

IX. *Observations on the Lepidopterous Family Cossidae and on the Classification of the Lepidoptera.* By A. JEFFERIS TURNER, M.D., F.E.S.

[Read March 20th, 1918.]

It has long been known that moths belonging to the family *Cossidae* present certain peculiarities in their neururation; but the importance of these peculiarities and the light they throw on the relationship of the different families of the *Lepidoptera* have never, I believe, been fully recognised. So far as I know, no monograph has appeared on the structure of the whole family. Mr. Meyrick in his "British Lepidoptera" deals with three genera, which he divides into two families rather widely separated in his scheme of classification. Sir George Hampson has dealt with the more numerous Indian genera as one family in his "Moths of India," and has also kindly lent me an MS. key to the world genera represented in the collection of the British Museum. Mr. Barnes and Mr. McDonough have revised and tabulated the North American genera ("Contrib. Nat. Hist. Lep. N. Amer.," i, p. 3). Without attempting a systematic revision of the world genera, I have endeavoured to describe all the more important structural modifications exhibited by them, and to discuss their significance. The accompanying figures are all original, and though roughly diagrammatic, for I have no skill as a draughtsman, they give, I believe, with accuracy the essential details of the neururation in each case.

Family COSSIDAE.

*Definition.*—Tongue and maxillary palpi obsolete. Forewings with an areole, usually large; the parting vein between areole and cell (the *chorda*) distinctly or strongly developed; \* a branched median vein distinctly developed in cell, very rarely unbranched; two anal veins 1c and 1b, the latter furcate at base. Hind-wings with a branched median vein in cell distinctly developed, very rarely unbranched; three anal veins 1c, 1b, and 1a, 1b often shortly furcate at base.

\* With one exception, which will be described.

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By this definition the genus *Paracossus*, Hmps., is excluded from the family, and will be dealt with separately.

To the definition the following particulars must be added: Moths of moderate or large, sometimes exceedingly large, size. The larvae so far as known, and probably in every case, are internal feeders living in wood. The frons is usually flat, but may have a projecting tuft of scales. The labial palpi may be moderate and porrect, or short, or obsolete. The antennae are rarely simple in both sexes, frequently bipectinate in both sexes to apex, in one genus unipectinate, frequently with a double row of long pectinations in the ♂ for part of their length, the pectinations

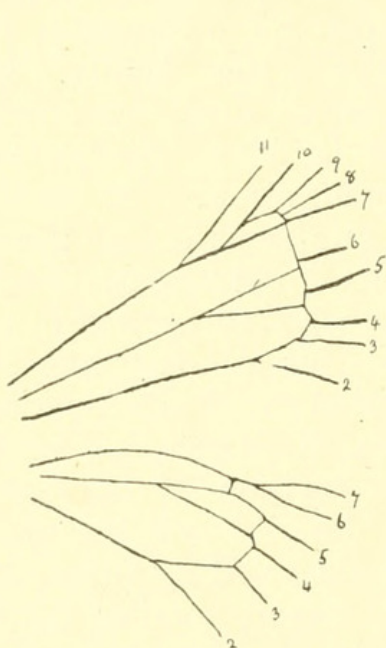


FIG. 1.—*Cossodes lyoneti*,  
White.

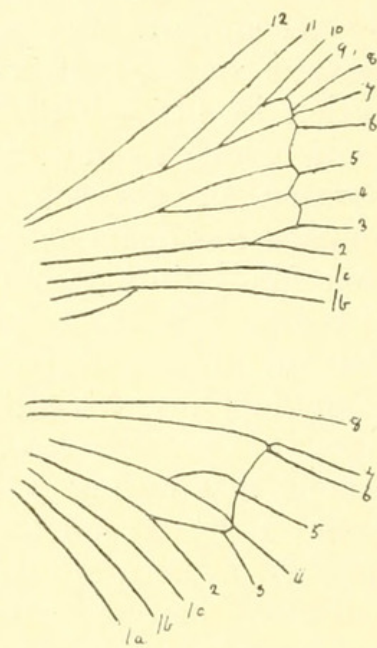


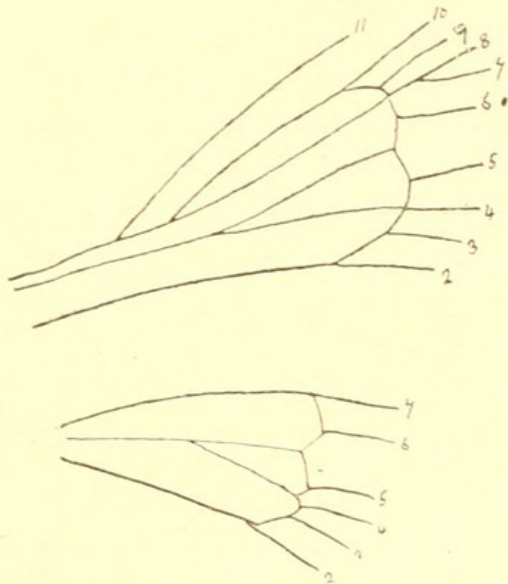
FIG. 2.—*Dudgeona actinias*,  
Turn.

usually ceasing or shortening abruptly, and the apices simple or shortly bipectinate, but simple or shortly bipectinate from base to apex in the ♀. The tibial spurs are long and well developed in some of the more primitive genera, but frequently very short or obsolete. The frenulum is sometimes short, not articulating with the retinaculum, and apparently non-functional.

We will commence our survey of the neururation with two of the most primitive genera, *Cossodes* and *Dudgeona*. Both genera have long, well-developed tibial spines and rather long palpi, which are unusual in the family, and confirm the conclusion, that I draw from their neururation, that they are primitive types. *Cossodes* has simple antennae



in both sexes, and contains one Australian species. The type of *Dudgeona* is Indian, and has the ♂ antennae shortly bipectinate to apex, and veins 6 and 7 of the hind-wings are separate; *D. actinias*, Turn., from Australia has the antennae simple in both sexes, and 6 and 7 of the hind-wings connate; there is a third unnamed species from Africa, which is intermediate, having the ♂ antennae simple, but 6 and 7 of the hind-wings separate. In view of their close specific relationship and agreement in all other structural details, it does not seem necessary to divide the genus. In neuration *Cossodes* and *Dudgeona* are closely allied. Both possess an areole of moderate size in the fore-wing, with a branched median nerve in both wings. The areole between 8 and 9 is completed not by the usual anastomosis, but by a short cross-bar, probably a more primitive arrangement. It is interesting to note that in one example of *D. actinias* examined this cross-bar was absent, leaving the areole open. The full importance of this observation will be seen later. The Australian genus *Ptilomacra* has, like many others of the family, lost its tibial spurs, the antennae of both sexes show a double row of long pectinations to the apex, in the ♂ very long, the palpi are small and very hairy, but in its neuration it agrees very closely with the preceding genera, the only differences in the fore-wing being a larger areole, and stalking of veins 7 and 8. The European *Cossus* is not very far removed from *Ptilomacra* in neuration (fig. 21), the principal difference being the smaller and more projecting areole, on the apex of which the origins of 7, 8, 9, 10 are crowded together, and the obsolescence of the dorsal half of the basal fork of 1b, which is vestigial. It has the antennae shortly and evenly bipectinate to apex in both sexes, the palpi moderately short, the tibiae without spurs, and the frenulum in the ♂, though stout, apparently

FIG. 3.—*Ptilomacra senex*, Wlk.

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functionless, being short and not articulating with a retinaculum. *Miacora* agrees in neururation with *Cossus*, but has occasionally, not always, an oblique bar from near the end of cell to vein 8 imperfectly developed; it is doubtfully distinct. *Eremocossus*, Hmps., has very

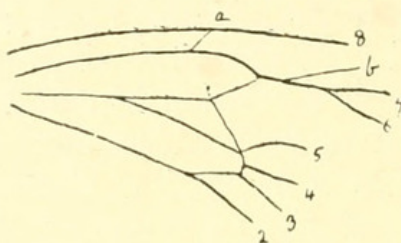


FIG. 4.—*Eremocossus foedus*, Swinh.

similar neururation. I take the opportunity of figuring an abnormal hind-wing of *Eremocossus foedus* ♀ in which two of the missing radial veins appear to be developed, one (a) running from the cell into 8, the other (b) running from the stalk of 6 and 7, quite distinct but ending in

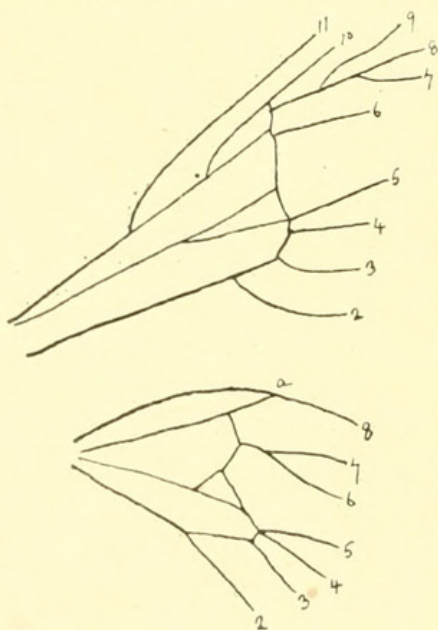


FIG. 5.—*Xystus robiniae*, Bdv.

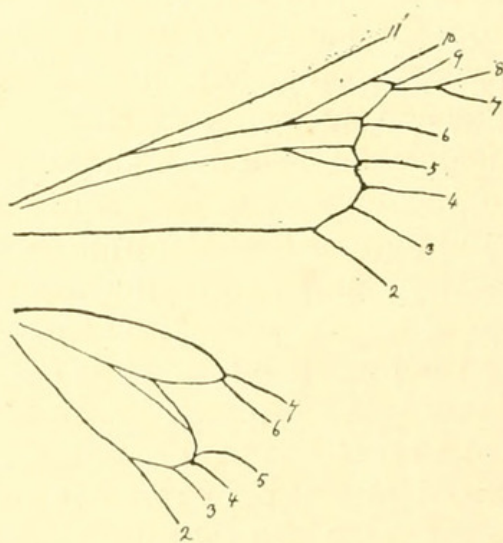


FIG. 6.—*Holocerus nobilis*, Stgr.

disc without reaching margin. On the other side of the same example and in both wings of a ♂ these extra veins are wanting. In the Nearctic genus *Xystus*, which is a member of this group possessing well-formed but rather small tibial spurs and moderate palpi, this vein (a) is constantly developed in the hind-wing. Except for this



the genus presents only minor peculiarities of neuration. The Palaearctic *Holocerus*, to which the African *Rethona* is closely allied, is another member of this group with moderately developed tibial spurs. In the hind-wing the

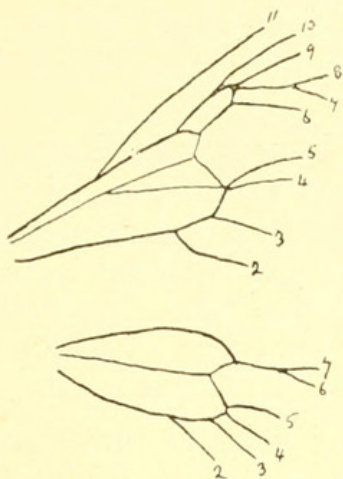


FIG. 7.—*Dyspessa ulula*,  
Bork.

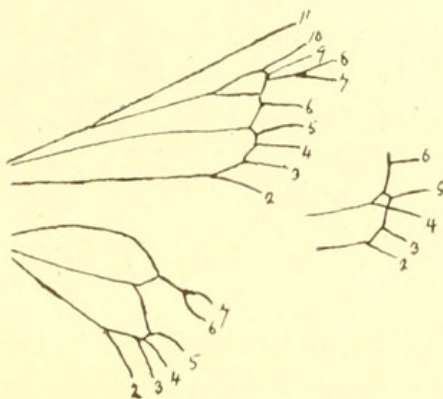


FIG. 8.—*Stygia australis*, Latr.

lower branch of the median is often so close to the lower discocellular as to be nearly fused with it. In *Dyspessa* this has actually occurred, so that the median of this wing appears single, only the upper branch being left. In a third Palaearctic genus of this series, *Stygia*, the median is unbranched in the fore-wing also, a rare degradation of the neuration in this family, though common in other groups. In one specimen the median in the fore-wing is just branched, forming a minute median cell, and I have reproduced this also in the figure; it is interesting as showing that the median cell has been obliterated in normal specimens by coalescence of the two primary branches of the median.

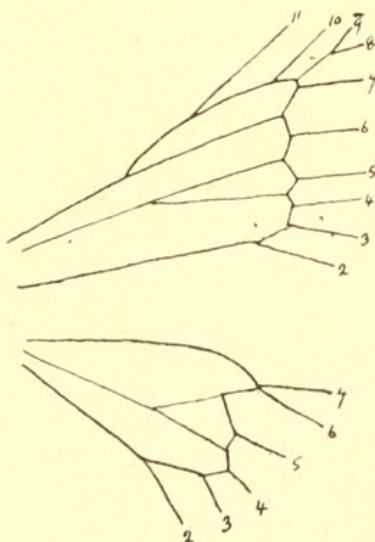


FIG. 9.—*Culama australis*,  
Wlk.

*Stygia* marks the extreme development along one branch of the *Cossidae*, and we must now hark back to a more primitive Australian genus, *Culama*, which differs from the ancestral form in only one point of importance, the origin of vein 11 from the areole, which is large. Veins 8 and 9



are stalked, but in *Culama expressa*, Luc. (fig. 22), which should form the type of a new genus,\* all the veins arise separately from the areole. Both forms have the tibial spurs well developed, as have the allied Neotropical genera *Schausiana*, Strand (*Hemipecten*, Dyar), and an undescribed genus (sp. *norax*, Druce), which differ from them in minor points only. The former has the antennae unipectinate in both sexes.

The section of the *Cossidae* with hypertrophied areole giving origin to vein 11 form a large proportion of the family, and, so far as I know, no similar structure occurs elsewhere in the *Lepidoptera*.† It may be explained in two ways: (1) the origin of the chorda has been displaced towards the base of the wing—that this has occurred is shown by the increased length of the areole; (2) the basal

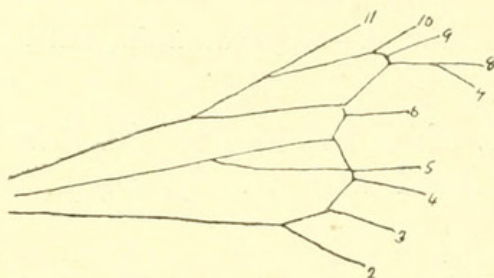


FIG. 10.—*Phragmatoecia parvipuncta*,  
Hmps.

part of vein 11 may have partly coalesced with the common stalk of the remaining radial veins (the radial sector) and with the common stalk of the 1st and 2nd radial. The latter factor has been also in operation, and it explains the displacement of the origin of 11 towards the

apex. The relative part taken by the two factors could be approximately determined by comparative measurements.

There are in the genus *Phragmatoecia* two types of

\* *Macrocyttara*, gen. nov. Frons with anteriorly projecting scales. Palpi moderately long, projecting beyond frons, longer in ♀, smooth-scaled; terminal joint stout, obtuse, in ♂ very short, in ♀ rather long. Antennae bipectinate to apex in both sexes; or in ♂ only, in ♀ simple. Thorax with a small posterior crest. Tibiae with all spurs present and well developed. Fore-wing with areole very large, median vein branching about middle, lower branch ending between 4 and 5, upper between 5 and 6; 2 from towards end of cell, 3 from angle, 4 and 5 separate, 6 from near upper angle, 7, 8, 9, 10, and 11 arising separately from areole. Hind-wings with median cell narrow, lower branch ending between 4 and 5, upper between 5 and 6, where discocellulars are sharply angled inwards; 2 from about  $\frac{2}{3}$ , 3 from angle, 4 and 5 widely separate, 6 and 7 stalked from upper angle, 8 free.

† Except, as pointed out to me by Mr. Durrant, the Tortricid *Phtheochroa*. In the *Drepanidae*, 11 sometimes arises from the areole, but in this instance 11 arises from much nearer the apex.



neuration in the fore-wing so different that at first sight one would pronounce them distinctive of two separate genera. In *P. parvipuncta*, Hmps., the structure of the fore-wing is substantially the same as in *Culama*, but in *P. castaneae*, Hb., the sector runs into the upper branch of the median and the shape of the areole is distorted. Although these two types of neuration seem so distinct, some other species, such as *P. impura*, Hmps., present intermediate forms, in which the anastomosis between chorda and upper median is incomplete. The hind-wing in this genus is similar to that of *Culama*, but is more

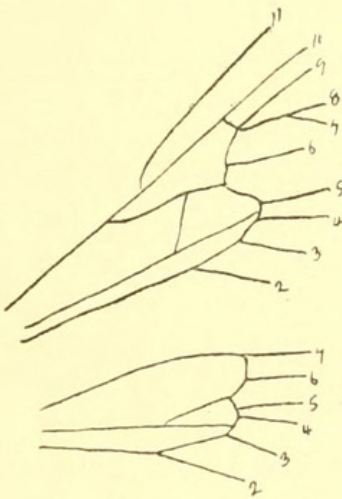


FIG. 11.—*Phragmatoecia castaneae*, Hb.

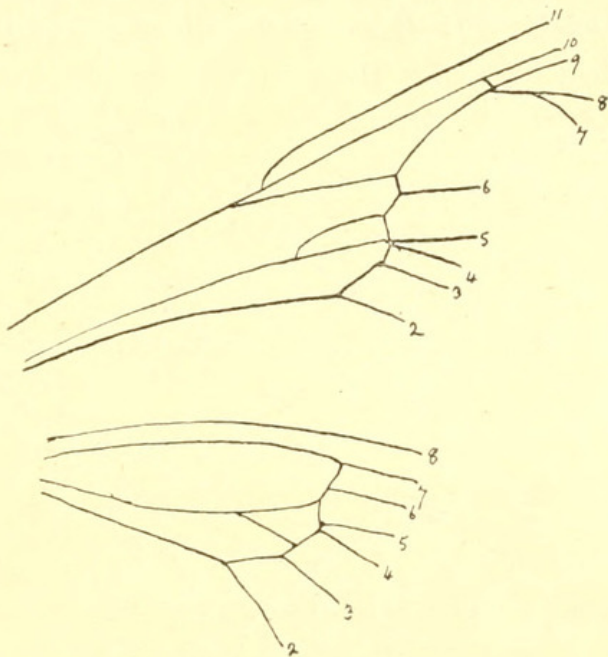


FIG. 12.—*Xyleutes crassa*, Drury (*polioplaga*, Hmps.).

primitive. In all the preceding figures the upper branch of the median, which is the common stalk of veins 5 and 6, terminates between those veins; but the median cell has been narrowed so that the lower branch, which is the common stalk of veins 3 and 4, terminates either opposite 4 or between 4 and 5. Also veins 6 and 7 are separate and parallel. For these reasons I am unable to regard *Phragmatoecia* as a direct derivative of *Culama*; but undoubtedly *Phragmatoecia* is derived from the stem from which *Culama* arose. The former genus is in other respects less primitive than the latter; it has the antennae shortly pectinated nearly to the apex in both sexes, but in the ♂ the pectinations are long for the basal  $\frac{2}{3}$  and then become



abruptly shorter, the palpi are short and hairy, and the posterior tibiae have a minute pair of terminal spurs only.

By far the largest genus in the family, *Xyleutes*, Hb., type *crassa*, Drury (= *Chalcidica*, Hb., *Endoxyla*, H.-Sch., *Duomitus*, Butl., *Himaeya*, Moore, *Azygophleps*, Hmps.), is represented in all the warmer regions, but most numerous in Australia. The neuration is that of the more primitive form of *Phragmatoecia*, and it differs from that genus only in the scaling of the head and palpi, but the fore-wing is very constant in structure, only slight differences existing, such as the short-stalking of vein 9, or the lower branch of the median terminating opposite 4 instead of opposite 5 as in *crassa*, or even from shortly before 4, but the median

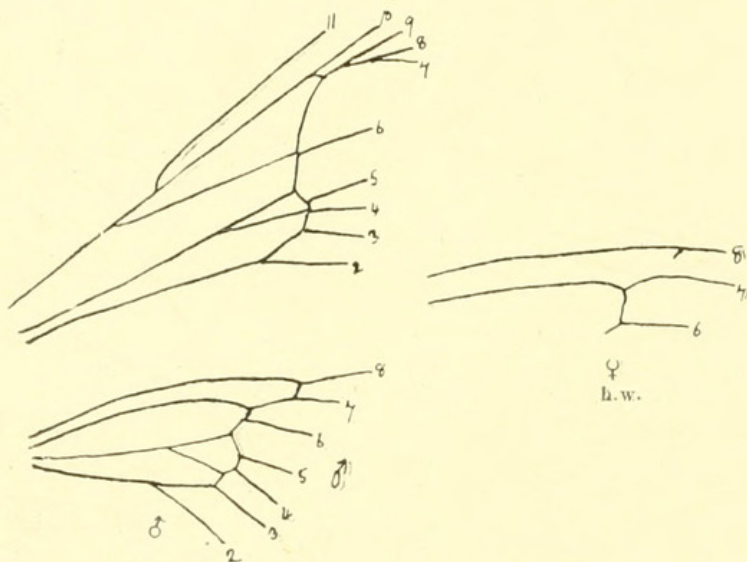


FIG. 13.—*Xylotrypa strigillata*, Feld.

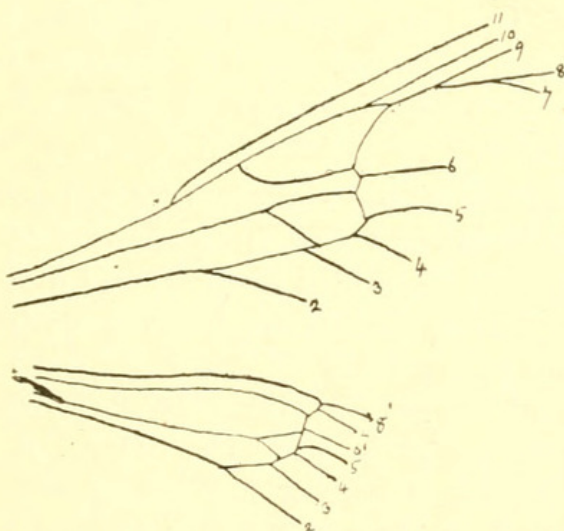
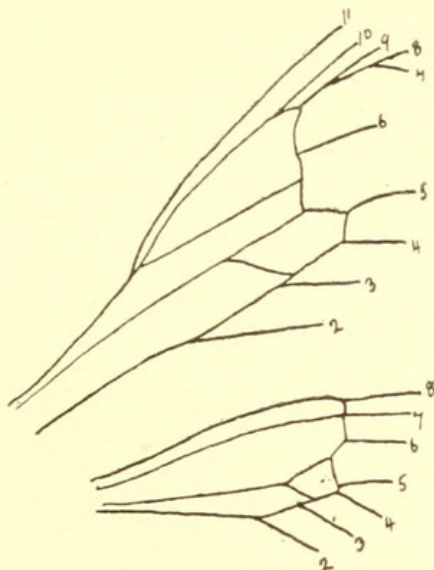
cell of the fore-wing is always narrow, not broad as in *Zeuzera*.

An undescribed genus,\* which contains the species *strigillata*, Feld., from temperate South America, is an interesting modification of *Xyleutes*. The fore-wing and antennae are the same, but the palpi and tibial spurs are obsolete, and in the hind-wing of the ♂ there is a branch running from vein 7 to 8. This, I think, represents one of the veins of that wing usually undeveloped. It is variable, and in a ♀ example represented by only a short spur on the dorsal side of 8. As there is only one example of each sex in the British Museum I cannot say whether the variation is sexual.

\* *Xylotrypa*, gen. nov.



The genus *Zeuzera* presents a curious mixture of characters, some specialised, others primitive. Of the former are the absence of palpi and tibial spurs, and the ♂ antennae, which have a double row of long pectinations to about  $\frac{3}{5}$  and then become abruptly simple. Of the latter is the termination of the lower branch of the median between veins 3 and 4 not only in the hind-wings, as in the preceding two genera, but in the fore-wings also. There is also a bar between vein 8 and the cell in the hind-wings, which may merely represent an anastomosis, but probably, as in *Xylotrypa*, represents the vein marked *a* in fig. 4. There is some variability in the genus. In *Z. coffeae* the areole is larger than in *Z. aesculi*, and vein 11 arises from

FIG. 14.—*Zeuzera aesculi*, Latr.FIG. 15.—*Zeuzera coffeae*, Neitn.

only just behind it. In *aesculi* 7 of the hind-wings arises from the connecting bar, in *coffeae* from the cell. *Z. indica* has the fore-wing as in *aesculi*, the hind-wing as in *coffeae*. In *Z. multistrigata* 9 arises from the areole, connate but not stalked with 8. In an unnamed species from South Africa the chorda runs into the upper branch of the median as in some species of *Phragmatoecia*. The fore-wing of *Zeuzera* being as regards the unnarrowed median cell more primitive than in any other genus, it must have arisen independently from the same stem from which arose *Xyleutes* and its allies, but at a lower level.

We complete our survey of the family with a group of Neotropical genera, some species of which have invaded North America, in which there is a tendency to reduction of



the areole and median cell, the latter being sometimes lost. Apart from the neururation they are characterised by small palpi and tibial spurs; the latter appear to be sometimes

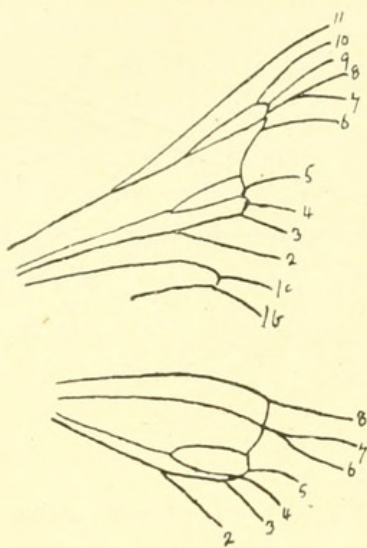


FIG. 16.—*Givira tristis*, Wlk.

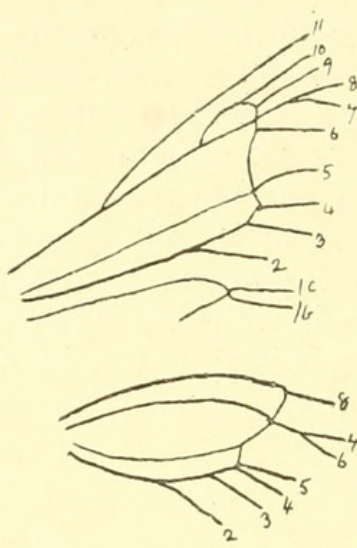


FIG. 17.—*Ingurimorpha basalis*, Wlk.

absent, and by the ♂ antennae being shortly bipectinate from base to apex. Sometimes the frenulum is short and apparently functionless. *Givira* resembles *Zeuzera*, and like

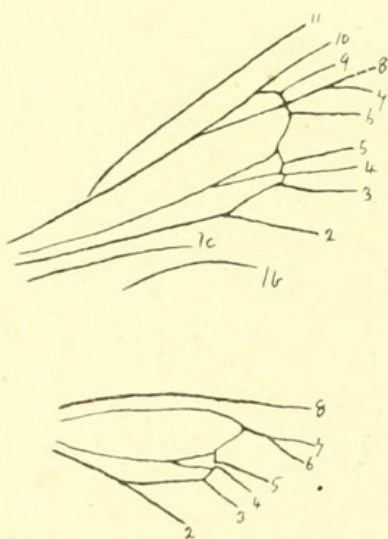


FIG. 18.—*Stenocyttara sabulosa*, Schaus.

it has a bar connecting 8 with the upper angle of the cell in the hind-wings, but both areole and median cells are narrower. A peculiar character not previously noted in this paper is a connecting bar between 1b and 1c of the hind-wings towards their distal extremities. This is, I believe, only paralleled elsewhere in the *Psychidae*, but I do not think it indicates any close relationship with this family. It has been probably an independent development. *Ingurimorpha* is a further development of the same stem, with median cell obsolete in both

wings. An undescribed genus containing *sabulosa*,\* Schaus, is near *Givira*, but lacks the bar in the hind-wings. Its median cells are narrow, that of the hind-wings being very

\* *Stenocyttara*, gen. nov.



small. The connection between 1b and 1c of fore-wings is not developed, the latter vein becoming obsolete before it reaches the point of connection in *Givira*.

*Lentagena* is remarkable for its minute areole, which if not carefully looked for might be thought to have been completely lost.\* It well illustrates the process by which the areole becomes obliterated by coalescence of its upper and lower enclosing vein-trunks. In the fore-wings there is an oval median cell of some size, but in the hind-wing there is none, and the unbranched median vein has been displaced towards the dorsal margin of the cell. At first sight it looks as though the upper branch of the median had become obsolete, but comparing it with *Ingurimorpha*, in which the termination of the median above vein 5 shows that the upper branch is represented, it seems to me at least equally probable that the median has become displaced dorsally after coalescence of its branches. In this genus the ♂ antennae are dentate or shortly bipectinate to apex, the palpi are rather small, and there appear to be no tibial spurs.

I have not seen any example of *Trigena*, Dyar, in which there is stated to be no areole, but there is certainly none in the species *tigrata*, Schaus, which I am unable to refer to any described genus.† In this the neuration of the hind-wing is that of *Lentagena*, excepting for the presence of a connecting

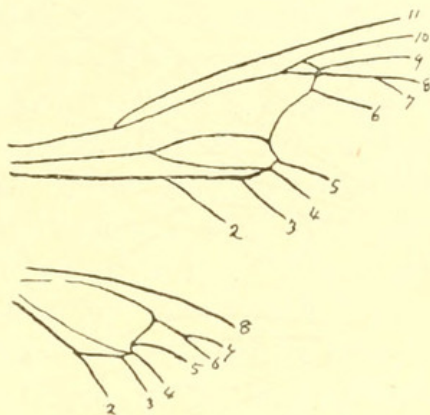


FIG. 19.—*Lentagena tristani*, Schaus.

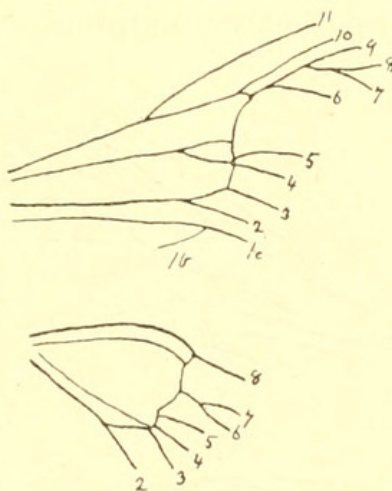


FIG. 20.—*Acyrtara igrata*, Schaus.

\* Mr. Dyar, Proc. U.S. Nat. Mus., xxix, p. 178 (1906), describes *Lentagena* as having no areole. This may, for all I know, be the case sometimes, but I have examined one example each (all that are accessible to me) of *tristani*, *albicosta*, and *nudaridia*, and found it present in all of them, though in the last, which is the type species, certainly very minute.

† I propose for it the name *Acyrtara*, gen. nov.



bar between 8 and the end of the cell. In the fore-wing there is a small median cell, but no trace of an areole, 6, 7, 8, 9 are stalked, and the anal veins anastomose, 1b running into 1c. The tibial spurs are obsolete; the palpi moderate, porrect; the frenulum well developed, and the ♂ antennae bipectinate to apex.

This concludes my present study of the neururation of the *Cossidae*. I have not attempted to figure every genus, but, so far as I know, I have not omitted any important deviation of structure. As a result I have convinced myself that this is a natural and compact family not divisible naturally even into subfamilies. There is, it is true, a considerable and very interesting degree of variation in several directions, but all these lines of development are linked together by forms of intermediate structure.

I have also convinced myself that the *Cossidae* have retained the most ancient form of neururation among the existing families of the *Lepidoptera Heteroneura*, and that from this neururation that of all the other families can be easily derived by a process of reduction, the stages of which can be readily traced. The study of this family has therefore appeared to be of fundamental importance, and it is this that has encouraged me to consider it in detail. But to establish my conclusion it is necessary to study also the neururation of these other groups, more particularly of those families that may be considered of primitive type, or at least to contain genera of primitive type. Naturally this survey cannot be undertaken in an exhaustive manner within the limits of a short paper. I can do no more than select one or two of the more primitive genera in the case of each family, paying particular attention to those families which agree with the *Cossidae* in the primitive character of possessing three anal veins, 1a, 1b, and 1c, in the hind-wing. These families are the *Tortricidae*, *Tineidae*, *Castniidae*, *Zygaenidae*, *Limacodidae*, *Psychidae*, and *Pyralidae*.

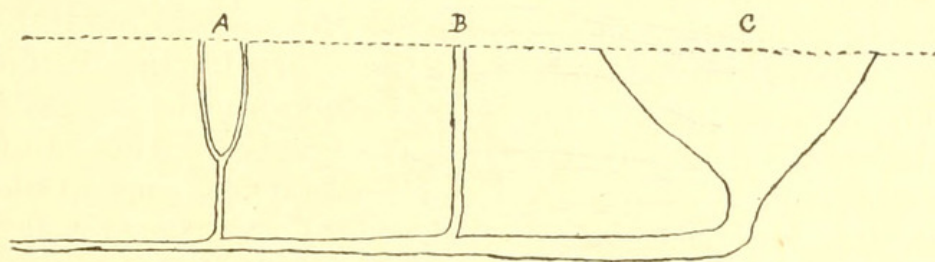
#### THE CLASSIFICATION OF THE LEPIDOPTERA.

Before considering the relationship of the *Cossidae* to other families it is necessary to make a few remarks on the classification of the *Lepidoptera*. It is now generally agreed that the primary division of this order is into two very unequal groups, (a) those with closely similar fore-



and hind-wing neuration, and (b) those with unlike neuration of the two wings, the number of the veins in the hind-wings being considerably reduced. For these two groups I accept the names proposed by Mr. R. J. Tillyard in a short but illuminating paper (Proc. Linn. Soc. N.S.W., 1917, p. 167) of *Lepidoptera Homoneura* and *Lepidoptera Heteroneura*. These names are preferable to *Jugatae* and *Frenatae*, for the number of the veins is of more importance than the presence or absence of the frenulum, and as the latter organ is present in two other orders of insects besides the *Lepidoptera*, namely, the *Mecoptera* and the *Neuroptera Planipennia* (Tillyard, *l.c.*, p. 174), it is probably more primitive than has been supposed, and its absence in the *Lepidoptera Homoneura* may well have been due to loss.\*

The *Lepidoptera Homoneura* consist of the *Micropterygidae* and *Eriocranidae* (if these are really lepidopterous) and the



*Hepialidae*. I regard them as offshoots of the primitive lepidopterous stem and not as part of the main line of development, as illustrated in the accompanying diagram.

The dotted line represents the present era. Deeply beneath it is the primitive lepidopterous stem, three branches of which reach the surface; A represents the *Micropterygidae* and *Eriocranidae*, B the *Hepialidae*, and C the *Lepidoptera Heteroneura*. There is no evidence that the two former were ever more numerous than at present, though that is quite possible, but the third are a dominant group at the present day, consisting of a vast number of genera and species, and are consequently represented by a wide-based inverted cone.

The structure of the *Lepidoptera Homoneura* is of great interest in the evolution of the order, but has small connection with the object of the present essay, the natural

\* Mr. Tillyard has since this was written sent me a drawing and photographs demonstrating that a frenulum is actually present in the *Micropterygidae*.



classification of the *Heteroneura*, and I shall reserve the former for future consideration.

It is also desirable to look at the neururation from a broad standpoint and to bring it into correlation with that of other related orders of insects. Without entering into fuller discussion, I may say that I consider the primitive lepidopterous wing possessed four main veins, which divided dichotomously, together with three, or perhaps four, *anal* veins. These veins (figs. 21 and 22) were the *subcostal* (the *costal* exists as a separate vein only in fossil insects),

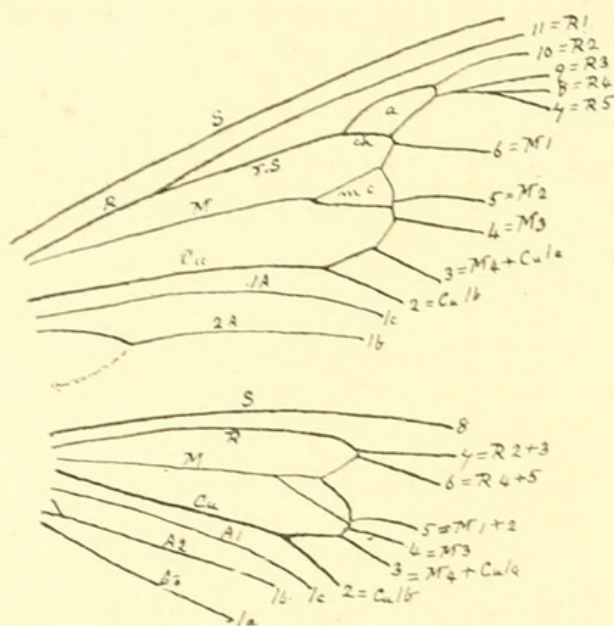


FIG. 21.—*Cossus cossus*, Linn.

S. Subcostal vein. R. Radius. M. Media. Cu. Cubitus. a. Areole. m.c. Median cell. r.s. Radial sector. ch. Chorda. R 1, 2, 3, 4, 5. The five radial veins. M 1, 2, 3, 4. The four median veins. Cu 1a and 1b. The two cubital veins. 1A, 2A, 3A. The three anal veins.

the *radius*, the *media*, the *cubitus*, the first *anal*, the second *anal*, which is furcate at base and probably represents two coalesced veins, and in the hind-wing the third *anal*. The nomenclature adopted is that of the Comstock-Needham system, and brings the lepidopterous neururation into correlation with that of at least several of the primitive orders of insects (Tillyard, *l. c.*, p. 173). In the accompanying figures of *Cossus* and *Macrocyttara* the Comstock-Needham notation is given, and in the former the commonly used numerical notation also. The *radius* divides dichotomously into the first *radial* and the common trunk of the second, third, fourth, and fifth *radials*, which is known in



other orders as the *radial sector*. This again divides into (a) the common stalk of the second and third *radials*, and (b) the common stalk of the fourth and fifth. The latter is of such importance in the *Lepidoptera* that it is necessary to give it a special name, and I have termed it the *chorda*. It is noteworthy that, although the original dichotomy is often obscured, the second and third radials, that is, veins 10 and 9, always arise by a common stalk. The enclosed space, completed by a bar or anastomosis between 9 and 8, is identified by Mr. Tillyard with the *discoidal cell*, but as that term has been used with a different sense in the *Lepidoptera*, I have thought it wiser to retain for it the

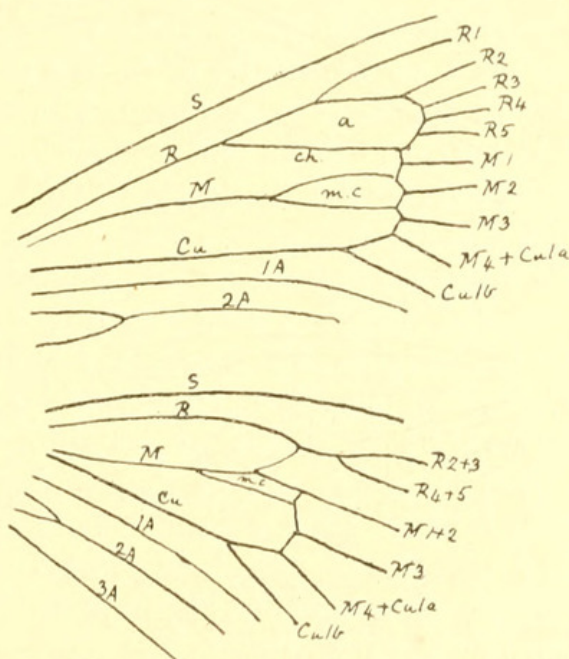


FIG. 22.—*Macrocyttara expressa*, Luc.

name *areole*. When *areole* and *cell* coalesce to form what I will call an *areocel*, it is evident that the original staking of 9 and 10 is obscured, so that they appear to arise separately from the *areocel* as in fig. 23. The *media* divides into (a) the common stalk of the first and second median, and (b) the common stalk of the third and fourth median; between them is the median cell. Mr. Tillyard has shown (*l. c.*, p. 169) that the fourth *median* has coalesced with the first *cubital*, thus closing the *lepidopterous cell*, which has hitherto been known incorrectly as the *discoidal cell*, but may be conveniently spoken of as the *cell*; it of course includes the median cell when that is present.

While the *Comstock-Needham* system is, so far as our



present knowledge extends, morphologically correct, and is the only notation which permits of comparison between the *Lepidoptera* and other orders, I am strongly of opinion that the numerical notation\* should be retained for morphological comparisons *within the order*, and for these reasons: (1) it is much simpler and at the same time absolutely unambiguous, while possessing the advantage of extreme conciseness; (2) it is free from morphological theories or assumptions, which however well established may be liable to future modification. In using it I would recommend that the origin of the numbered veins be always given as from the *cell* or *areole*, the *chorda* and *media*, when present, being separately described. In considering the serial morphology of the two wings there is no doubt as to their correspondence as far as vein 4, but the morphology of veins 5, 6, 7, and 8 of the hind-wings is a matter of interpretation, and subject to correction. It is, of course, obvious that 8 of the hind-wing does not correspond to 8 of the fore-wing (a fact that involves no difficulty if the numerical notation be regarded as a convenient form of shorthand). Mr. Tillyard considers 8 of the hind-wing to be the first *radial*; I consider it the *subcostal*, and identify the first radial with the short vein marked *a* on several of my diagrams. I think Mr. Tillyard has probably made the mistake of identifying as the subcostal a precostal basal spur which is sometimes present but does not represent any vein, being merely an accessory process of recent development for the support of a precostal basal expansion of the hind-wing.

The *lepidopterous cell* is usually spoken of as closed by the *discocellulars*, upper and lower, their junction being at the median notch. This may be convenient, but it must be recognised that morphologically the discocellulars are of complex origin. Their complexity is clearly indicated in their angulated outline in *Culama* and other primitive genera. For instance, in the fore-wing the *cell* is closed (1) by a short bar connecting the *areole* with the first *median*; (2) by the diverging bases of the first and second *median*; (3) by a short bar connecting the second and third *median* and closing the *median cell*; (4) by the diverging bases of the third and fourth *median*; and (5) by

\* Sir George Hampson informs me that this was invented by Herrich-Schäffer.



the base of the first *cubital* before it coalesces with the fourth *median*.

*Tortricidae*.—At first sight the neuration of the fore-wing of *Tortrix*, a closed cell from which ten veins arise separately, appears simple and primitive, and in marked contrast with the more complex neuration of the *Cossidae*. Nevertheless, if the principles just enunciated are correct,

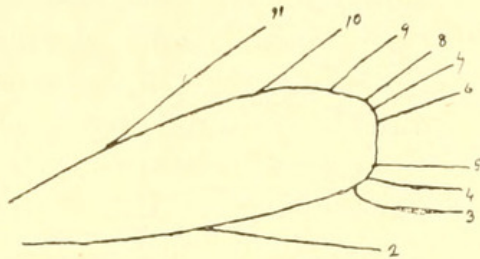


FIG. 23.—*Tortrix viridana*, Linn.

this simplicity is not primitive but acquired; it originated from a more complex scheme by a process of loss or asthenogenesis. It needs but little research to confirm the accuracy of this anticipation. In many genera both *chorda* and *median* vein are developed, certainly very slenderly but quite distinctly. The *areole* is usually narrow, the *chorda* running from a little before 10 to just above 7 in *Eucosma*, or just opposite 7 in *Carpocapsa*. The *media* is unbranched,

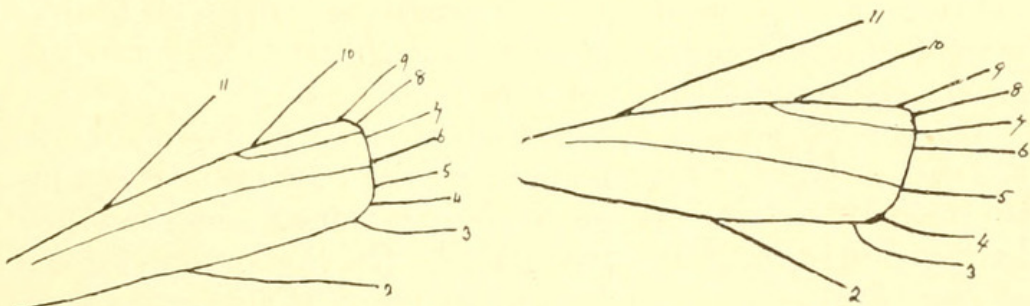


FIG. 24.—*Eucosma variegana*, Hb. FIG. 25.—*Carpocapsa pomonella*, Linn.

its exact course through the cell varies, it terminates between 5 and 6 in *Eucosma*, just opposite 5 in *Carpocapsa*. The *media* is more rarely distinguishable in the hind-wing, but a branched *media* is plainly to be seen in that wing of *Isotrias*. In this genus the *areole* is larger than usual, the *chorda* arising shortly after 11 and ending opposite 6, while the *media* ends opposite 4. I have not observed a branched *media* in the fore-wing in any of the *Tortricidae*



that I have examined. It will be noted that the cell of *Tortrix* really represents a compound structure, the combined areole and cell, and I propose to call it an *areocel*.

Mr. Meyrick in his "British Lepidoptera" has noted

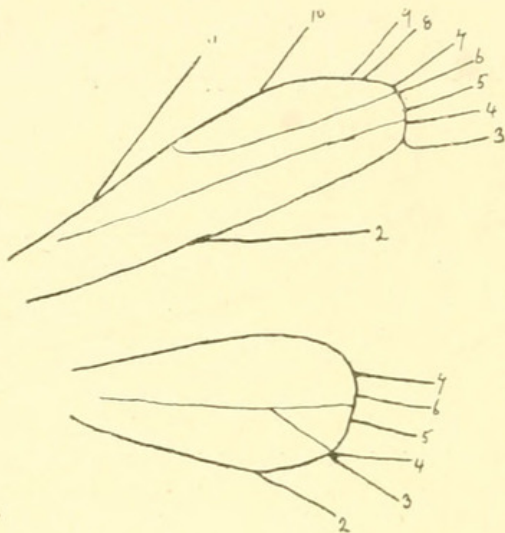


FIG. 26.—*Isotrias hybridana*, Hb.

and figured the occasional occurrence of chorda and media in the *Tortricidae*. He declares them to be inconstant and valueless in defining the genera. This may be so, but they are exceedingly valuable in indicating the true relationship of the family.

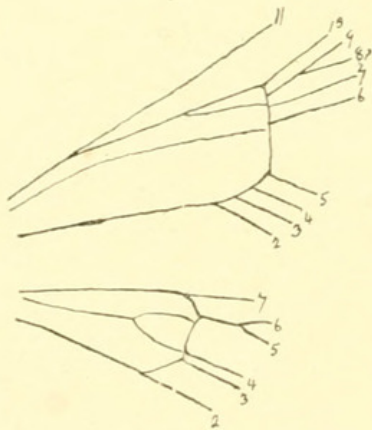


FIG. 27.—*Nemophora swamerdamella*, Linn.

*Tineidae*.—In this great family asthenogenesis among the *Lepidoptera* runs to its extreme. In many of the more minute forms the neuration is so degraded as not to be recognisable as of the lepidopterous type, were it not that they are linked to the more typical forms by intermediate gradations. These aberrant forms need not concern us in this essay, for they are certainly derivative, and the affinities of a family are entirely determined by those of its most

primitive genera. The genus *Nemophora*, with its five-jointed maxillary palpi and long antennae is certainly a primitive type, and in spite of its small size preserves a primitive neuration. In the fore-wing both sector and media are present, while the hind-wing has a branched



media. *Cerostoma* has an even more primitive neuration in the fore-wing, the media being branched; but less so in the hind-wing, the media, although well marked, being

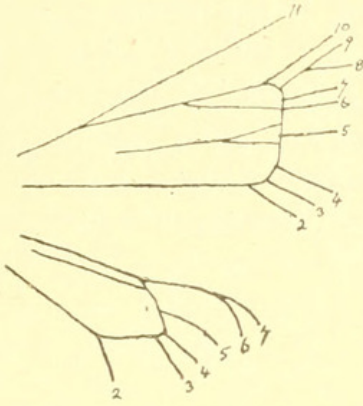


FIG. 28.—*Cerostoma radiatella*, Don.

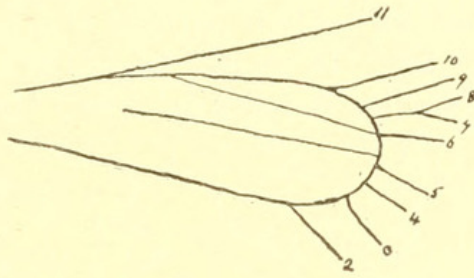


FIG. 29.—*Chimabacche jagella*, Fab.

single and running near the costal edge of the cell. Evidently in this instance it is the lower branch of the media that is undeveloped. In *Chimabacche* the areole is large, the chorda and media are, however, extremely feeble, though traceable. A little further obsolescence would have resulted in an apparently simple areocel. The most cossid neuration that I have found among the *Tineidae* occurs in *Titanomis*, Meyr.,\* a rather large form from New Zealand, to which my attention was directed by Mr. J. H. Durrant. It is evidently of an early undifferentiated type with all the veins present and separate. If we ask ourselves by what

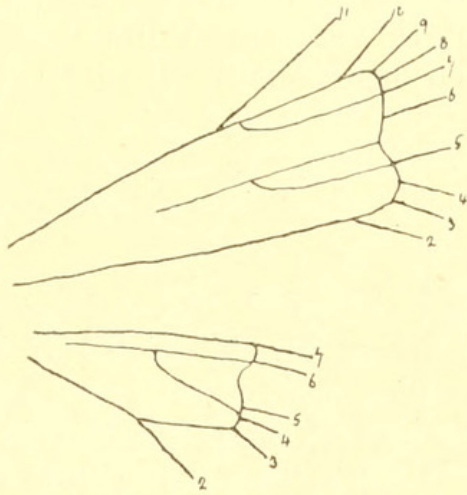
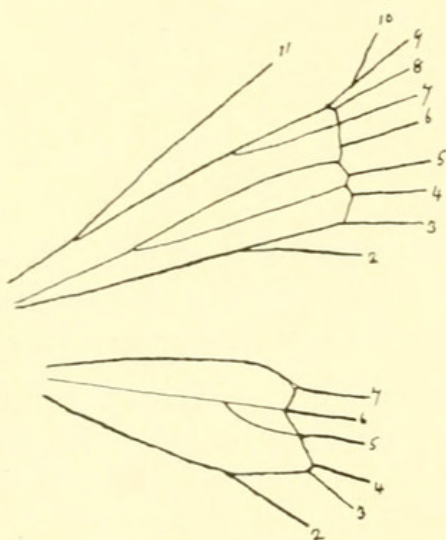
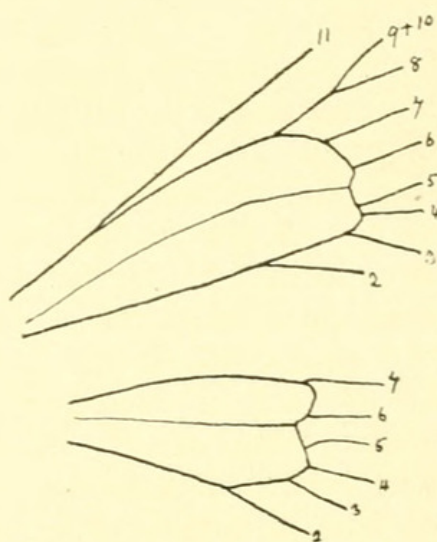


FIG. 30.—*Titanomis sisyrota*, Meyr.

\* *Nosymna*, an equally large form from Borneo, has somewhat similar neuration with large areole and strongly developed chorda, but the media is unbranched in both wings. It has smooth posterior tibiae as in the *Hyponomeutinae*, but those of *Titanomis* are densely hairy. *Incurvaria pectinea*, Haw., has nearly the same structure as *Titanomis*, but the chorda and branched media of fore-wings are very slender, almost vestigial.



structural points this genus can be differentiated from the *Cossidae*, we can only reply that the chorda and median veins, though present, are very slenderly developed, and that there is a well-developed tongue, with distinct though rudimentary maxillary palpi. In fact, the affinities of the *Cossidae* with the *Microlepidoptera* are so close that they must be included among them, if the latter term has any scientific meaning, although the former include the largest known *Lepidoptera*, if body bulk is estimated, for some Australian species of *Xyleutes* are about as big as a sparrow. It would be better to acknowledge that *Microlepidoptera* is not a scientific term and has no more meaning

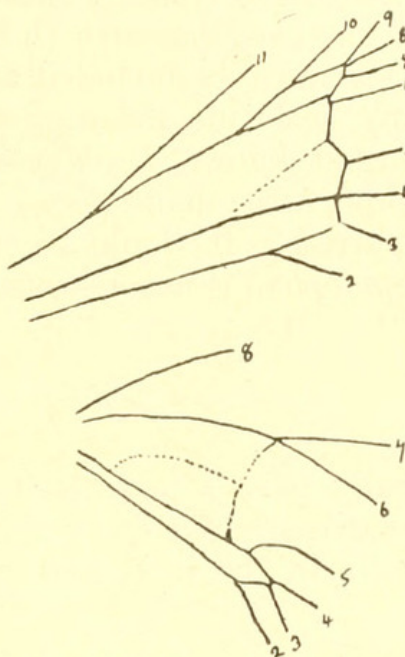
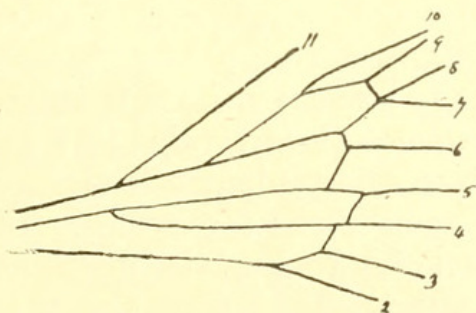
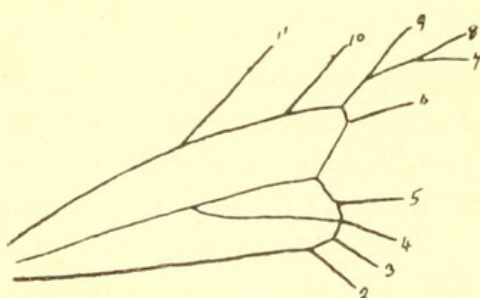
FIG. 31.—*Cnissostages oleagina*, Zel.FIG. 32.—*Arrhenophanes perspicilla*, Stoll.

than the word *Microcoleoptera*. While I am quite unable to accept Mr. Meyrick's division of the *Cossidae* into two families, he is certainly correct in his opinion as to the true affinities of the genus *Cossus*.

The genera *Cnissostages* and *Arrhenophanes*, to which my attention was called by Mr. J. H. Durrant, contain some large Tineids from South America with curiously specialised ♀ antennae. In the former there is a small narrow areole and well-branched median veins in both wings. In the latter, though an allied genus, the neurotation is much less primitive; there is no trace of a chorda, which suggests that it has disappeared by coalescence and not by obsolescence, as usual in this family; 9 and 10 are coincident, and both medians are unbranched.



*Castniadae*.—Though this and the three following families present structures linking them to the *Zeuzeridae*, the affinity is not so close as in the two families I have just dealt with. In the genus *Castnia* there is a narrow areole, partly projecting beyond the cell, the media with its lower branch is strongly developed, while the upper branch is completely absent. In the hind-wing the upper median branch is absent together with the discocellulars, except for a short spur arising from the strongly developed lower median branch shortly above the origin of vein 5. This apparently anomalous neuration is elucidated in the diagram by drawing dotted lines to represent the missing veins. So far as the fore-wing is concerned this explanation is demonstrated to be correct by the neuration of the genus *Gazera*, which has a larger areole, and a media with two long branches. In the genus *Synemon* the neuration of the hind-wing agrees with that of *Castnia*; the media in the fore-wing is of the primitive type, but the areole has disappeared,

FIG. 33.—*Castnia atymnus*, Fab.FIG. 34.—*Gazera linus*, Cram.FIG. 35.—*Synemon sophia*, White.

probably by coalescence of the chorda with the margin of the cell, so producing the type of neuration characteristic of the next three families. Before passing on to them I will draw attention to a peculiarity in the neuration of *Gazera*. In the fore-wing of this genus vein 10, which is rather weakly developed, becomes closely approximated to vein 9.



Had these two veins anastomosed they would have formed a new cell, which might be called a secondary areole. The importance of this point will become evident later.

*Zygaenidae*.—In *Cyclosia*, as in all the genera of this

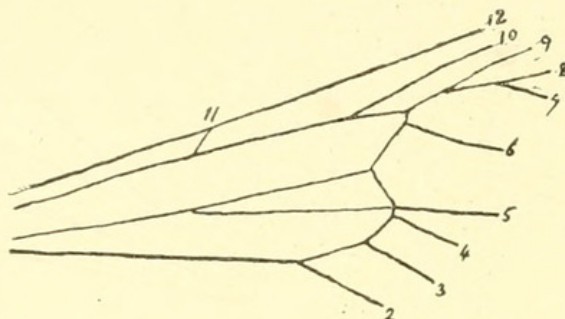


FIG. 36.—*Cyclosia panthona*, Cram.

family that I have examined or seen figured, the areole has disappeared as in *Synemon*. There is a long-branched media in the fore-wing, and vein 11 runs into 12, but in

the hind-wing the media is single as in *Chalcosia*. Sir George Hampson figures *Chelura* with a branched media in the hind-wing in his "Moths of India," but I found it to be unbranched in all the examples of this genus examined. I conjecture that Sir George Hampson may have figured an abnormal specimen. *Chalcosia* has vein 11 free, and the median cell is very small in the fore-wings. In the hind-wings the media is unbranched, and there is a short oblique vein connecting the cell with 8.

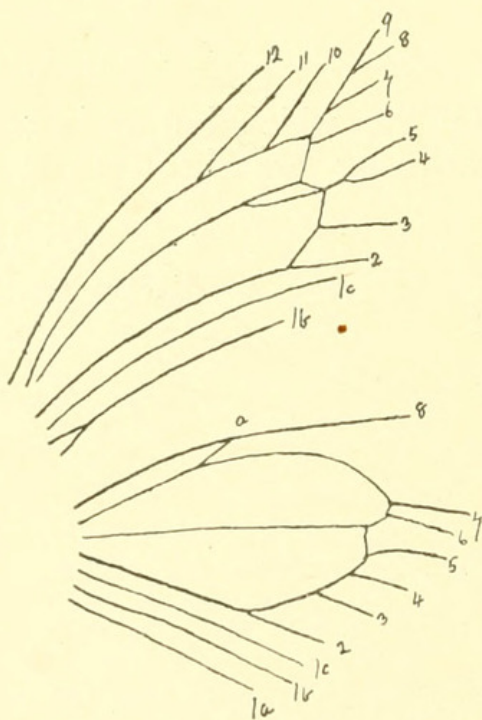


FIG. 37.—*Chalcosia affinis*, Guer.

Comparing this with the fore-wing of *Cyclosia*, we can hardly doubt that this connection represents one of the missing branches of the *radial* in the hind-wing, probably the first *radial*. The same vein is present in *Zygaena*, which has the media unbranched in both wings, the median cell having been



apparently extinguished by coalescence. In this genus, as in *Procris*, the median veins are developed feebly.

From this analysis it will be evident that the *Zygaenidae* are less primitive in their neurulation than the *Cossidae*, and

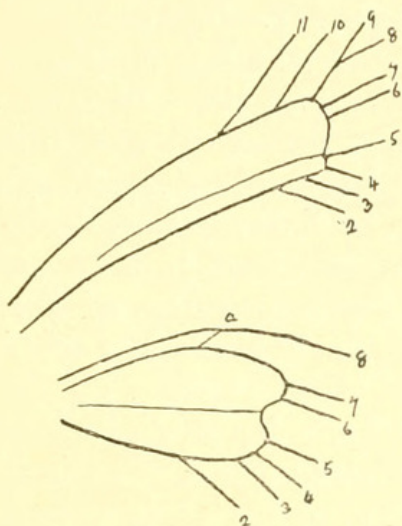


FIG. 38.—*Zygaena filipendulae*, Linn.

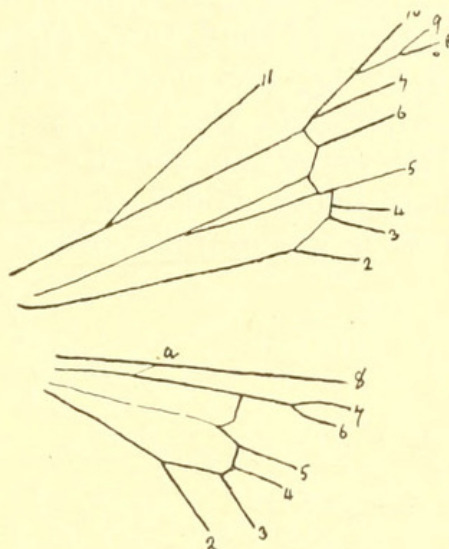


FIG. 39.—*Susica (Miresa) corones*, Fab.

that it is quite impossible that the latter family should have originated from the former, as maintained by Sir George Hampson in his "Catalogue of the Lepidoptera Phalaena" (i, p. 12). This conclusion is strengthened, although such confirmation is unnecessary, by the absence of tibial spurs in the former family.

*Limacodidae*.—That this family is structurally closely allied to the *Zygaenidae* is sufficiently shown by the accompanying figure of the neurulation of *Susica*, which in the absence of the areole and the structure of the media of fore- and hind-wings and in other points agrees closely with *Chalcisia*.

As a less primitive genus I have figured *Apoda*, in which the median cell has been lost in both wings. The short vein *a* present in *Susica*, which I believe to represent the first radial, is here replaced by a short anastomosis.

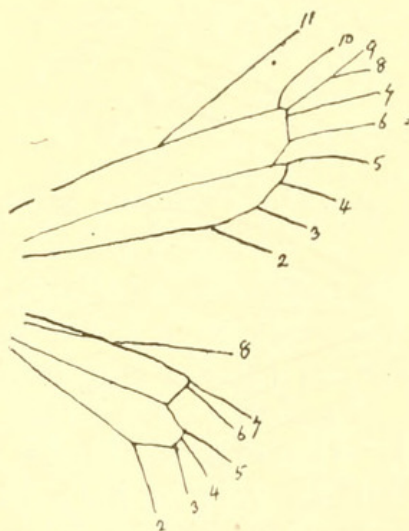


FIG. 40.—*Apoda avellana*, Linn.

At this point we will consider the genus *Paracossus*,  
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Hmps., which is represented in the British Museum by two solitary types, *P. parva*, Hmps., ♂, from Ceylon, and *P. furcata*, Hmps., ♀, from Pegu. They are of somewhat peculiar facies and very similar, but the former has short porrect palpi, and the latter longer palpi curved upwards in front of the frons. The tongue is absent. The antennae in the ♂ are shortly bipectinate to the apex, in the ♀ simple, and the posterior tibiae have two pairs of spurs. The neurulation shows no areole, an unbranched media in both wings, and 7, 8, 9, 10 of fore-wings stalked. Though this is structurally different from any known *Cossidae*, I

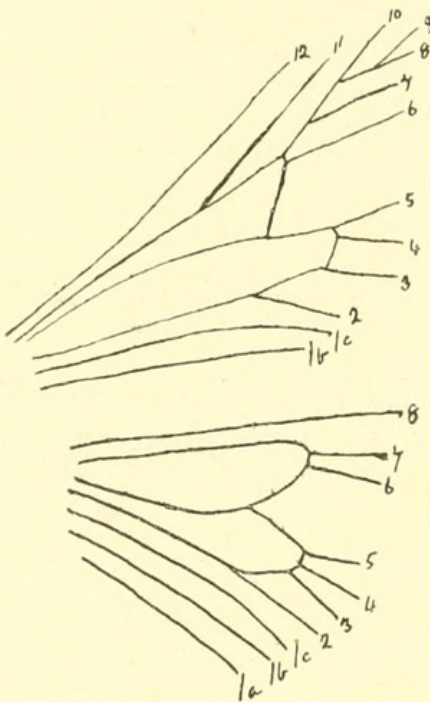


FIG. 41.—*Paracossus parva*,  
Hmps.

will not say that it may not be an aberrant genus of that family. In *Stygia* and *Inguri-morpha* the media is unbranched in both wings, and in *Lentagena* the areole is so small that a very small change would bring about its absence, and in *Acyttara* this has actually happened. But these genera are connected to the typical *Cossidae* by allied intermediate forms, the first belonging to a small Palaearctic, the remainder to a Neotropical group, while the Oriental *Paracossus* stands isolated. Again, stalking of 10 with 7, 8, 9 does not occur elsewhere in the family. On the other hand,

the neurulation of *Paracossus* agrees well with that of the *Limacodidae* in the unbranched median veins as in *Apoda*, and in the stalking of 7, 8, 9, 10 as in *Susica*.

*Psychidae*.—This family is related to the Zygaenid group by the absence of an areole and the development of a median vein in both wings, as shown in the figure of the neurulation of *Clania*, which has a branched media with narrow median cell in both wings. But it also presents peculiar features in the anal veins of the fore-wing, 1c anastomosing with 1b, and 1a being apparently present. In the hind-wing there is a short vein emitted from 8 on its costal side. Whether these are peculiarities developed in the family, or whether they represent some ancestral



features, are points on which I am not prepared to express an opinion without further study.

*Pyralidae*.—This family need not detain us long. It is a dominant group of more modern origin than the preceding families. In spite of the frequent presence of maxillary palpi and the three anal veins in the hind-wings, the neuration is of a modern type without any areole and usually without any median veins. In *Schoenobius* I have observed unbranched median veins slenderly developed in both wings, and probably they would be found in some other genera if careful search were made.

We now pass on to the numerous families which have only two anal veins in the hind-wings and one in the fore-wings. I cannot do more than deal with a few of these, and that in a summary fashion.

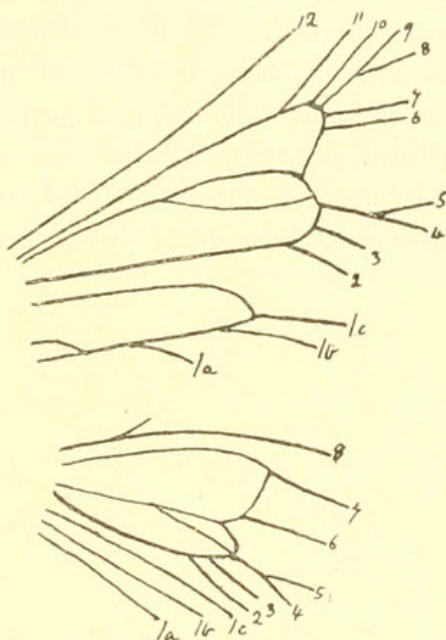


FIG. 42.—*Clania variegata*, Snell.

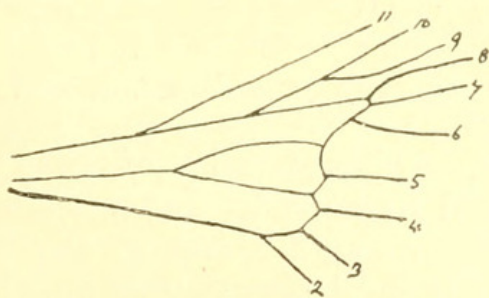


FIG. 43.—*Dudgeona actinias*, Turn.  
Abnormal neuration. Compare Fig. 2.

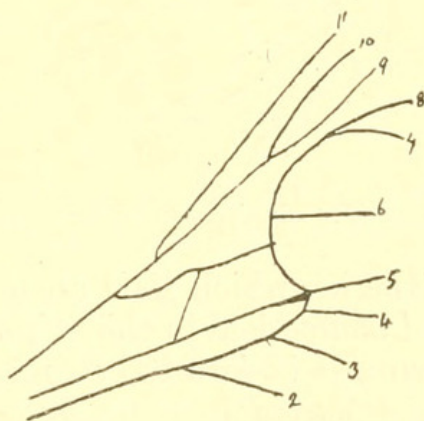


FIG. 44.—*Phragmatoecia castaneae*, Hb.  
Abnormal neuration. Compare Fig. 11.

*Lasiocampidae*.—This family, however, deserves rather fuller treatment. I have already pointed out that the areole may be lost in two ways, by obsolescence of the chorda, or by coalescence of the chorda with the common stalk of the second and third radials. There is yet a third way. As already mentioned in one example of *Dudgeona*



*actinias* (fig. 43), the bar between 8 and 9 which completes the areole is undeveloped. Similarly in an example of *Phragmatoecia castaneae* (fig. 44) the usual anastomosis between 8 and 9 is absent. In both these instances the areole has coalesced with the discal area outside the lepidopterous cell. These abnormalities illustrate, I believe, the normal structure of the *Lasiocampidae*. In the figure of *Lasiocampa* the letters *ar* mark the site of the undeveloped areole. There is a small cell with a slenderly developed unbranched media, and this cell is, I believe, the primitive lepidopterous cell, not an areocel, as in all the preceding

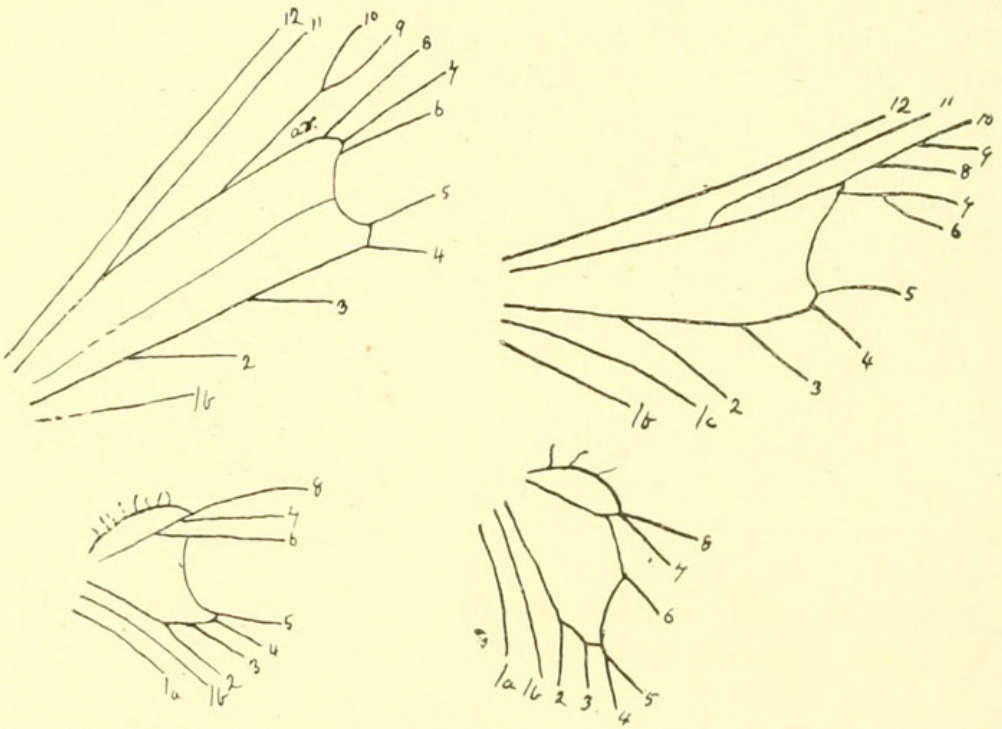


FIG. 45.—*Lasiocampa quercus*, Linn.      FIG. 46.—*Bhima undulosa*, Wlk.

families which lack an areole. This separation of 8 and 9 of course leaves the veins 9 and 10 stalked. But when an areocel is formed, as may be seen at a glance at any of the figures up to fig. 42, 9 and 10 are left arising separately from it. Usually 9 is attracted to 8, the instances in which it becomes again stalked with 10 are rare and exceptional; but in the *Lasiocampidae* 9 and 10 are *invariably* stalked. In the Indian genus *Bhima* the ancient structure is obscured by the stalking of 8, 9, 10, but this is a rare and late modification; in the great majority of genera 8 is separate or stalked with 7. But *Bhima* has one primitive character in the retention of *lc* of the fore-wings. The hind-wings of the *Lasiocampidae* usually differ very much



from those of the other families dealt with in this paper. The cell is small, without any media, 7 arises from its costal edge rather near the base and is connected with 8 by a short oblique vein *a* as in *Lasiocampa*, or by an anastomosis as in *Bhima*. I regard the former as more primitive. The offshoots from 8 are not veins, but chitinous thickenings developed to strengthen the precostal expansion of the hind-wing, which compensates for the absence of a frenulum in this family. In an undescribed genus from West Australia, for which I propose the name *Neurochyta*,\* the fore-wing differs from *Lasiocampa* only in the stalking of 7 and 8, and the absence of the media. The hind-wings are very exceptional in the family in the origin of 7 from very near the end of the cell, as is usual in other families, and the cell is of the normal lepidopterous form. I regard this as a fortunate discovery in preventing me from attaching too much importance to the peculiarly formed hind-wing cell usual in the *Lasiocampidae*, and as indicating, by the preservation of a more primitive form, how it may have developed. Yet *Neurochyta* has a lasiocampid hind-wing, for 8 anastomoses strongly with the cell near the base, and though the pre-costal cell so formed is very small, it gives rise to two strong branching spurs or pseudoneuria.

There seems, therefore, no real difficulty in deriving the *Lasiocampidae* from the cossid stem, although it is an isolated and early development from it.

\* *Neurochyta*, gen. nov. Palpi moderately long, porrect, reaching beyond frontal tuft, densely hairy. Fore-wings with 2 from  $\frac{1}{3}$ , 3 from  $\frac{2}{3}$ , 4 and 5 approximated from angle, 6 from upper angle connate with 7, 8 which are short-stalked, or 6, 7, 8 stalked, 9, 10 stalked, 11 from  $\frac{2}{3}$ , free, but running close under 12. Hind-wings with 2 from middle of cell, 3 from shortly before angle, 4, 5 stalked from angle, 6 from upper angle, 7 from shortly before angle, 8 anastomosing with cell from near base to  $\frac{1}{3}$ , precostal cell minute, two precostal pseudoneuria arising together near base and diverging. Type *N. edna*, Swinh.

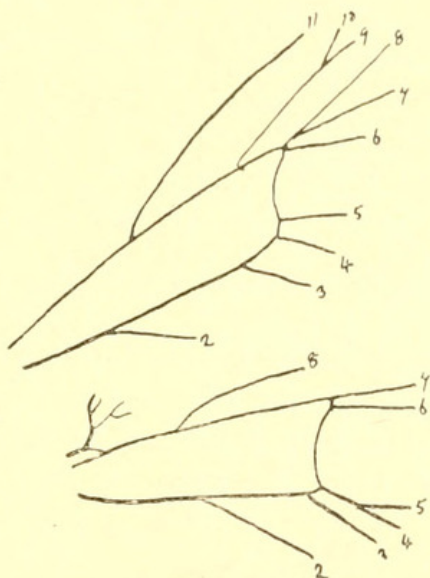
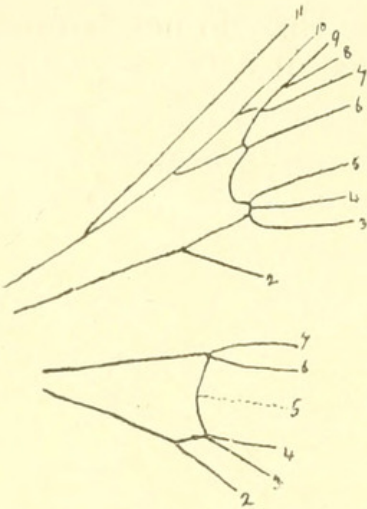
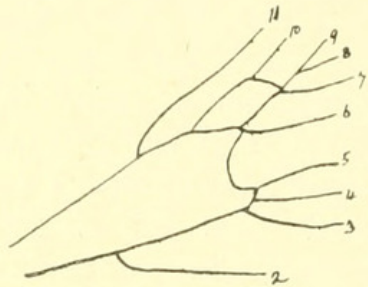


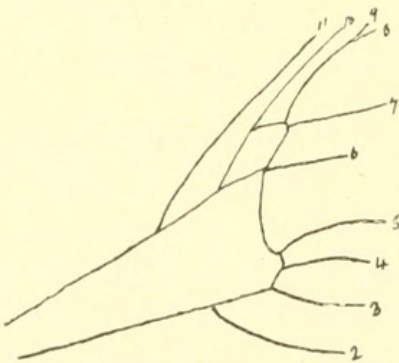
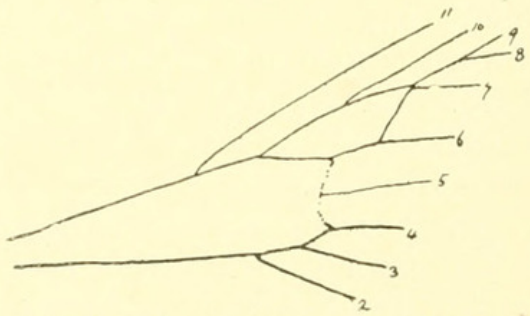
FIG. 47.—*Neurochyta edna*, Swinh.



*Noctuidae, Arctiadae, Liparidae, Notodontidae*.—We will consider these four families together. I have picked out one genus from each showing a well-marked areole and chorda of typically cossid form. I see no reason to doubt that it is actually a primitive areole. A secondary areole not homologous with the primitive areole is a possibility,

FIG. 48.—*Agrotis pronuba*, Linn.FIG. 49.—*Palaeosia bicosta*, Wlk.

as I have pointed out when describing the neurulation of *Gazera*, one of the *Castniadae*, and if such a structure was formed in a genus, in which areole and cell had coalesced to form an areocel, it might even be impossible to dis-

FIG. 50.—*Orgyia mendosa*, Hb.FIG. 51.—*Gargetta costigera*, Wlk.

tinguish it by inspection from a primitive areole, although morphologically of different origin. But there are two strong reasons for believing that this has not occurred in the *Noctuidae, Arctiadae, Liparidae*, and *Notodontidae*: (1) in these families there are genera which demonstrate the gradual obliteration of the areole by coalescence, but no genera exist in which there is any approach to the



formation of an areole; (2) the areole exists in the more primitive genera of the four families, and there is good reason for holding that the genera which have no areole have descended from forms which once possessed it. In the *Noctuidae* the neuration is remarkably constant. As Sir George Hampson informs me, the typical noctuid neuration, as illustrated in *Agrotis*, is present in the vast majority of the genera, and in those that do not possess it

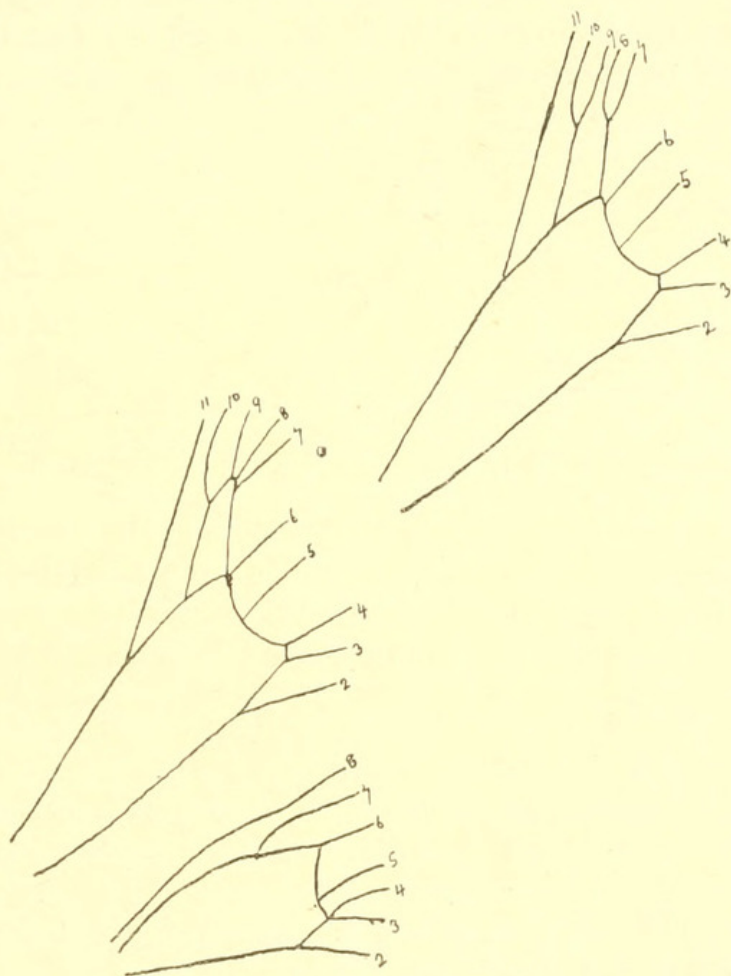


FIG. 52.—*Thyatira batis*, Linn.

it has been lost\* (see Introduction to "Cat. Lep. Phal.," vols. iv and x). In the other three families there is more variability, and it would take a much more lengthy examination than I can afford at present to prove that the forms which possess an areole are the more primitive. I can only express my belief that it is so.

While in the *Zygaenidae*, *Limacodidae*, and *Psychidae*

\* The primitive genus *Hyblaea* which possesses maxillary palpi has, however, lost the areole and cannot therefore be in the primitive noctuid stem, but must be an early branch from it.



the cossid areole and chorda have been lost, but the media has been retained, in the *Noctuidae*, *Arctiadae*, *Liparidae*, and *Notodontidae* the former have been retained and the latter lost. It follows that the descent of the second group of families from the first is an impossibility; they have developed from the cossid stem by a separate branch. How far this applies to those families which have lost both structures I will not inquire at present. It is advisable, however, to note that although the media is not developed as a vein, which occurs rarely in the higher families, it is frequently represented, either branched or unbranched, by

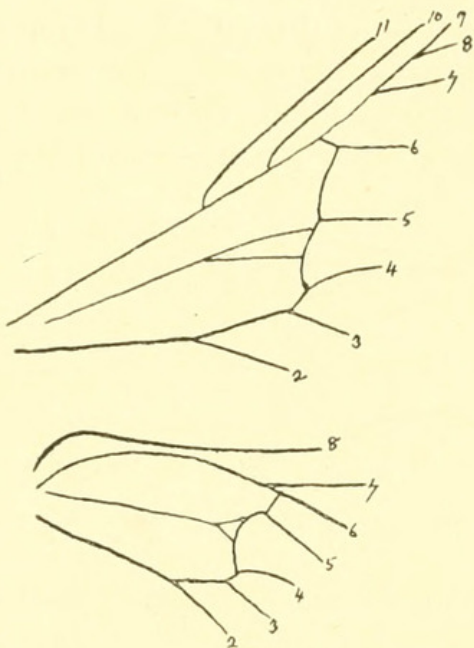


FIG. 53.—*Monoctenia falernaria*,  
Gn.

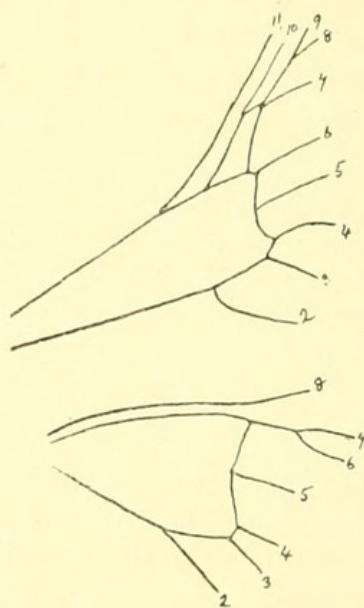


FIG. 54.—*Diceratucha xenopis*, Low.

a fold in the wing-membrane. These folds I have not reproduced in my diagrams.

*Thyatiridae* (*Cymatophoridae*).—The explanation that I have given as to the fate of the areole in the *Lasiocampidae* is to some extent supported by the analogous structure in the *Thyatiridae*. As Sir George Hampson has pointed out, the areole in this family is frequently not closed, the variation occurring rather frequently in the limits of a single species. There does not appear to be here any instance of the development of a new structure, which would be shown by a gradual change in a series of related genera, but of the loss of part of a structure in a proportion of individuals of a species perhaps owing to the absence of



some Mendelian factor. This curious variation is illustrated in the figure of *Thyatira batis*, Linn. The hind-wing shows some similarity to that of the *Lasiocampidae*, 7 arises from well before the angle of the cell, and, although there is no anastomosis, 8 is approximated to 7, but there is a well-developed frenulum, and I do not think the similarity points to any real community of descent. Whether the areole is really a primary and not a secondary areole in this family is not quite certain, but I think the former is more probable.

*Geometridae*.—This large family affords very interesting studies in neurulation. By neurulation alone it may be divided into at least five perfectly natural subfamilies. I have figured two of the most primitive genera in the most primitive subfamily *Monoctenianae*. They show remarkable differences. In *Monoctenia* there is a slender but

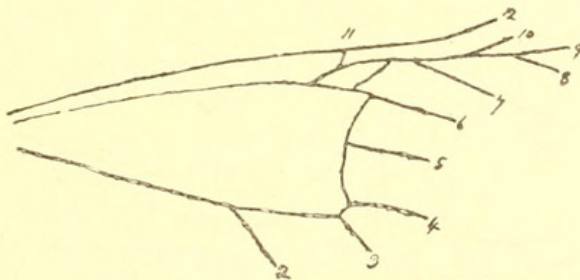
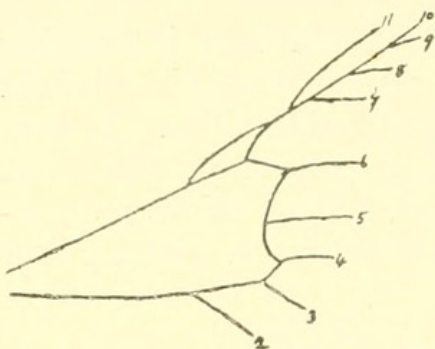
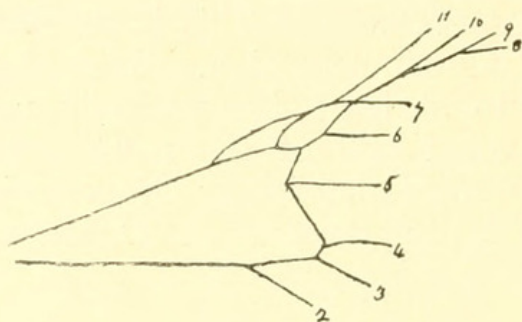


FIG. 55.—*Bupalus piniarius*, Linn.

distinct branched media in both wings, the areole being absent. In the three Australian genera *Diceratucha*, *Dirce*, and *Xenogenes* the media has been lost, but a large areole and well-marked chorda retained. These are very primitive genera, and I have no doubt this is a primitive areole, which in most of the family has been lost. It so happens that veins 10 and 11, which arise from the areocel separately and remain free in *Monoctenia*, often vary remarkably, not only in allied genera but in the same genus, and often in different individuals of the same species. This is especially the case in the subfamily *Boarmianae*. Here 10 and 11 may be separate or stalked at origin, and there is a strong tendency for 11 to anastomose with 12 and 10 with 9. In *Bupalus* 11 runs into 12 and 10 anastomoses with 9 to form a secondary areole, which has no relationship to the areole present in *Diceratucha*. In the *Geometrinae* 10 is usually stalked with 9 and there is a tendency for 11 to anastomose first with 12 and then with 10, but



an areole is never formed. In the *Acidalianae*, on the other hand, an areole is present in most genera, and those that do not possess it have lost it, the stages of its loss being often still preserved. The *Acidalianae* are a specialised, not a primitive subfamily, and their areole is evidently a secondary one. Similarly the *Larentianae* have nearly always a secondary areole, originally double, but with its internal partition often not developed, formed by an anastomosis of 11 with 10, and of 10 with 9.\*

FIG. 56.—*Eois aversata*, Linn.FIG. 57.—*Hydriomena dotata*, Linn.

#### CONCLUSION.

To sum up the results obtained by this inquiry. All the *Lepidoptera Heteroneura* are descended from a group with cossid neuration, to which, for convenience, I will give the name *Protocossidae*. The *Protocossidae* possessed a spiral proboscis or tongue with at least rudimentary maxillary palpi;† it had well-developed labial palpi, porrect or ascending; the tibial spurs were long and all present. The neuration of the fore-wing was that of *Zeuzera*, except that all the veins from the areole arose separately as in *Macrocyttara*. The neuration of the hind-wing was that of *Xyleutes*, except that a short oblique vein connected the cell with 8 as in *Xystus*. Perhaps the nearest living genus to the *Protocossidae* is *Titanomis*, a primitive Tineid, and from a form resembling this have descended the *Tortricidae* and a very large proportion, if not all,‡ of the *Tineidae*. From the *Protocossidae* arose

\* These conclusions may possibly be modified by a more exhaustive study of the family than I am able to give to it at present.

† Either the *Protocossidae* had five-jointed maxillary palpi, or those *Tineidae* which possess them, together with their immediate allies, descended from the heteroneurous trunk by a separate stem at an earlier level, and the *Tineidae* contain the descendants of two separate lines of descent approximated by convergence,



also (1) the *Castniidae* by a separate stem; (2) the *Zygænidæ*, *Limacodidæ*, *Psychidæ*, and *Pyrælidæ*, the first two from a common stem, the exact relationship of the last two being less certain; (3) the *Lasiocampidæ* by a very distinct stem; (4) by yet another stem the *Noctuidæ*, *Arctiidæ*, *Liparidæ*, and *Notodontidæ*, together probably with the *Geometridæ* and *Thyatiridæ*. If so much be admitted, we have already a classification in outline of the *Heteroneura*. The assignment of the other families of this great assemblage to their positions within this outline must be reserved for another occasion.

It is apparent that this phylogeny is based mainly on the neurulation. No one is more anxious than I to consider all the characters of all the stages of the Lepidoptera, but the value of all the characters must be carefully weighed. The great problem of phylogeny is the distinguishing of resemblances due to community of descent from those due to evolution in a common direction usually but perhaps not always under the influence of the environment, that is to say, to adaptation to common conditions. Or, as my old teacher, Prof. Ray

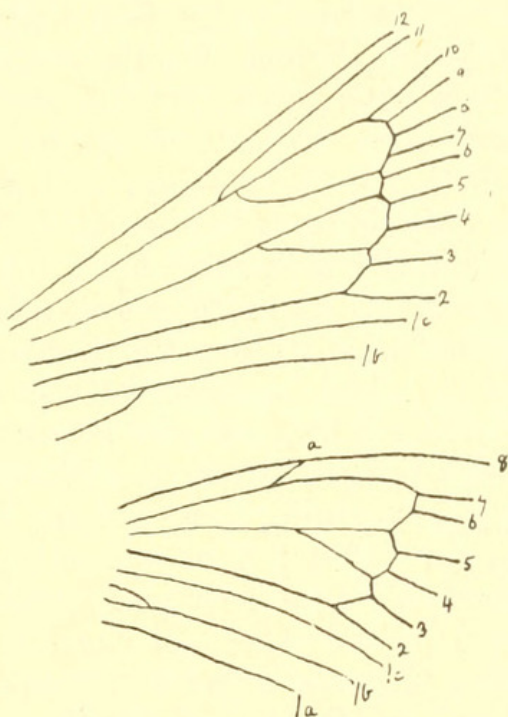


FIG. 58.—Neurulation of the hypothetical family *Protocossidae*.

Lankester, used to say in his lectures, we must distinguish *homogeny* from *homoplasy*. No better illustration of homoplastic resemblances can be found than among the larvae of Lepidoptera, for instance, in the resemblance of some Noctuid larvae to those of the *Geometridæ*, of other Noctuid larvae to those of the *Bombycine* families. Lepidopterous larvae are peculiarly exposed to adaptational modification. They are in no sense embryonic forms, that is to say, forms recapitulating the phylogeny of the insect, but secondary adaptations to a phytophagous existence departing more widely from the primitive insect than do the imagines, and morphologically much degraded. Their



characters within the various families have sometimes considerable phylogenetic value, but little value in indicating the true relationship between the families. To attempt a classification of the Lepidoptera from the relative position of the tubercles on the larval skin, as has been done by Mr. Dyar, seems to me as profitless as it would be to classify the whole order by the form of the palpi, or the shape of the outlines of the wings in the perfect insect.

The pupal and oval characters advanced by Dr. Chapman appear to me to stand on a better foundation. I am quite ready to admit that forms with a greater number of movable pupal rings, his *Incompletae*, are more primitive than those with fewer movable rings, his *Obtectae*; but this does not carry us far. It seems probable also that the distinction between forms with vertical eggs having a central micropyle from those with flat eggs in which the micropyle is on the side may have important phylogenetic significance. In the former group are the four families *Arctiadae* (from which arose the *Syntomidae*), *Noctuidae*, *Liparidae* (with which I associate the *Hypsidae*) and *Notodontidae*, families which, it will be observed, I have associated on neurational characters. The only other family with upright eggs, excepting those usually known as *Rhopalocera*, whose origin I am not at present prepared to discuss, are the *Castniadae*, and these I regard as an isolated group. In the *Cossidae* the oval characters appear to have remained in a fluid state, for Dr. Chapman states (Trans. Ent. Soc. 1896, p. 579) that while *Cossus* has a vertical egg, that of *Zeuzera* is flat. If this is so it is admissible to assume that the same held true of the *Protocossidae*, and that these have given origin not only to the above-mentioned families with vertical eggs, but to other families in which the eggs are always flat.

The neuration is by far the best guide to lepidopterous phylogeny that we possess; it is a hidden structure protected from the direct action of outside influences to a large extent, rarely affected by directly adaptational changes, and, in short, the best field in which to search for *homogeny* unobscured by *homoplasy*. Yet even here *homoplastic* influences are at work, and cautious interpretation is necessary, for there is a widespread tendency in many different families towards a simplification of the neuration, which often proceeds along parallel lines.



The *Lepidoptera* have specialised in colour and wing-pattern, not in structure. The great achievement of the order in structure was the development from the maxillae of the spiral proboscis, and this happened long since. Among existing families structural evolution has had but trivial results, consisting (I am writing, of course, of the imagos) of little more than secondary sexual characters.\* On the other hand, there has been a strong tendency in nearly all the families to progressive reduction in structural complexity, to a progressive simplification by structural loss, on parallel lines. Unless this is fully recognised no progress will be attained in the true phylogeny of the different groups. I will enumerate some of these lines, and point out how remarkably they have been followed even within the very ancient and primitive *Cossidae*.

(1) The proboscis and maxillary palpi have been lost in the *Cossidae*, *Psychidae* (only the ♂ can be brought into comparison, the ♀ being degraded to an extreme degree), *Limacodidae*, *Lasiocampidae*, *Liparidae*, and in other whole families, as well as in many isolated genera.

(2) The labial palpi have been lost in some genera of *Cossidae* and quite independently in many genera of other families.

(3) The tibial spurs have been lost or much reduced in most *Cossidae*, in the *Zygaenidae*, *Psychidae* ♂, and in other instances.

(4) The frenulum has become shortened and non-functional in a few *Cossidae*, wholly lost in all the *Lasiocampidae*, *Endromidae*, *Uranianae*, and in some genera of the *Drepanidae*, and *Bombycidae* and the *Geometrinae* subfamily of the *Geometridae*; in the last instance every grade between full development and complete loss can still be traced.

(5) The median vein is always present in the *Cossidae*, but in a few genera, the first step in its obsolescence, the obliteration of the median cell has taken place. It is completely lost or merely vestigial in most *Lepidoptera*.

(6) The areole and chorda are lost in at least one genus of *Cossidae*, in all genera of most other families, and in those families that retain it, it has been lost in some, if not

\* I leave out of consideration the basal abdominal cavities, as to which I have no precise knowledge.



most, of the genera. This is a striking instance of parallel involution in independent groups.

(7) The peripheral veins are partly or wholly coalesced to some extent in nearly all families. In the *Cossidae* this does not proceed beyond partial coalescence (stalking).

Other instances might be mentioned, but these are sufficient.





Turner, Alfred Jefferis. 1918. "Observations on the Lepidopterous Family Cossidae and on the Classification of the Lepidoptera." *Transactions of the Entomological Society of London* 66, 155–190.

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