XV. *On the Phylogeny and Evolution of the* Lepidoptera *from a pupal and oval standpoint.* By Dr. THOMAS ALGERNON CHAPMAN, M.D., F.E.S.

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THE title of this paper is perhaps too ambitious, and would require a volume rather than a short paper to elucidate it. It is incorrect, in so far that I do not propose to do more than state, as clearly as I can, what I believe to be the special dominating condition that underlies the evolution of the lepidopterous pupa, from its earliest to its latest forms. It is obvious that if there be such a condition, and it can be at all successfully apprehended, it will give us much greater certainty in using the details of pupal structure as guides to the true phylogeny of the Lepidoptera, and will show us in what respects they are of value, and where they give less definite indications.

Though I cannot claim to present the subject in more than a tentative form, I am emboldened to do so by the encouragement given by our President in his last address to the use of the "scientific imagination," of which I hope this is a legitimate instance.

What I have to advance may be stigmatised as a mere speculative hypothesis. Perchance it may prove to be so and nothing more. My own belief is that it will be useful and valuable in guiding the study of pupal forms and understanding their significance, even if it should finally appear that it has a very secondary, instead of a primary, place in marking out the lines of lepidopterous evolution.

The precise lines by which the quiescent, inactive pupa, say of bees or beetles, was derived from the active larva-like pupa, if the term is indeed at all applicable, such as those of bugs or crickets, hardly concerns me here; but it is of interest to note that the great mass of *Coleoptera* and *Hymenoptera* have a pupa of very uniform type, helpless from its quiescence, and hence resorting for protection to some cocoon or other cavity. Probably as secondary to such protection, being of very delicate cutaneous structure and possessing no hard chitinous parts, the imaginal appendages are all present, quite distinct and separate from each other, but incapable of any movement.

The exceptions in these two orders in which the pupa is exposed, and consequently of harder external texture, are by no means few in actual number, but are isolated to single species, genera, and rarely families, and seem nowhere to have given occasion to any further evolutional development.

Actually numerous as these exceptions may be, in comparison with the totals of these large orders, it is hardly erroneous to neglect them, and say that the protected pupa of delicate texture is universal throughout these two orders, and that no further development by departure from this rule has taken place within them.

In all protected pupæ the problem has to be faced, how is the imago to free itself from the cocoon or other envelope protecting the pupa. In the *Hymenoptera* and *Coleoptera* this is effected by aid of the imaginal jaws. The imago becomes perfect within the cocoon; it not only throws off the pupal skin within the cocoon, but remains there till its appendages have become fully expanded and completely hardened, and then the mandibles are used to force an outlet of escape. Throughout these orders it is the rule that the imago requires its jaws for other purposes—purposes that we may regard as the primary reason for their existence. Still, their use to extricate the insect from its pupal residence can hardly be called a secondary matter, and in many cases, even in some whole families, they are of no use whatever to the imago except in this one particular; the *Cynipidæ* are perhaps the most striking instance of this circumstance.

Certain families of the *Neuroptera* struck out a new line in this matter. One or two families appear to have followed the same lines precisely as the *Coleoptera* and *Hymenoptera*. Whether the new departure was a development from these, or whether it was in some way a partial retention of the characteristics of the active pupa, I have no materials to decide; but the fact is, that in a group of families the pupa, otherwise quiescent and of delicate structure, retained well-developed mandibles, and by aid of these the pupa extricates itself from the cocoon immediately previous to the emergence of the imago.

When we note that the most neuropterous of these families retain active and useful jaws as imagines, and that some of these, as the *Hemerobiidæ,* have jaws of a remarkably modified structure, we may at any rate conclude that in this group of families the mandibular structures were in a highly plastic condition for development in any direction that appeared advantageous.

This peculiar method of escape from the cocoon associates with these *Neuroptera,* the *Phryganeidæ,* and the *Micropterygidæ,* families whose affinities with the *Neuroptera* on the one hand, and the *Lepidoptera* on the other, have long been recognized, as well established on other grounds.

This relationship between the *Lepidoptera* and the *Neuroptera* was first clearly established by McLachlan at a time when it was rank heresy to make such a suggestion, and to whom sufficient credit for so definite a breaking of new ground has hardly yet been accorded.

I believe Dr. Sharp quite agrees with me in assimilating the *Phryganeidæ* and the *Micropterygidæ* together, as being, though somewhat far apart, still nearer together than either is to the Neuroptera on one hand, or to the Lepidoptera on the other. I believe he sets more value on their neuropterous than on their lepidopterous affinities, whilst I take rather the contrary view, regarding the lower *Adelidæ* as being very probably directly derived from the *Micropteryges.* No doubt the question is more a question of personal equation than of fact, and I would agree that Dr. Sharp, taking a broader standpoint than mine, is possibly able to secure a more correct view.

There are two points that I may claim as making them *Lepidoptera* rather than *Neuroptera.* The first is that *Neuroptera* are carnivorous, *Lepidoptera* phytophagous. The phytophagous habit is strong in the *Phryganeidæ,* absolute in the *Micropteryges.* The other, which more concerns the subject of the present paper, is that they have lost the imaginal jaws. *Micropteryx* has a distinctly lepidopterous haustellum. Looking to the more neuropterous families with pupal jaws, we find they have also imaginal jaws; it is therefore apparently correct to conclude that the loss of the imaginal jaw is secondary to the acquirement of active pupal jaws, and that the discovery thus made that an imago without jaws was a satisfactory organism, opened up the whole field for the evolution both of the *Lepidoptera* and *Diptera*. I may say that I see every reason to believe that the *Diptera* also originated here, along with the *Lepidoptera*, and that they had to face the same problems that beset the *Lepidoptera* as to the escape of the imago from its cocoon, without the use of imaginal jaws. Up to a certain point their solutions were very similar, but later the *Diptera* made one or two remarkable advances, of which we find no trace in the *Lepidoptera*.

The history of the evolution of the Lepidoptera, from a pupal point of view, is, then, from the very beginning, a history of the solution in various ways and degrees, of the problem of how to escape from the cocoon without the aid of imaginal jaws; if this was not the dominant feature in lepidopterous evolution, it was at least so important as to leave distinctive features on almost every family of *Lepidoptera*, up to the point at which the problem appears to have received the most satisfactory possible solution, or rather *a* most satisfactory possible solution. When this point was reached, and it appears to have been reached by several different roads, their pupal structure presents a great similarity amongst a large number of very distinct and unallied families—those, in fact, which are classed together as *Macro-heterocera*.

Taking, then, the *Micropteryges* as being the lowest Lepidoptera from our present as from most other points of view, we find a method of escape from the cocoon that differs in several important respects from that in which the perfect imago accomplishes this by the aid of its own jaws.

We may note, however, that though it is nominally the pupa that escapes from the cocoon, it is in reality still the imago, the imago clothed in the effete pupal skin. To rupture the cocoon, it uses not its own jaws, but those of the pupal skin, energising them, however, in some totally different way from ordinary direct muscular action, their movements being the result of the vermicular movements of the pupa, acting probably by fluid pressure on the articular structure of the jaws, by some arrangement not altogether different perhaps from the frontal sac of the higher Diptera.

How this extraordinary method of escape originated and was developed from the earlier and simpler method, is a matter deserving of investigation, and will no doubt yield many interesting facts. That I say nothing about it is due to sheer ignorance, and not the ostensible reason that it is outside the *Lepidoptera.*

In the *Micropteryges* the jaws of the pupa not only rupture the cocoon, but appear to be the most active agents in dragging the pupa through the opening in the cocoon and through any superincumbent earth, being merely assisted by the vermicular action of the abdominal segments, and we find in accordance with this circumstance that the pupal envelope is still very thin and delicate, and has little or no hardening or roughness by which to obtain a leverage against the walls of the channel of escape.

There are no doubt many lost families at this point, and we do not find precisely the next stage in the progress of pupal evolution. In all other instances we not only find the pupal jaws absolutely lost, and also a general hardening of the pupal skin, with a development of roughness across the abdominal dorsum, but, perhaps, inevitable with the hardening pupal skin, we find also a considerable consolidation of previously separate and movable parts.

No doubt it was soon found that great assistance to the emergence from the cocoon was obtained by a hardened and rough abdominal integument, and this directly led to the further step that by a little weakening or valvular structure of the cocoon, the jaws might be absolutely dispensed with.

In *Limacodes* we find all the segments of the abdomen still free, and the appendages, though fused together, are fused so slightly as to be easily separated without injury, and the cocoon is provided with an easily separated lid.

In the lower Adelids the segments are more fused together, and by aid of a beak more or less developed, and the cocoon being made of a valved larval case, exit from the cocoon is achieved. It would seem that a beak was early adopted as a weapon for breaking open the cocoon, as it exists in nearly all the *Incompletæ,* except the *Limacodid* and *Nepticulid* section.

In all these instances the pupa emerges from the cocoon precisely as in the *Micropteryges,* that is, the moth it really is that emerges, but does so encased in the pupal skin. To achieve this object, it seems to have been found most efficient to have three, four, or five abdominal segments capable of movement, but to have the terminal sections soldered together. So few as two free segments is found only in the *Gracilariidæ*, and is, therefore, probably a number disadvantageously small.

A cremaster is very rare in this section, and its use, where it exists, appears to be to enable a cable of silk not to retain the pupa within the cocoon, but to restrain it at precisely that degree of emergence from the cocoon that is most desirable; this is usually attained when the movable segments have so far emerged from the cocoon that they are no longer capable of acting in the cocoon as locomotor organs. The pupa usually retains this position by the elasticity of the cocoon gripping it tightly, but in many Tortrices and others a cremaster and loose cable as just mentioned exists.

The next step, that intermediate between the *Incompletæ* and *Obtectæ*, I have so far only met with in the genus *Epermenia* (*Chauliodus*). It probably results in some instances from a cremaster preventing the escape of the pupa from the cocoon, and a slender cocoon permitting the escape of the moth.

We want many more facts at this point, if perchance they are attainable. The transition is a very notable one, we pass from what we might almost call the true lepidopterous (if it were not also equally dipterous) process of emergence, emergence within the pupal skin, to the direct emergence of the imago from the cocoon, leaving the pupal skin behind it, precisely the process in the bees and beetles, with the important difference that imaginal jaws are not required, and the less important one that some final expansion and hardening have still to be accomplished.

It puzzled me a great deal to understand why the *Obtectæ* always had the fifth and sixth abdominal segments free and no others, both sexes being the same. The exceptions being almost literally none, and *Epermenia* being, so far, the only transitional form I had met with.

Now throughout the *Obtectæ* there are many devices for breaking through the cocoon: specially constructed weak places in the cocoon, special softening fluid, applied by the moth, assisted by special appliances of diverse sorts, such as in *Hybocampa* and *Attacus*, and so forth, but all adhere to the special obtect formula of the fifth and sixth abdominal segments only being free.

I conclude that this structure of the pupa is that which affords far beyond any other, at once, a solid basis and an extensible ladder, by which the imago can attain a pupal fulcrum from which to reach and rupture the cocoon and force itself out.

The questions of animal mechanics involved are, however, I must admit, too complex and difficult for me to analyse them successfully.

A remarkable confirmation of this hypothesis is, however, presented by the butterflies.

It seems very probable that when the Skippers had but recently obtained obtect rank, they were not only still capable of further evolution in the direction of consolidation of pupal segments, but had, if it is legitimate so to express it, a distinct impulse towards further consolidation. They would, however, no doubt ordinarily have adhered to the usual obtect formula, but for one circumstance, viz., they succeeded in doing without any sort of cocoon.

The mechanical problem of how to escape from the cocoon by the way of least resistance, no longer dominated them ; and accordingly we find in each group of butterflies, that certain families have lost the power of movement in one, two, or all three of the incisions that are movable in the *Obtectæ*. That the families with least movement in each division happen to be the highest, may be the result of what I have called the impulse to such progress, existing in the Skippers. Much more probably the loss of movement occurred in each instance for some special reason, probably in pursuance of protective devices that so dominate the evolution of butterfly pupæ, and as there was no going back, it results inevitably that in each line of development, the most solid pupa must be the most recent.

In my first paper presented to the Society in 1893, I believe I gave the impression that I believed that all the Lepidoptera might be arranged by their pupæ in one line ; I had not this idea myself, but I had not formed any alternative view with sufficient definiteness to enable me to advance it.

I do not know that I can go much further yet, but I may state what I believe to be the law on this point in this way. The Lepidoptera certainly cannot be arranged in one line by their pupæ, but the Lepidoptera of one line can be arranged by their pupæ.

Two forms having different pupæ, are either—

1. Not related (that is not nearly enough for definition).
2. If related, then the pupæ will tell which is descended from the other or which is furthest from the common ancestor.

A pupa with more movable segments cannot be descended from one with fewer; broadly, one that is more consolidated or has lost certain parts, cannot be ancestral to one with more movable parts, or that retains appendages.

I have been forced to conclude that there have been several lines of evolution in the Lepidoptera all more or less parallel. That the *Obtectæ* in fact are not a homogeneous group and were not derived from the *Incompletæ* at one point only, and then diverged, but that the obtect pupal form was reached from several different stirps of *Incompletæ* independently under the pressure of the problem placed from the first before the Lepidoptera, viz., what is the line of least resistance by which the imago may escape from pupa case and cocoon without the aid of mandibles? I am not prepared to say how far back it was that these several stirps diverged. I still see many reasons for deriving them from different branches of the Palæolepidoptera; on the other hand, I see that it is necessary to admit that, if there can be parallel lines in the neolepidoptera, there may equally be lines in the neolepidoptera parallel to others in the Palæolepidoptera, just as we have parallel families in the marsupials and placentals, and even in the Reptilia.

My arch heresy in this respect is in claiming a relationship between *Cossus* and *Hepialus*. *Hepialus* (starting from *Micropteryx*) presents many characters similar to *Cossus*, and in some respects is even further removed from *Micropteryx* than *Cossus* is. If we grant a parallel progression to *Cossus* and *Hepialus*, some of my objections to the orthodox view would be diminished.

It is no doubt very difficult to admit that neolepidoptera with the subcostal vein of the hindwing simplified in precisely the same manner, should be equally derived from a Hepialid and Micropterygid source, but there are so many forms missing that it is not safe to form any very precise theories. I am less puzzled by the question of frenum and jugum. The jugum is certainly a remains of a wing lobe well-developed in many Neuroptera, and appears to have no such function as is attributed to it of combining the wings in flight, whilst there are distinct traces of a commencing frenulum in some stronger hairs in *Eriocephalids.*

With regard to the *Macro-lepidoptera,* I have not been able to find any definite pupal characters on which they may be classified, still less distributed in accordance to their phylogeny. A closer examination of a larger series of species may throw more light on the matter, but this is very doubtful, since, for example, I find in the *Geometrides,* pupæ as thoroughly obtect as the highest Noctuæ, whilst in some groups there are pupæ with dorsal head plates, and in some instances these even carry the eye-covers, a very parallel condition to that in the Skippers. Dorsal head plates also occur in Lasiocampids, Thyatyrids, Notodontids and some others. Obviously these remains of earlier structure appear in the lower families of each division.

It occurred to me to recur to some old ideas I had about the eggs of Lepidoptera, in hope of finding some solution of this difficulty.

It seems very probable that the eggs of Lepidoptera should give characters useful for classification, not only for the simple reason that every structure and habit does so, but because it is not merely a structure, but the whole individual at one stage of its existence, and because the circumstances of its environment being different from those of the later stages, it cannot have responded in the same manner as they have, and may, therefore, afford us differences and resemblances when they do not do so, or have them overlaid by various characters of more modern acquirement and less fundamental significance. Especially being the most ancestral stage, it may probably have some earlier characteristics, in spite of having varied in many particulars like the other stages.

We all know that in many genera the eggs of the different species are easily recognisable, as in Vanessa, Pieris, Ennomos, Acronycta, Cerura, &c. It is less easy to find characters from eggs of families, yet most of us can recognise a *Noctua* or a *Geometra* egg, one of a butterfly or of a sphinge.

Can we then find any characters of ova that will enable us to determine the probable relationships of the different families to each other. In studying the significance of any structure, one must be led entirely by what it teaches, in nowise straining the facts to meet preconceived ideas, and not until this is done must one compare the results with those otherwise attained, and then see whether the differences in results are to be reconciled by a fresh interpretation in the newer or older studies.

Approaching the question of egg form in this spirit, lepidopterous eggs are seen at once to present at least two very definite types of egg, which we may name the upright and the flat egg.

The *upright egg* has the *Micropylar axis* vertical to the surface on which the egg is laid, and the two axes at right angles to this are equal in length, and in fact not definite in position, the egg being circular on any horizontal section.

The *flat egg* has the *Micropylar axis* parallel to the surface on which the egg is laid, whilst the other horizontal axis and the vertical axis are usually of different lengths.

When we examine the distribution of these two forms of eggs in different families, we find that there is rarely if ever an exception to the rule, that one form only exists in each family, and even in each superfamily, and that, broadly, there appears a very strong presumption that, at least amongst the macros, there is never an abrupt transition from the one form to the other, and that whilst the flat egg is probably the earliest form, and may still retain a capacity for reaching the vertical form, any reversion in this respect is very doubtful.

If we confine ourselves to the true *Macro-lepidoptera*, we find the upright egg occurs in the butterflies and in the Noctuæ, whilst the flat egg is characteristic of the Geometræ and the Bombyces.

Now I think nineteen times out of twenty, perhaps ninety-nine out of a hundred, I should recognise a butterfly egg from any other, but I have so far failed to find any one definite character that can be predicated of all butterfly eggs and will at once distinguish them from all other upright eggs. Notwithstanding this, I think, we may properly divide the upright egg into two divisions—the butterflies and the Noctuæ.

I feel satisfied that the flat egg in the *Macro-heterocera* has also two (at least) different forms, the difficulty of defining them does not deter me from this conclusion, since the greater difficulty in the case of the upright egg is, nevertheless, merely a difficulty, and not a reason for refusing to accept two forms of upright egg.

The two forms of *flat egg* are the Geometrid and the Bombycid. The former is marked by greater roughness, the lines or ribs forming the network or sculpturing, are larger and coarser, the Bombycid egg is smoother and more polished, yet many instances could be quoted in flat contradiction to this distinction. The tendency of the Geometrid egg is to have a denser harder shell than the Bombycid, though here, again, many of the larger Bombycids have very firm eggshells.

Whether this division between Geometrid and Bombycid eggs will hold good, it remains true that both divisions are, in their typical forms, very distinct from the upright egg, and whilst I am, for reasons that may or may not be sound, inclined to derive the two forms of flat egg from distinct origins very low down in the evolutionary scale, it appears probable that the two forms of upright eggs, moths and butterflies, had a common origin, though very low down, and have long been separate.

In placing together all the families (of Macros) that have upright eggs, and looking for some other character they may have in common that will confirm such a collocation, we find a most valuable one in the chin glands of the larvæ. This curious structure is of so special a nature, that it would require very strong evidence to make one believe that it was separately acquired in different families, and so when we find that it occurs in butterflies, in Noctuæ, and in Notodonts, but nowhere amongst the families with flat eggs, the conclusions derived from the egg seem very strongly confirmed.

No one can doubt that the butterflies are widely separated from the Noctuæ, and the evidence of the Hesperid pupa shows that the butterfly separated from the Noctua stirps a very considerable way below any Noctua-like form, usually placed with the Macros. But this evidence of egg and larval chin gland suffices to show that they jointly separated from the Geometrid and Bombycids still lower down.

If we take Mr. Meyrick's classification of Macros, based on unstated grounds, but obviously chiefly on venation, we find that he has collected together into his *Caradrinina* all the Macro-heterocera with upright eggs, with the single exception of the *Notodontidæ*.

It is interesting here, in passing, to note that though we may gird at the earlier classifications, we have to admit that, with no doubt some very important exceptions, they had a grip of the main outlines, at least, amongst the Macros.

The four chief groups that I make on egg characters are, as I have stated, largely the four old ones of Butterflies, Noctuæ, Geometræ, and Bombyces, and these are also practically the groups framed by Mr. Meyrick, though I think he has missed the real value of these groups in placing the Notodontas and sundry Bombyces in the Geometræ. He would also, though that is a small matter, have pleased me and many others had he kept the time-honoured names for the groups.

If we are to attach any value to the egg evidence, it is clear that the *Rhopalocera* are not derived, as Mr. Meyrick surmises, from any Pyralid form, since the Pyralids are of a higher type than the Hesperids, and still belong very markedly to the flat egg stirps, or one of them. The pupæ of the two groups are not derivable from a common form, without going very far back, much further back, than is implied in an immediate common ancestor.

A consideration of great weight, that I ought perhaps to have placed earlier, deserves attention, that is, the great fixity of the two types of egg, the upright and the flat, throughout the *Macro-heterocera*, which is still true, if we add the *Pyralidina*, as of nearly Macro rank. There is no clear indication, amongst all the upright forms, of derivation from a flat form or *vice versa*.

A few Geometrid forms are hardly even apparent exceptions to this, such, for instance, as *Ennomos*, where the packing together of the eggs has placed them in a sloping position, so that, so far as position goes, they can hardly be called flat; and, further, there is a certain amount of rim or crown round the micropylar end; but there is perhaps no clearer instance of the secondary axes being distinct amongst all the flat eggs than the eggs of *Ennomos* present to us.

Again, in the *Lasiocampidæ* we find the flat egg set up on end in much the same manner as in sundry Geometras.

In our common *Neustria* and *Lanestris* the eggs are set up on end, so that, regarding the mere terms of the definition, they are vertical eggs. They have, however, three distinct axes, and may be regarded as being laid not on the twig at the nadir from the micropyle, but really as being laid on one another, a further development of the condition presented in Endromis and some Saturnids, where the eggs are piled up on one another.

It must be noted, however, that in some families of Geometræ the eggs present a gradual development of the hexagonal pitting into a regular ribbing of the noctua or nymphalid type. These still retain the pitting over the nadir of the micropylar area, and in the *Acidalias* preserve three unequal axes, though in *Acidalia imitaria* they even present a tendency to be laid on the end. These are the nearest approach to an exception to the general rule that I have met with, and they suggest that the upright egg is the higher form, and that nymphalid ribbing is also a late development, and that the Geometrid egg is still capable of progress in these directions. It would be interesting to find a similar progress amongst Bombycid ova.

It is therefore obvious that the two forms of eggs, as we find them in the *Macro-heterocera*, must have been derived the one from the other, or both from some other form, at some much lower point in the phylogenetic series.

In trying to trace backwards the several forms of eggs, we find amongst the lower (Micro) forms a great preponderance of groups with flat eggs. This appears to be so, after making full allowance for the fact that our (or at least my) ignorance of the eggs of Micro-lepidoptera is considerable. The lowliest form with upright eggs is *Cossus*; this fact is curious, since both Zenzera and Tortrix, to which it is allied, have flat eggs. It is probable, therefore, that we here have the point where the two forms are still unfixed and capable of easy variation. The alliance (by pupa) of *Castnia* to *Cossus* would probably point to this being the origin of the butterfly stirps.

But branches, by the way, are exceedingly scarce. *Sesiidæ*, that I had surmised to be, perchance, a low branch of the butterfly stem, cannot be so, as the eggs are flat.

Choreutidæ find their location somewhere low down, no doubt on the Noctuid division of the stem. This position explains at once the difficulty that systematists have felt to be unsolved, whether they place it on the Tineids or Tortricids. The egg is of a most beautiful and typical upright form.

The dorsal armature of the pupa of some genera is of a form I have met with nowhere else, being a close-set row of nearly spherical cups instead of the usual spines.

Nolidæ are possibly a branch from a point tolerably high up, but below the Notodontid division, advancing separately, so as to take rank, as judged by the pupa, at least as high as the summit of the Noctuid crown. The egg is extremely curious in one remarkable point; it is clearly an upright egg, ribbed, and broadly not unlike a Noctua egg, but is the only upright egg I have met with in which the horizontal section is not circular; this suggests an origin from the main stem low enough down to admit of such a variation taking place. The young larva, according to the opinion of Mr. Dyar, who kindly examined them, agrees very well with this position, whilst the loss of one pair of prolegs is a very ancient variation, no trace of the missing pair being discoverable even in the newly-hatched larva.

The pupa is also quite anomalous, regarded as a Macro; but would be explicable in the position I assign to it. It has only one movable segment, the fifth abdominal, and the terminal segments are very curiously abridged, so as to produce a flat end to the pupa, reminding one of Hepialus; the arrangement of the appendages is also inconsistent with a definite Macro position, the tarsi of the second and third pairs of legs projecting side by side beyond the wings and antennæ as a free process as far as the incision between the fifth and sixth segments. The detection by Mr. Hampson of maxillary palpi in a Nolid would not, in this view, be surprising; but would possibly suggest that *Nolids* are really a branch of the Tineid stirps that retains the maxillary palpi; the unequal axes of the egg would be a record of more recent and separate derivation from a flat egg form.

Chrysocorys, which almost certainly belongs to this stirps, in which flat eggs are the rule, has a remarkable egg, which is distinctly upright, and proves the transition from one form to the other not to be difficult at this point. It also shows that families with upright eggs may have more points of origin than the one apparently common to butterflies and Noctuæ.

The *Chloephoridæ* have also an upright egg; the vertical axis is extremely short, the general form being an exaggeration of the very depressed egg of the Acronyctas; but the ribbing is of a different type, it does not fall in line with the *Noctuæ*, still less with *Liparids* or *Arctiids*. The larva and pupa also suggest differences difficult to seize and impossible to put into description; that is to say, that they agree with, say Noctuæ, in any point I can put into words, and yet leave me with the impression that there is a fundamental difference. If this be a correct impression, there is no doubt some feature capable of observation and description that I have overlooked.

The *Noctuæ* have a spherical egg, ribbed vertically and with secondary transverse ribs. I do not know any egg that departs widely from this; *Acronyctas* are probably the extreme as to flatness. In some few the ribbing is obscure, apparently from being lost again. This egg is essentially the same as the *Piero-nymphalid* egg amongst the butterflies; that the higher development of the upright egg in each of its two great branches should be so similar is remarkable. We have already noted that the Geometrid egg tends in the same direction. The greatest difference is that the Noctua egg tends to have the micropylar axis shorter than the transverse (Acronycta, etc.), whilst the Piero-nymphalid egg tends to have it longer in nearly all groups.

The *Arctiid* egg is nearly spherical, smooth, and polished, with a netted surface very faintly marked.

The *Liparid* egg is not unlike the *Arctiid*, but with a denser texture, duller surface, and often with a depression at the summit. There is greater variation here than, say, in the *Noctua*. *Pudibunda* egg might almost be a Notodonta. *Monacha* is very like an *Arctia*. *Salicis* is enveloped in a curious foam-like gum, and one is not prepared to refuse a place to *Coryli*, *Ludifica*, and some others, although their eggs are distinctly Noctuan.

The *Notodonta* egg is dense, dull-surfaced, opaque, and is a hemisphere laid on its flat side. *N. bucephala* has a spherical egg very like *Liparids*. *Cerura erminea* shows the capability of the Notodontid egg to become very depressed.

The Notodontids are a lower family than the other three typical ones, and it is interesting to find that as the *Noctuæ* are parallel in egg specialisation to the *Piero-nymphalids*, so the Notodontids are parallel with the Hesperids, the forms being very similar.

Notodontids have been placed in more varied positions in classification (always, however, within the Macros) than almost any other family, and have especially been supposed to be on the way up to Sphinges, etc.

It seems to me impossible to intercalate a group like *Notodonta* between any two families with flat eggs, or even to make it a terminal branch (as in one sense all families are) from a flat-egged stirps. The chin-glands of the larva are a very strong item also. Mr. Dyar's researches on the larvæ do not seem to me to indicate with any certainty in which of the three great divisions of the Macro-heterocera it should be placed. He places it, however, with the Noctuæ. Mr. Meyrick places it with Geometræ, between the *Eupterotidæ* and the Sphinges (both Bombyces), apparently entirely on the evidence of the neuration.

Now it is unquestionable that the neuration of the *Noctuæ*, *Arctiids*, and *Liparids* is of a different character from the mass of the *Notodontids*, especially as regards vein 5; but this does not appear to disagree with the position to which I assign them, viz., in the Noctuid stem, some way below its final division into the three (with other exotic) highest families. In this lower position the venation is less specialised but more variable than in them; now the typical Notodontid venation is less specialised than in Noctua, but it varies more, in some instances into quite a Noctuid form, in others vein 5 is practically absent, and in some few forms there is even so definite a trace of a lowlier origin as indications of veins within the cell.

When we come to the pupa, we meet with the same difficulty that affects all the *Macro-heterocera*, viz., that the differences between different families are often less than between different genera or even species within the same genus.

A Geometra pupa is difficult to distinguish from a Noctua, especially a deltoid pupa, and so on.

Most species of Notodontids possess the dorsal head-plate (cephalo-thoracic piece) dwindled to a small, but quite definite portion. This does not at all settle its position, but shows that it is below the summit level of heteroceral, pupal evolution. The texture is distinctly noctuid, but this has reference to the subterranean position of the pupa. *Cerura*, with a different habit, might almost be Saturnian.

The cremastral development, consisting of two or four short spines, seem to be processes of the pupa rather than separate spines or bristles, as in most Noctuæ in some species they are quite obsolete (as in many Arctians), in others (Clostera) they are at the extremity of a long slender process. The chief feature in which they differ from Noctuæ is in the appendages falling short of the wings, but in this there is a great variety within the group. The way in which the abdominal segments do not materially taper till the 8th or 9th segment is distinctly Noctuan, but both this and the short appendage covers might be claimed as Lasiocampid.

The *Lithosiidæ*, *Euchromiidæ*, and *Syntomidæ* are hardly distinguishable from *Arctiidæ*. The *Agaristidæ* (*Alypia octomaculata* is the only species I have had from the egg) is very close to *Noctuidæ*. Of other (exotic) families and subfamilies (*Pericopidæ*, etc.) I am very ignorant.

The *Lithosiidæ* and some *Arctiidæ* (*Spilosoma*) are the only Macro-heterocera I know whose pupæ seem fairly on the way to lose all movement; in some instances, possibly, they have achieved that result. This is probably associated as cause and effect with their possessing a soft flimsy cocoon from which escape does not much depend on the nature of the support and fulcrum afforded by the pupal skin.

When we come to the Bombycid stirps, there appear to be very good reasons for associating together a certain group of families, and these all are characterised by possessing a flat egg—that is, an egg so laid that the micropyle is not on top but at one end. This egg has three axes of different length, the micropylar being the longest, the vertical the shortest; it has generally a very smooth surface, the sculpturing being very slight and shallow, the texture often firm, but tending to be delicate, and it has, I think, always both ends of equal size—that is, it is not more narrowed towards the micropylar end or at all pear-shaped, and it tends less than the Geometrid egg to narrow towards the ends.

Packard's description of the egg of *Dryocampa rubicunda* may be taken as typical: "Oval, a little flattened, the shell yellow, thin parchment-like, the surface smooth, polished; under one-half inch objector showing no traces of pits or polygonal areas. The shell is so thin that unfertilized eggs collapse irregularly."

This group has three (at least) branches, the Lasiocampida and Eupterotida; and two branches of which, Endromidæ is possibly the base passing by *Aglia* to Citheronidæ and Sphingidæ on the one hand and to Bombycidæ and Saturnidæ on the other.

The form of egg is so similar to that obtaining in *Anthroceridæ* and *Megalopygidæ*, that I cannot resist the conclusion that this series originates in my "Micros whose larvæ are external feeders," though intermediate forms to bridge over the great distance between *Limacodes* and *Lasiocampa* are unknown to me. My observations on the spines of *Limacodes* and *Eacles*, and again of these and *Sphinges* and *Saturnids*, together with the much larger series on this subject published by Packard, and the observations of Poulton and Weissman, on larvæ of Aglia, Sphingidæ, etc., leave no room for doubt that all these families are related, to the exclusion of the Geometrid stirps. Most Macro pupæ, except, perhaps, the upper families of the Noctuid series, present some indications of a Micro derivation. Here the Lasiocampids (like the Notodontids) preserve traces of the dorsal head-piece; but a more important feature that is preserved is that of pupal locomotion. Some Lasiocampids can travel to and fro in their cocoons, whilst *Endromis* and *Sphinx* actually present instances of the pupæ emerging from their cocoons, this seems to be a feature distinctly binding this group together. They are all thick bodied.

The Geometrid section has a thicker egg than the Bombycid, usually with a bold raised netted sculpturing, the ends are often narrower making the egg distinctly ovoid, the micropylar end being the narrower. The moths are slender, the pupæ of not a few groups possess the dorsal head-piece; in some few Geometers the eye-pieces actually separate in connection with this piece, there are others in which the pieces separate without adhering to the head-piece. These forms are no doubt the lowest of the group; they occur in Eupithecia, Thera, and some allied genera.

In tracing these series downwards, we find the same form of egg in Crambus, in many Pyraloids, and in not a few *Tineina,* such as Chauliodus and Orneodes. In many of these we find, as in most Geometers, but never I think in Bombycids, that one end of the egg is narrower than the other, making the egg pear-shaped.

This stirps in fact includes nearly all the lower forms. The egg in different groups of these varies within wide limits. In some families it is very depressed and scale-like; as, indeed, is the Bombycid egg in many Limacodids, if we are correct in tracing the Bombycid egg to that origin.

If the Geometræ really belong to this stirps, we must note that the majority of the stirps culminating in the Pyralids preserve the maxillary palpus, and that the Geometrid Macros must be derived from branches lower down which have lost the palpus.

The *Cymatophoridæ* (*Thyatiridæ*) unquestionably, on the evidence of their ova, belong to the Geometrid division, many of them are still characteristically slight bodied. The larvæ of some genera preserve the Micro habit of living between leaves, though they have Macro legs. A trace of dorsal head-piece is always present in the pupa, which has the tapering hind segments of the Geometrid type. The Brephidæ almost certainly belong here and not to the Bombycids. The egg proves they are not Noctuæ.

The *Drepanulidæ* are very puzzling. I incline to place them here, they are probably like the *Nolidæ* on the Noctua stem, a form as high as any other, but with a separate origin low down. The egg is rather Bombycid than Geometrid, the larva is very isolated, the prolegs are of the same formula in the newly-hatched as in the adult larva, the pupa is of high Macro type. Whilst the imago is slender-bodied, preserves a frenulum, and has rather a Bombycid than Geometrid type of markings.

The complete circles of hooks on the larval prolegs in stage 1, with traces of the outer series of crochets in the adult larva, prove that it cannot be closely associated with any other Macro-heterocera, and whether we associate it with the Bombyces or Geometræ, it must have departed from the main stem very low down, probably so low that it would hardly be correct to recognise the stem so low down by its Macro name.

Mr. Dyar associates the Drepanulids with the Geometræ, the fashion of the young larvæ fastening leaves together flatly (like Cymatophorids) is the only character that is difficult to recognise, as, perchance, Bombycine.

On submitting an outline of this classification, by ova, to Mr. Dyar, it appears from the short criticism with which he favours me, that it substantially agrees with his larval classification, except on one point—that is, the position of the *Lasiocampidæ*, which he derives from the *Notodontidæ*. This, I find it extremely difficult to agree with. I find a great many points in the Notodontid pupa, in which it agrees with the Lasiocamps, so many as to prevent my saying there may not be some way of reconciling the differences. But I certainly do not see any, and think the agreements are instances of parallel variation or evolution, the two families being at very nearly the same level on their respective stems.

Mr. Dyar derives Lasiocampids from Notodonts. The Notodonts are higher in having less mobile pupæ and in having a vertical egg. Since the flat egg is probably the earlier form, it is improbable to a degree, for which impossible might not be too strong a term, that it should revert from the upright form in Notodonts to a flat one in Lasiocamps.

The *Notodontas* are, therefore, claimed both by Mr. Meyrick and Mr. Dyar as presenting an instance of a *per saltum* transition from a flat to a vertical egg, or *vice versa*, but with very different results as to the positions in which they place it. Whilst admitting that the conclusions I derive from egg structure will probably have to be largely modified by the acquisition of wider knowledge and a closer comparison with other structures, I do not think they will be so far overturned as to justify the position assigned to the Notodontids, beside *Lasiocampa* by Mr. Dyar, or beside Geometræ by Mr. Meyrick, their results being as mutually incompatible as they are with mine. Mr. Meyrick placing Notodonta amongst

Geometræ and *Sphinges*, and deriving it (with them, and at some distance) from *Lasiocampa*.

Mr. Dyar really agrees with me as to *Notodonta*, placing it in *Noctuina* (Mr. Meyrick's *Caradinina*), but differs as to *Lasiocampa*, which he places above *Notodonta*. On each point, therefore, I have the agreement of one of these authorities, as against the other. I also agree with them as to the many points of resemblance between *Notodonta* and *Lasiocampa*, but differ in regarding them as the result of parallel and not of derivative variation.