPTERA

(1) Tettigometriidae (*Tettigometra*)
(2) Acanalonidae (*Acanalonia*)
(3) Tropiduchidae (some)
(4) Nepidae (Fig 2 e, g)
(5) Miridae (*Termatophylidea*)
(6) Miridae (some Cylapinae)

Plate I

Figs 1–4. Plastron network of side of shell of various species of Syrphidae.
Fig. 1. *Syrphidius ribsii* (L.).
Fig. 2. *Episyrphus balteatus* (Deg.).
Fig. 3. *Rhingia campestris* Meig.
Fig. 4. *Platycheirus peltatus* (Meig.).
Fig. 5. Side of shell of *Platypalpus pallidiventris* (Meig.), Empididae.
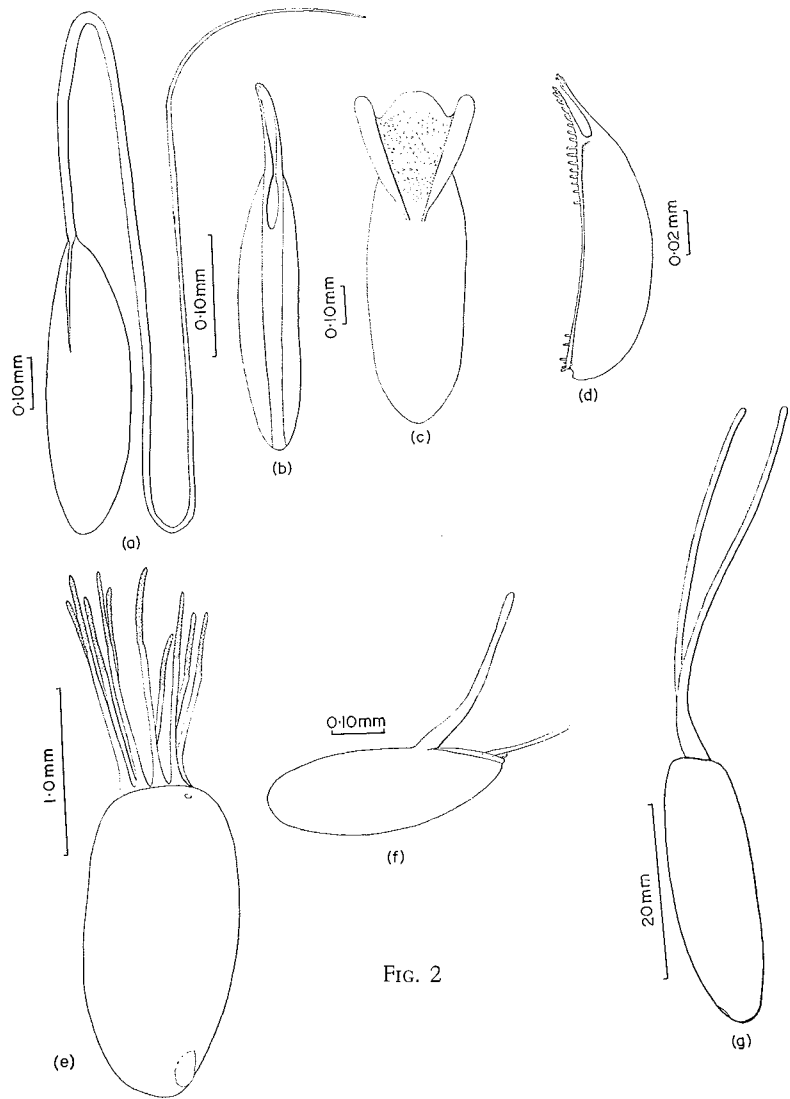Fig. 6. Plastron of median area between hatching lines of *Polietes lardarius* (F.), Muscidae.

Fig. 2 (a, b, c, d, e, f, g). Eggs with plastron-bearing respiratory horns. (a) *Sepsis violacea*
Meig., Sepsidae. (b) *Musca (Eumusca) autumnalis* Deg., Muscidae. (c) *Scopeuma
stercorarium* (L.), Cordiluridae. (d) *Hebecnema umbratica* (Meig.), Muscidae. (e)
Nepa rubra L., Nepidae. (f) *Drosophila gibberosa* (Patt. & Main.), Drosophilidae.
(g) *Ranatra fusca* Beauv., Nepidae.

HYMENOPTERA

(7) Encyrtidae (some)

DIPTERA

(8) Dryomyzidae (*Dryomyza*)
(9) Sepsidae (many, Fig. 2a)
(10) Coelopidae (*Orygma*)
(11) Sphaeroceridae (*Coprophila*)
(12) Sphaeroceridae (some *Leptocera*)
(13) Drosophilidae (some *Drosophila* s.lat., Figs 1a and 2f)
(14) Cordiluridae (some, Fig. 2c)
(15) Muscidae (some *Eumusca*, Fig. 2b)
(16) Muscidae (*Myospila*)
(17) Muscidae (*Mydea*)
(18) Muscidae (*Hebecnema*, Fig. 2d)
(19) Muscidae (some *Limnophora*)

Plastron-bearing horns appear to be a primitive feature in only one family of insects, bugs of the family Nepidae (Hinton, 1961). All other families that contain species with plastron-bearing horns also contain numerous species without such structures. It may be noted that there are in fact more than 19 instances of independent origin in the groups cited above. For instance, I have cited the Drosophilidae as a single instance of the independent origin of such horns, but within the genus *Drosophila* 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.* (*Phleridosa*) *flavicola* Sturt. and *D.* (*Hirtodrosophila*) *sexvittata* Okada. In the subgenus *Hirtodrosophila* there are species with and those without horns.

SOME OBSERVATIONS ON THE PRINCIPLES OF CLASSIFICATION

Statements about independent origins are statements about relationships, and their validity is necessarily dependent upon the degree to which nomenclature reflects phylogeny. In speaking of the independent evolution of structures, it has to be borne in mind that at any taxonomic level the preferred nomenclature is that which most nearly reflects the relative times of divergence of the different groups. Polyphyletic taxa are inevitably created when relative times of divergence are reversed. For instance, as I have shown elsewhere (Hinton, 1958), to
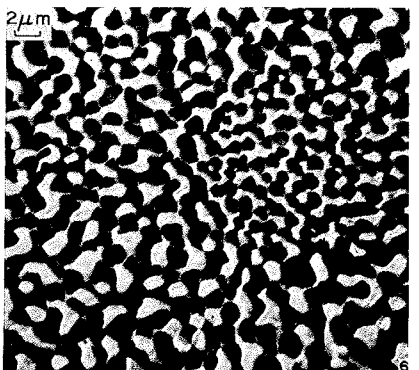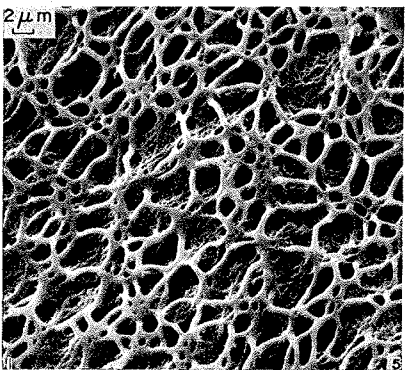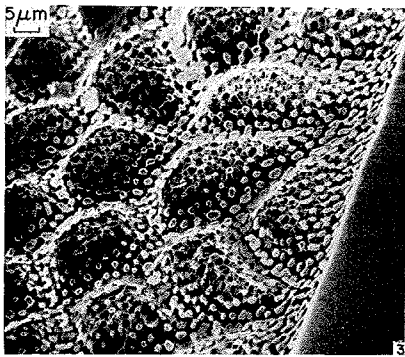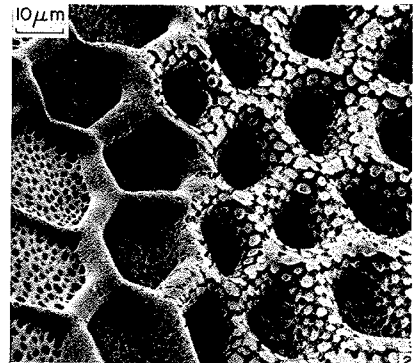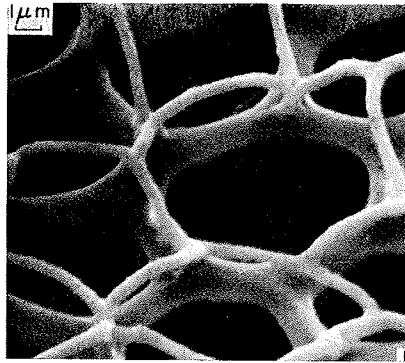
place the Permian Orthophlebiidae (or related families) in the order Mecoptera with recent Mecoptera is to create a polyphyletic order in terms of other panorpoid orders. To place the Orthophlebiidae in the Mecoptera is to say that they are more nearly related to the Mecoptera than to other panorpoid orders. In other words it is to say that they are more nearly related to the Mecoptera than are the Siphonaptera and Diptera to the Mecoptera, which is absurd. It must always be remembered that *one taxon can only be polyphyletic in terms of another, never in terms of itself.* In short, all living organisms could be placed in one family and this would not be polyphyletic although it would not be a useful classification because it would give no indication of phyletic relationships.

Mistakes in systems of classification arise essentially in three different ways: (1) because not enough facts are known about the taxa under consideration; (2) because the available evidence is misinterpreted, or; (3) because of a failure to understand the relation between nomenclature and the facts of evolution so that polyphyletic groups are created without intention. The first two kinds of mistakes do not require further explanation. Mistakes arising because of the failure to understand the relation between nomenclature and the facts of evolution can easily be avoided and have been much discussed since the 1950's by Hennig (1950) and others. Even so, there is still a widespread belief that phylogenetic systems should take into account the relative amounts of divergence from the primitive form, that the amount of divergence from the primitive form should be reflected in the nomenclature used. In other words, it is thought that differences in the rates of evolution should affect the position of the group in the nomenclatorial system. It is necessary to state most emphatically that in phylogenetic classifications we are in no way concerned with the amount of divergence. Concern with the degree or amount of divergence from the primitive plays so large a part in many supposedly phylogenetic classifications that it may be considered in a little more detail. In the first place, many of the ways chosen to portray phylogenetic systems, such as trees without a time scale,

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Plate II

Fig. 1. Side of shell showing the coarse and fine plastron networks of *Fannia armata* (Meig.), Muscidae; the fine network is more resistant to wetting by high hydrostatic pressures than is the coarse network.

Fig. 2. Plastron of mesal side of wing of the eggshell of *Fannia coracina* (Loew).

Fig. 3. Plastron of side of wing of shell of *Fannia atripes* Stein.

Fig. 4. Same of *Fannia nidica* Collin.

Fig. 5. Plastron of ventral side of wing of shell of *Fannia canicularis* (L.).

Fig. 6. Plastron of side of shell of *Chrysopa* sp., Neuroptera.
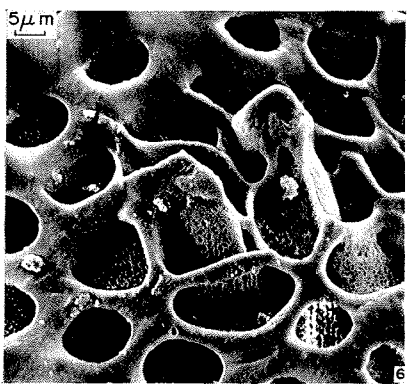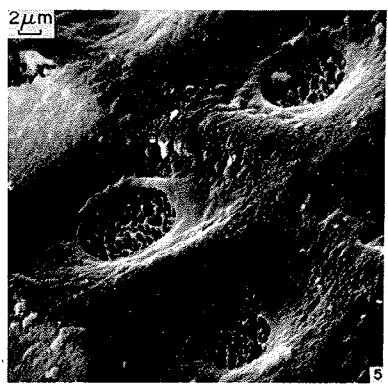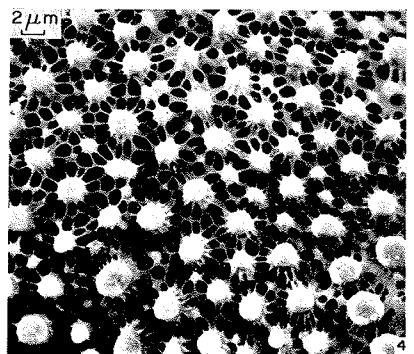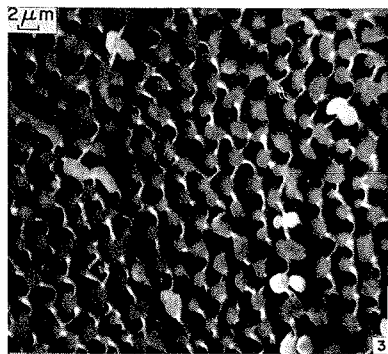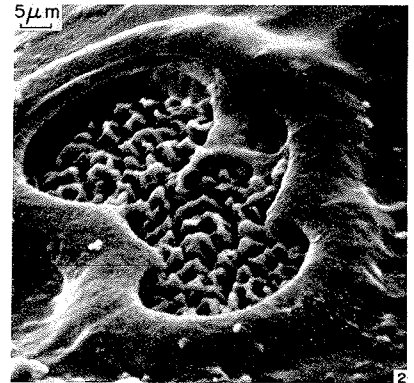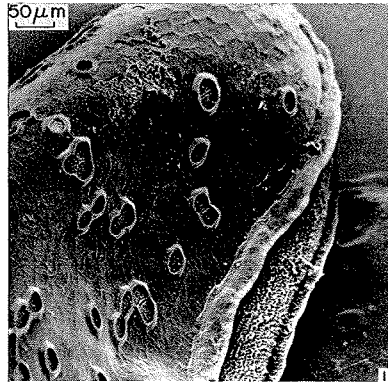
almost inevitably mean that allowance is being made for the amount of divergence from the common ancestor. However, it should be clear that if the amount of divergence of two or more groups from their common ancestor is allowed to influence the structure of a phylogenetic tree, it can only do so by altering time relations, that is, by reversing relative times of origin and therefore making polyphyletic groups.

The amount or degree of divergence from the primitive is an indication of the rate of evolution. Because the amount of divergence is an indication of the rate of evolution it has no necessary bearing upon the time of origin. For instance, the rates of evolution may be entirely different in very closely related groups. To consider but a single example, some insects enter ants' nests and in due course become what we call true guests or symphiles of the ants. There is a very great selective pressure on symphiles for a circumscribed range of structure. The very heavy selective pressure exerted upon the morphological features of a species that has become an ant guest means that its rate of evolution towards a different form and structure is vastly accelerated as compared with its relatives that remain outside ant nests. A particularly striking example of this is to be found in some ground beetles (Carabidae) of the tribe Ozaenini. In the early or middle tertiary one or more groups of Ozaenini became ant guests. Their rate of morphological change was so greatly accelerated that the Ozaenini found today in ant nests so little resemble their relatives outside that until recent years they were placed without question in a family of their own, the Paussidae. Thus in this instance the fact that the rate of evolution was allowed to affect classification resulted in making the Carabidae polyphyletic in terms of the family Paussidae. In short, polyphyletic categories are inevitably created when relative times of origin are reversed. In a phylogenetic classification no account can be taken of different rates of evolution because the rate of evolution is not related to the times of origin but to outward circumstance that has nothing to do with times of origin.

One of the most general laws of evolution is what I have called the law of unequal development (Hinton, 1958), borrowing a name from the 19th century

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Plate III

Fig. 1. Anterior end of shell of *Musca sorbens* Weid., Muscidae.
Fig. 2. Plastron crater of same species.
Fig. 3. Plastron network of side of shell of *Orthellia caesarion* (Meig.), Muscidae.
Fig. 4. Plastron network of side of shell of *Culex pipiens fatigans* Wied., Culicidae.
Fig. 5. Plastron craters of side of shell of *Idiostatus aequalis* (Scudder), Tettigoniidae.
Fig. 6. Plastron craters around a micropyle of *Idionotus siskiyou* Hebard, Tettigoniidae.
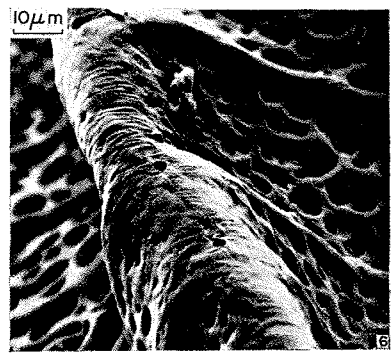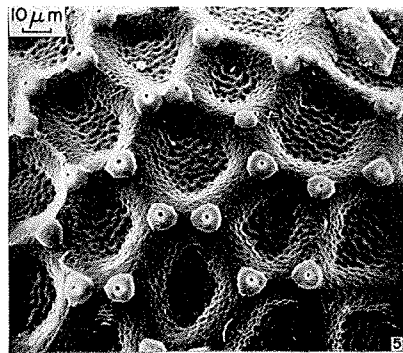
economists who were concerned with the evolution of different social systems. This law states that not only do different groups evolve at different rates but within any taxon the organ systems themselves evolve at different rates. This necessarily follows because the selective pressure of the physical and biological environment can never be expected to be exactly equal on every organ system for long periods of time. This is why so many animals and plants are such mixtures of specialized and primitive features. The idea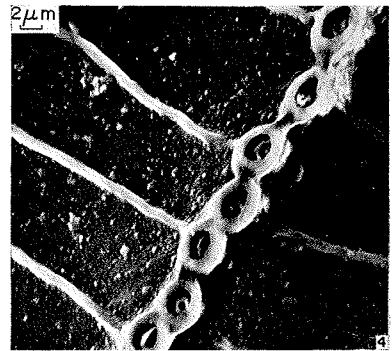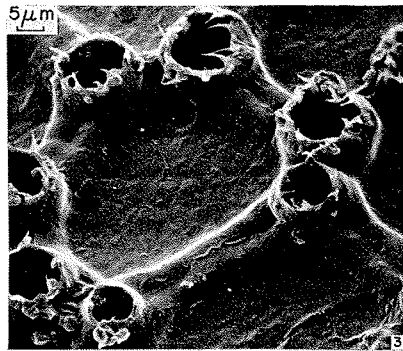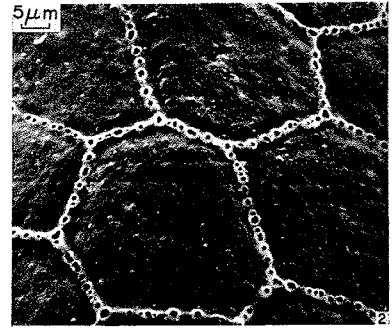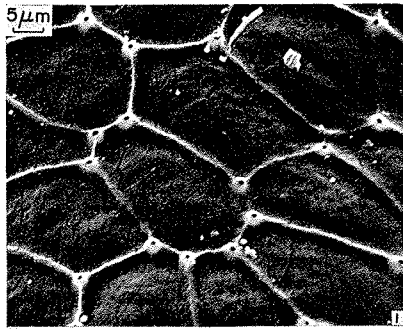 of unequal development has been referred to a number of times in the work of D. M. S. Watson, and De Beer (1954) has referred to what I call the law of unequal development as "Watson's Rule".

Attempts are often made to assign values to different characters and to estimate the degree of specialization or the degree of primitiveness by summating these values. For instance, a primitive leg with the trochanter unfused to the femora is given, say, 5 points and one where the femora and trochanter are fused together is given, say, 0 points, and so on. When this has been done for a large number of structures or characters of one kind or another the total scores are then supposed to provide an answer as to which group is more specialized and which is more primitive. However, looking at the matter a little more closely, it will be seen that attempts of this kind are based upon a failure to understand that different morphological characters have no universal equivalent. They cannot be weighed one against the other any more than the use value of a shirt can be compared with the use value of a pair of shoes. The value of commodities with different use values can, however, be compared in terms of their value or price in money. That is, money functions as a universal equivalent for comparisons of this kind between different commodities but there is no universal

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Plate IV

Fig. 1. Aeropyles of side of shell of *Arctia caja* (L.), Arctiidae.

Fig. 2. Aeropyles of side of shell of *Phragmatobia fuliginosa* (L.), Arctiidae; the total water-air interface of the aeropyles when the egg is flooded is about 1 to 2% of the surface, which in an egg of this size is sufficient to make plastron respiration of some significance.

Fig. 3. Aeropyles of side of shell of *Antheraea pernyi* Guér., Saturniidae; the aeropyles are greatly enlarged and the total area of the openings is about 12% of the surface of the egg, and there is therefore hardly any doubt that in this egg plastron respiration is significant when it is covered by water.

Fig. 4. Aeropyles of side of shell of *Ochropleura plecta* (L.), Agrotidae.

Fig. 5. Aeropyles of side of shell of *Semiothisa signaria dispuncta* Walk., Geometridae.

Fig. 6. Aeropyles on one of the longitudinal ridges of the eggshell of *Argynnis selene* (Schiff.), Nymphalidae.
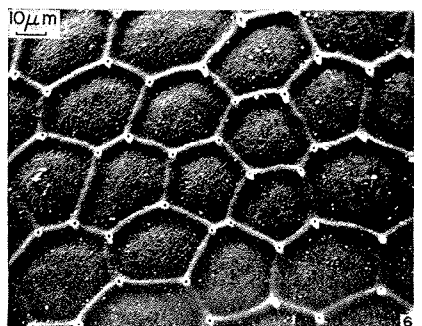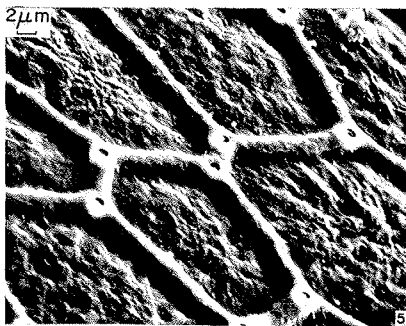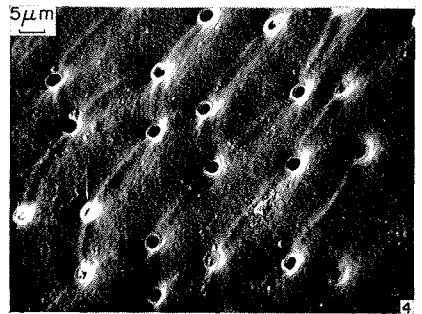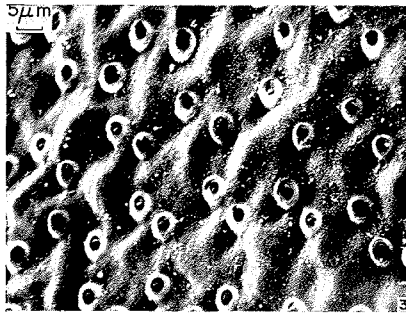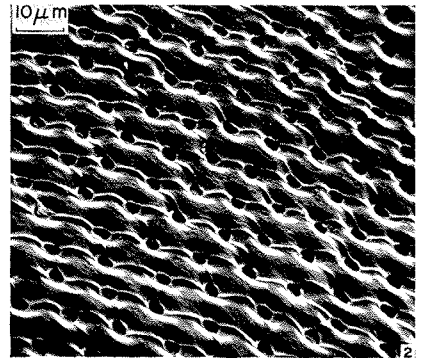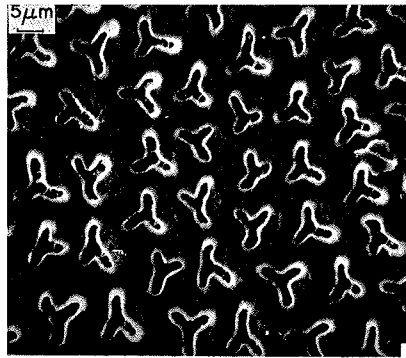
equivalent that can be used for comparing the value of morphological characters.

During the last decade there have been many papers published on what may be described as numerical taxonomy. In nearly all of these papers is the assumption, always implicit but occasionally explicit, that there is some kind of universal equivalence between characters. However, it seems clear enough that many pairs of taxa could converge in evolution to such an extent that 99% of all their characters were the same but the groups were nevertheless distantly related, that is they came from different stocks. Conversely, it often happens that two groups that share a common ancestor more recently than any other groups diverge so widely during the course of evolution that hardly any of their characters are the same. The numerical taxonomist has not yet invented a method of taking these circumstances into account. To put it another way: (1) the similarity might be due to convergence, i.e. the structures were not identical in all ancestors of the two groups *and* in the common ancestor of both, or (2) the present similarity of structures is due to the fact that they were possessed by the common ancestor of the two groups and in both have remained unchanged. If the first proposition is true, then the similarity, however great, should be given absolutely no weight in deciding relationships. If the second proposition is correct it is proof of a relationship. Most numerical taxonomists simply make lists of characters without distinguishing whether the first or second of these propositions applies to them, and it is difficult to see any value in the exercise apart from the fact that it is always useful to discover characters that may have been overlooked by others.

STRUCTURE IN RELATION TO DENSITY-DEPENDENT AND DENSITY-INDEPENDENT SELECTIVE PRESSURES

I am not aware that anyone has previously drawn attention to the bearing of structure upon the question of whether the total number of individuals of a

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Plate V

Figs 1–6. Aeropyles of the side of the eggshell of various species of moths of the family Notodontidae.

Fig. 1. *Pheosia gnoma* (F.).

Fig. 2. *Pheosia tremula* (Clerk).

Fig. 3. *Ichthyura albosigma* Fitch.

Fig. 4. *Notodonta dromedarius* (L.).

Fig. 5. *Nadata gibbosa* (A. & S.).

Fig. 6. *Heterocampa manteo* Doubl. In the species of *Pheosia* the aeropyles are sufficiently numerous and large to constitute an effective plastron, whereas in *Nadata* and *Heterocampa* the aeropyles are too few and too small to constitute an effective plastron.

species existing at any one time are, by and large, determined by density-independent factors or by density-dependent ones. When the functional significance of the structures of an organism is understood, it becomes possible to decide whether most of the structures have been evolved as the result of selective pressures of a density-independent kind or as the result of selective pressures that can properly be called density-dependent. It is first necessary to digress a little and define terms in order fully to appreciate how the structure of an organism can assist in choosing between two quite different views about how numbers of individuals are regulated in nature.

By density-independent factors is meant those that affect the average individual of the species irrespective of population density. Climate is usually regarded as the most important density-independent factor. The quality and quantity of the available food are other density-independent factors.* Density-dependent factors, on the other hand, are those the effect of which on the average individual of a species depends upon the population density of that species. Intraspecific competition and predators, parasites, and pathogens are density-dependent factors. Intraspecific competition is the only density-dependent factor that is affected solely by numbers. Predators and parasites cannot be expected to show an unfailingly exact response to changes in the population density of their hosts because they have environmental relations that are quite independent of their hosts. The amplitude of the population density fluctuations of any species is regulated by a complex of factors which we speak of as the natural control of the species.

Broadly speaking, there are two sharply opposed schools of thought about natural control. Some writers claim that the total number of individuals of a species that are present at any one time depends only or chiefly upon density-dependent processes and they believe that density-independent factors do not limit density. Other writers assert that densities are determined by density-independent factors and sometimes go so far as to claim that it is not necessary to evoke density-dependent factors to explain either the maximal or minimal numbers of individuals of a species in nature. Long ago Milne (1957) pointed out that the density of each species fluctuates only within limits imposed by the total effect of the density-independent environment. My own view (Hinton,

* Competition for food is a density-dependent factor. Sometimes climate, which is ordinarily density-independent, is said to have a density-dependent action. For instance, when there are a more or less limited number of protected niches in the environment, individuals in excess of the number that can occupy the niches may be destroyed by unfavourable climate. But it is not the climate but the competition for the niches that is density-dependent.

1957) is that the fluctuations of pressure upon a species that result from variations in the total effect of the density-independent environment, especially climate, determine the fluctuations of its maximum potential density. But these potential densities are never attained because of (a) the action of imperfectly density-dependent factors such as parasites and predators, or, more rarely, because of (b) both the effect of imperfectly density-dependent factors and intraspecific competition. In short, the fluctuations of density permitted by the density-independent environment are nearly always dampened by imperfectly density-dependent factors, and only exceptionally is the combined effect of both so benign as to permit any significant degree of intraspecific competition.

Those who take the view that it is density-dependent factors that are chiefly responsible for natural control have a great deal of experimental evidence in support of their views, and it is therefore necessary briefly to examine the nature of the experimental evidence on which they rely. The total number of individuals of a species in nature is distributed as a greater or lesser number of more or less discrete communities. Each year, according to climate and other density-independent factors, some of these communities are wiped out and another year, when conditions are better, the sites where they previously existed are once more populated from not too distant communities that managed to survive.

In practically all experimental work a very small population or community of a species is kept in conditions where the density-independent factors are adjusted to levels at which the community multiplies, and density-dependent factors therefore become the important ones in stopping further increase. It is for this reason that so much attention is focused upon density-dependent factors, and the conclusions from such experiments are applied to the whole population of the species in nature. But it is quite clear that nobody setting up an experiment in a laboratory would adjust density-independent factors so that the population failed to multiply: to do so would appear absurd. The experiments are therefore done under conditions where no other conclusion is possible but that it is density-dependent factors that regulate numbers. In other words, the answer is pre-determined by the nature of the experiment.

More rarely, a small community in nature is studied. Such communities have been studied over a short period of years, and even when something like 95% of the mortality is due to density-independent factors the writer nevertheless insists that these do not regulate density. However, work done with populations in nature is usually done only with extremely small natural communities that survive over a period of years simply because the density-independent factors have, during the period of observation, never been severe enough to wipe out the community. For instance, work has been done on the density fluctuations of

a community on a few trees over a period of years when the climate was benign enough for the community to survive during the period of observation. But the species in question may occupy thousands or even millions of square miles. Conclusions based on a study of such small segments of the population are then treated as if they were relevant to the total population of the species. However, work on a small natural community is subject to precisely the same defects as the laboratory experiments. It is simply not possible, for the reasons already mentioned, to believe that the results from a study of a small community, surviving only where density-independent factors are benign, is necessarily relevant to what happens in nature where the total number of individuals of a species is distributed among a very large number of more or less independent communities, some of which survive and some of which are exterminated each year.

The relevance of all this to structure is simply that if the chief selective pressures on a species were density-dependent then we should expect to find this reflected in their structure or habits. If, on the other hand, the chief selective pressures are those resulting from density-independent processes we should expect to find that the chief variations in their structure were concerned with their relation with the density-independent part of their environment. To distinguish the effect of these two kinds of factors—density-dependent and density-independent—is particularly easy in the egg stage. This follows because in the egg stage the insect has to a large extent disrupted relations with the external physical and biological environment. Speaking loosely, the only demands that the insect egg makes upon its external environment are that it shall have an adequate supply of oxygen, not lose too much water, and that it shall be left alone. The insect in the egg stage has no social nor sexual behaviour, and it is thus structurally more simple than other stages where many of the structures are associated with social and sexual behaviour. Furthermore, the insect egg does not feed and is unable to move, which further makes for the simplicity of the shell and the possibility of apprehending the significance of its structure. When eggshells are examined from this point of view, it immediately becomes evident that the chief variations in structure between one species and another result from relations with the density-independent part of the environment. That is, they are concerned with the way in which the egg obtains its oxygen supply and conserves its moisture. Only relatively rarely are the variations in structure related to density-dependent factors such as parasites and predators. In fact, structures of the eggshell that are concerned with defence against parasites and predators, or against attack by larvae or adults of their own species, are so infrequent that they immediately command attention.

The enormous variation of sculpture to be seen in Plates I–V is related to the density-independent environment and in no way that I can see to the density-dependent environment. Nearly all the variation of structure reflects differences in the respiratory systems of the eggshell. These variations can be enormous even between related groups. For instance, Plate I, Figs 1–4 show the variation of the plastron of eggs of flies of the family Syrphidae. Plate II, Figs 1–4 show the enormous variation that can exist in closely related members of a single genus, in this case Muscid flies of the genus *Fannia*. The kind of variation to be found in a single family of moths is shown in Plate V, Figs 1–6. The primitive microsculpture of the outer surface of the eggshell consists of a pattern of polygons determined by the shape of the follicular cells that secreted the shell. This pattern is secondarily modified in many of the illustrations shown (Plate I, Figs 1–6; Plate IV, Figs 4 and 6; Plate V, Figs 1 and 2), but it does not appear that any of the secondary modifications here are related in any way to density-dependent selective pressures. Sometimes the boundaries of the polygons are elevated and the openings of the aeropyles are lifted well above the surface. The selective advantage of this is clearly that the egg is able to utilize atmospheric oxygen even when covered by a thin layer of water. It should also be noted that the structure of the respiratory system below the surface of the shell differs enormously even between closely related species: the chorion may have different numbers of layers, and the form of the internal chorionic meshworks can be very different.

Objections may be made to my thesis on the grounds that I have chosen a stage of the insect which has relatively uncomplicated relations with its physical and biological environment. Stages of the insect such as the larval stage or the adult stage with much more complex relations with the environment will undoubtedly show many more structures which are related to the density-dependent environment. However, a preliminary survey does not indicate that the *percentage* of structures evolved in relation to density-dependent selective pressures is any greater although the absolute number is of course much greater. I hope to be able to discuss this in more detail elsewhere.

SUMMARY

The geometry of the respiratory structures of insect eggshells has been surveyed with the aid of the scanning electron microscope. It has been shown that many structures that are identical in fine detail are polyphyletic in origin, and some of the principles of classification are considered in relation to polyphyletic origins of structures. The functional significance of most of the chief structures of eggshells has been determined. In so doing, it has become possible to distinguish

sharply between two kinds of selective pressures, namely, those resulting from the density-independent part of the environment and those arising from the density-dependent part of the environment. The distinction that can be made between the two types of selective pressures has made it possible to assess the relative importance of these two kinds of selective pressures in the natural regulation of the numbers of individuals of a species, at least in so far as the egg stage is concerned.

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