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ORIGIN OF THE LEPIDOPTERA, WITH DESCRIPTION OF A NEW MID-TRIASSIC SPECIES AND NOTES ON THE ORIGIN OF THE BUTTERFLY STEM

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ABSTRACT. Part I presents data on two new fossil wing impressions, identified as early Lepidoptera of a homoneurous type, from the Insect Bed at Mount Crosby, Queensland, now recognized to be of Mid-Triassic age. They represent a new family, the Eocoronidae, a new genus, *Eocorona*, and species, *iani*.

The status of a previously described genus and species from the same horizon in Triassic time, *Eoses triassica* Tindale, 1945 is examined and evidence given for its validity as a member of the Lepidoptera. Evolution of the homoneurous stem of the Lepidoptera is discussed in light of several living members of the family Lophocoronidae (Common, 1973), the Agathiphagidae (Dumbleton, 1952), and the recent finding of *Neotheora* in Brazil (Kristensen, 1978).

Part II offers observations on the origin of the Rhopalocera stem of the Lepidoptera, based in large part on study of tracheal systems in the wings of newly formed pupae of several superfamilies. The observations lead to the conclusion that the Butterfly stem may be rather closely linked with an ancestral line of the Castnioidea, or Butterfly-moths.

The recent discovery (Durden & Rose, 1978) of Mid-Eocene butterflies of two existing families reinforces earlier ideas that the origin of the stem should be sought in the Mesozoic, and not in the Tertiary Period.

PART I. NEW EVIDENCE ON THE ORIGIN OF THE LEPIDOPTERA

Recent discoveries of new familial representatives of the homoneurous Lepidoptera by Common (1973) in Australia, by Kristensen (1978) in Brazil, and added information about the Neopseustidae by Davis (1975), has prompted reconsideration of the origin of elements of the Lepidoptera stem.

New evidence suggests that between the end of the Permian and the Jurassic differentiation of early branches of the Lepidoptera stem and their separation from the Mecopteroid stem may have occurred. This necessitates further discussion of the Triassic fossil described as *Eoses triassica* Tindale (1945: 39). When published it was considered an ancestor leading toward the homoneurous branch of the Lepidop-

tera and was placed in a separate suborder, the Eoneura. This view has been rejected by some researchers. Thus Riek (1955), who subscribed to a view that the Lepidoptera only became separate relatively recently, said that consideration of an early Mesozoic appearance would be premature. He said of *Eoses* that it would be difficult to maintain it as a primitive lepidopteran although it conceivably might be ancestral to that order.

New discoveries have encouraged consideration of an earlier Mesozoic origin. Finding of early Cretaceous moths close to *Sabatinca* in amber from Lebanon (Whalley, 1977) and of Eocene Papilionoidea relatively close to the living *Baronia*, by Durden and Rose (1978), has strengthened the view of an earlier Mesozoic origin of the Lepidoptera stem.

After attempting to place *Eoses* correctly, a further pair of wings from the same Mount Crosby Mid-Triassic bed will be described. This fossil suggests differentiation of the Lepidoptera had already begun at that time, especially in forms classified by venational characters as Homoneura.

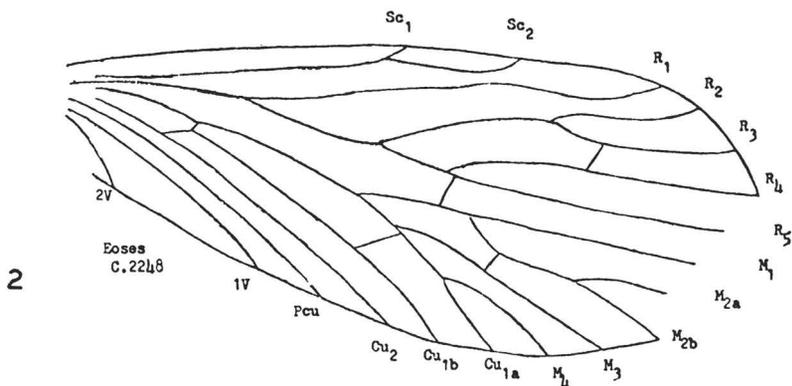
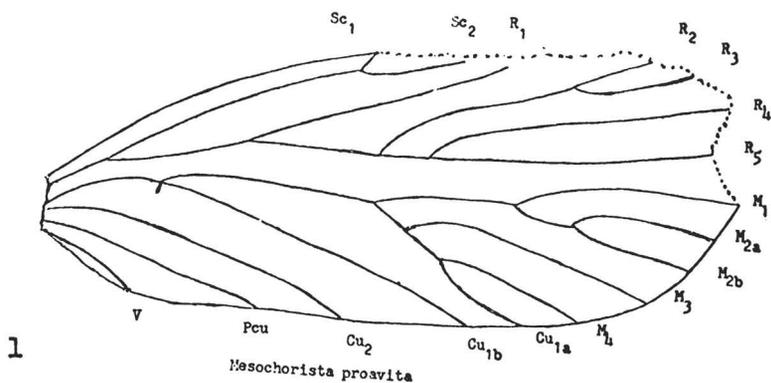
Dodds (1949: 3) confirmed that the Insect horizon of the Mt. Crosby bed under consideration is beside the track between Portion 92 and Portion 172, Parish of Chuwar, in Queensland. In the view of findings of Jones and de Jersey (1947) the bed lies at the top of the Mid-Triassic. I worked in the bed at various times between 1942 and 1944.

Historical and Taxonomic Review

Preliminary discussion on the taxonomy of *Eoses triassica* is in order. Riek (1955: 661) suggested that the generic name *Eoses* was a *nomen nudum*. He failed to notice that in the original paper the genus was described in the same terms as the species. There was a description and a direct discussion on the likely position of *Eoses* in the development of the Lepidoptera stem. Riek further considered it to be a direct synonym of the Upper Triassic *Mesochorista proavita* Tillyard (1916: Pl. 2, Fig. 2), an insect to which it has some resemblance, but which belongs in the Mecoptera. Of *M. proavita* he says that, save for differing structural details of the vein Sc it could be placed, almost, in the Recent genus *Chorista* Klug (Mecoptera, family Choristidae). Fig. 1 in this paper is based on Tillyard's original figure.

When comparisons are made in detail between *Eoses triassica* and *Mesochorista proavita* there are significant differences:

- a) In the forewing the hm vein is present in *Eoses* and extends along the costa; it is not in the *Mesochorista*.
- b) The ir vein is present in *Eoses* between R_3 and R_4 , but it is absent in *Mesochorista*.

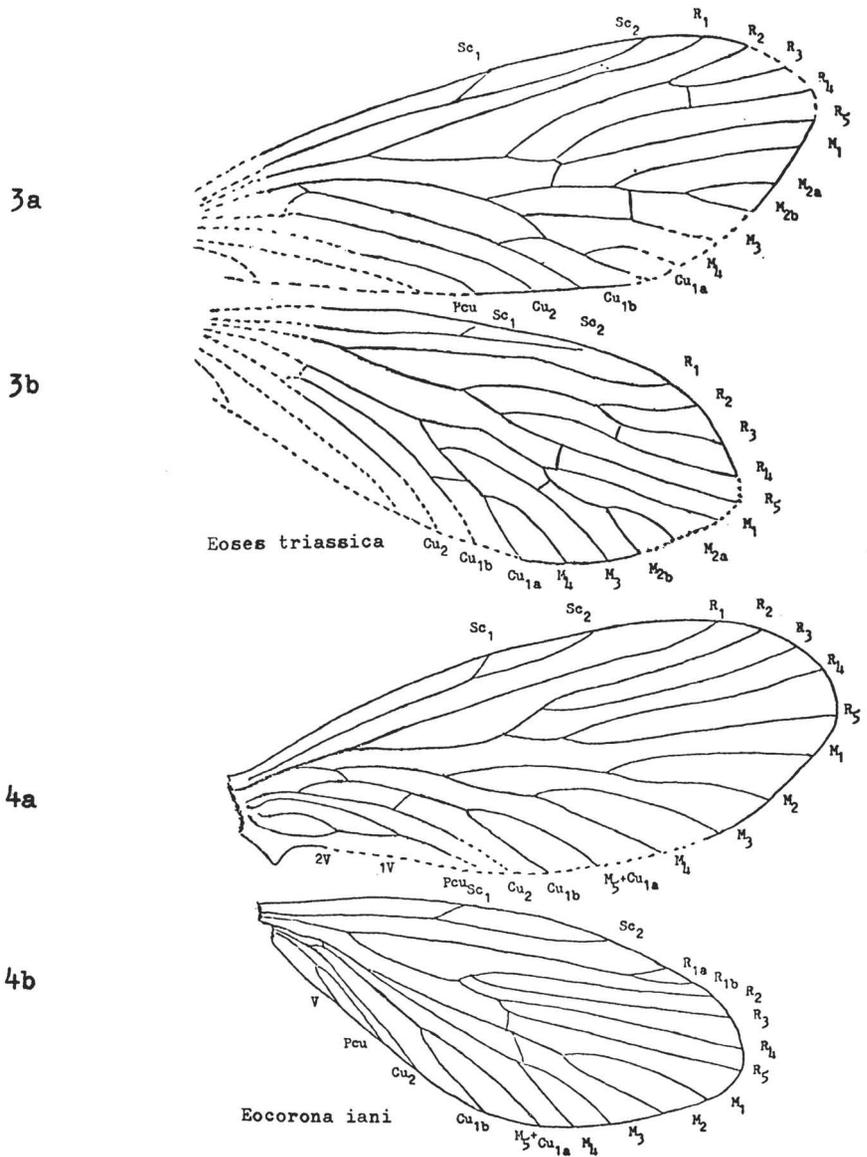


FIGS. 1-2. Upper, *Mesochorista proavita* Tillyard, 1916, Upper Triassic (after Tillyard); Lower, Specimen C.2248, Middle Triassic, *Eoses* identified as *M. proavita* Riek (nec Tillyard), after Riek.

- c) The *rm* vein is present in *Eoses*, but not in *Mesochorista*.
- d) The *im* vein is present in *Eoses*, but not in *Mesochorista*.
- e) Cu_{1a}/Cu_{1b} fork is present in *Eoses*, but is not in *Mesochorista*.

Some of the above differences may be, in part, due to the difficulties of observing the fossils but I question their being the same. When drawn to similar scales, by taking the distance from the fork of R_1 and R_5 to the fork of M_1 and M_2 as base, the wings also are different in form. Finally, they are from very different horizons in the Triassic.

In the Australian Museum collection in Sydney, Riek found a linked pair of wings, their specimen F.39230, which he was able to match



FIGS. 3-4. **3a**, *Eoses triassica* Tindale, 1945, original specimen, F.7853, with data from C.2248 superimposed in dotted line. **3b**, paratype specimen F.7855 with additions suggested in dotted line. **4a**, *Eocorona iani* gen. et sp. nov. Mid-Triassic, Site A, Mount Crosby, Queensland, holotype. **4b**, the same, paratype, identified as a hindwing, from same horizon as holotype.

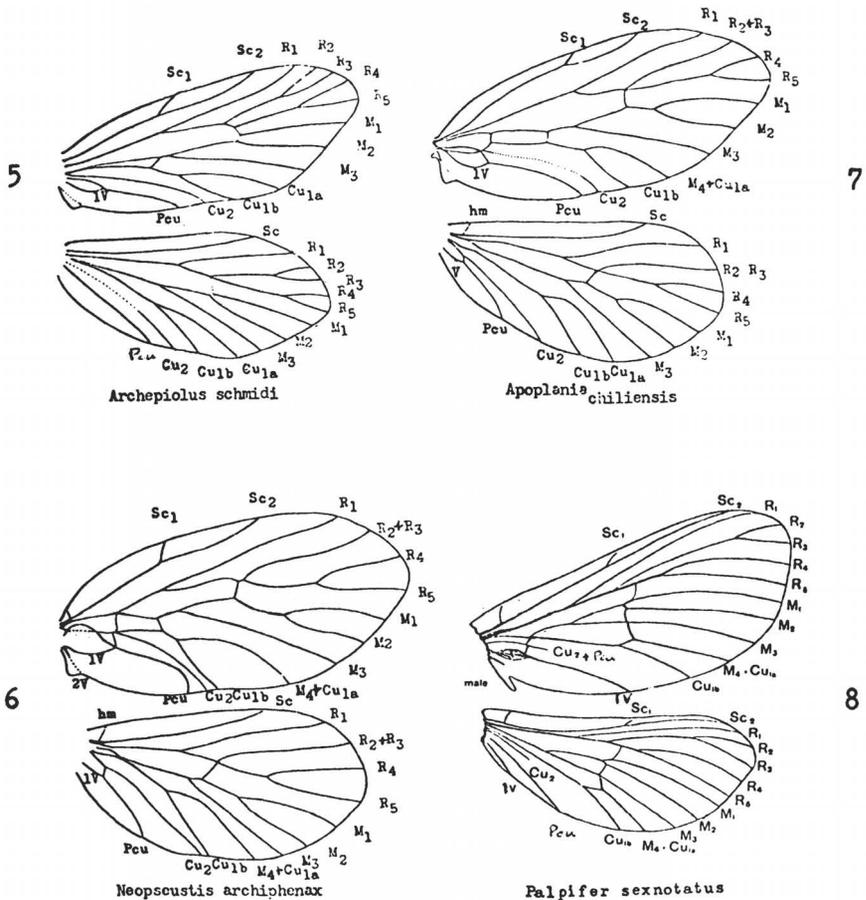
with the type specimen of *Mesochorista proavita* Tillyard, thus confirming that it was a forewing. Therefore, it appears safe to accept the view that it is the forewings that are being compared between *Eoses* and *Mesochorista*. Unfortunately Riek did not figure the hindwing of this pair. He also obtained a further specimen, C.2248, from the Mount Crosby bed. This he believed to be a *Mesochorista* and thus equated it with *Eoses*. He did figure the new find. It shows similar differences from *M. proavita* as outlined above and definitely is not *M. proavita*.

Specimen C.2248 is smaller than the type forewing of *Eoses triassica*, necessitating an adjustment of the order of 8.7 as against 11.0 to obtain any close match of comparable parts of the venational pattern. Conceding all the imperfections claimed by Riek, as present in the specimen F.7853, a composite drawing affords some substantiation, but suggests that there is less of an apical wing point than suggested in the original interpretation. Figure 3a incorporates in dotted outline additional information suggested by C.2248.

According to Riek the paratype specimen of *Eoses triassica*, F. 7855, is not a hindwing as described, but another forewing, despite its different size and shape. Parenthetically, in the original published drawings of *Eoses* a printer's error in the reduction of the figures made the hindwing proportionally far too large. This is apparent when the published dimensions are noted. It is smaller than the supposed forewing and matches C.2248 in size. I believe that they both are hindwings. When they are directly superimposed there is little need for adjustment and there is considerable correspondence even in small details. The result is shown in Fig. 3b.

Accepting a view that we have present matched fore- and hindwings of a single species, known as *Eoses triassica*, consideration must be given to the specimen C.1595 of Riek (1955: 658, Fig. 5) which he regards as a hindwing. This specimen differs in wing pattern and it is too small to be an actual hindwing of the species under discussion. It seems safe to dismiss it from further consideration as part of the immediate problem. Thus, in my opinion, we have strong indications of the existence of an early member of the Lepidoptera stem, and I believe that Riek has incorrectly synonymized its name with that of a species, *Mesochorista proavita* which belongs in a different order of mecopteroid insects, a group from which it is removed both by structure and by time. The three wings of *Eoses triassica* now known provide us with a useful picture of a Mid-Triassic, and very early lepidopteran.

As summarized by Razowski (1974: 7), the position of *Eoses* has generated several divergent points of view. The finding of the addi-



FIGS. 5-8. Upper left, *Archepiolus schmidi* Matuura, 1971, Assam (after Davis, 1975) with altered vein designations. Lower left, *Neopseustis archiphenax* Meyrick, 1928, Burma, China (after Davis; vein designations added). Upper right, *Apoplania chiliensis* Davis, 1975, Chile (after Davis; vein designations added). Lower right, *Palpifer sexnotatus* Moore, 1879, Sikkim (Hepialidae).

tional material by Riek (his specimen C.2248) eliminates the Bourgogne (1951) view that *Eoses* was a pathological specimen. Hennig (1969) followed Riek (1955) in considering it a mecopteran, a position disputed in this paper. The supposed similarities to the Diptera seem specious if both fore- and hindwings are accepted as present. It seems that these authors thought that the Lepidoptera originated at a very late date, implied although not stated, as Tertiary time. The presence of a relatively advanced homoneuran from the Lower Cretaceous im-

TABLE 1. Two estimates of the geological time scale. Age in millions of years before present.

| Eras | Periods | Epochs | First estimate | Second estimate |
|-----------|------------|-------------|----------------|-----------------|
| | | Recent | 0.01 | 0.015 |
| | Quaternary | Pleistocene | 3 | 1 |
| | | Pliocene | 6 | 11 |
| | | Miocene | 23 | 25 |
| | | Oligocene | 35 | 40 |
| | | Eocene | 55 | 60 |
| Cenozoic | Tertiary | Paleocene | 65 | 70 |
| | | Cretaceous | 135 | 130 |
| | | Jurassic | 200 | 180 |
| Mesozoic | | Triassic | 210 | 225 |
| Paleozoic | | Permian | 235 | 270 |

plies earlier development must have occurred in the Jurassic, thus pointing to at least a Triassic base for the order. The inferences of Jeannel (1949) that early Lepidoptera were inhabitants of Gondwanaland in the earliest Mesozoic, and that lines leading to the Cossidae and to the Castniidae were already represented in the Jurassic, are likely to be true.

Time Scale in the Development of the Lepidoptera

A frequent question is how much time has elapsed since the Lepidoptera first appeared. Geologists are not yet in agreement as to time scale, but an origin of the stem in the Triassic would take us back more than 210 million years.

Radiometric records by Banks (1973: 669) suggest the Permian-Triassic boundary at about 235 million years before present, with the Triassic-Jurassic changeover near the 200 million mark. Whalley (1977) in reporting the *Sabatinca*-like species from amber, in Lebanon, of Early Cretaceous date, allowed "at least 100 million years," and quoted another assessment of "an absolute age of 130 million years before the Present." Table 1 is based principally on Banks.

I will now discuss another species from the Mid-Triassic of Mount Crosby, Queensland, which may qualify for recognition as an early member of the Order Lepidoptera.

Wing Impressions from the Mount Crosby Insect Bed

Order Lepidoptera

Family **Eocoronidae** nov.

This family is erected to contain the monotypic species and genus described below. It is from an upper level in the Mid-Triassic of Mt.

Crosby, Queensland. The looped vannal veins of the forewing differentiate this taxon from what is considered to be its nearest known relative, *Eoses triassica* Tindale, 1945, which belongs in a separate family, the Eosetidae, present in the same Triassic horizon. Descriptions of the family, genus, and species are combined below, and are followed by a discussion on its relationships with other early fossil Lepidoptera.

Eocorona Tindale, new genus

Description. Forewing moderately broad, margins well rounded, with rather rounded apical area at about R_5 . Costa with Sc_1 and Sc_2 present; R_1 and R_8 parting at one-quarter. Second radial fork near one-half, thereafter both tertiary forks are short-stalked and evenly parting. Presence of *rm* crossvein suspected but not clearly shown in the primary type specimen. Median fork near base, second fork well before middle, thereafter both veins long stalked. M_1+M_2 stalk twice as long as M_3+M_4 . M_5 joining *Cu* near one-third, separating again before the margin. Cubital fork well defined, intercubital crossvein present. Cu_2 extending strongly towards hind margin so far as preserved in the specimen under consideration. *Pcu* a strong vein running towards margin parallel to Cu_2 . Veins IV and 2V in anal area looping up to join with *Pcu* well before margin. A broad jugal lobe present.

Type. *Eocorona iani*. From the Mid-Triassic of Mount Crosby, Queensland. The single species so far recognized in this genus appears to be a member of the Suborder Eoneura of the Lepidoptera, as envisaged by Tindale (1945), but its position is subject to revision when more is known of its relationships. A broader discussion of its status and relationship with *Eoses triassica* and other Lepidoptera is given later in this paper.

Eocorona iani Tindale, new species

Description. Characters as set out in the above generic description. Virtually the whole of a forewing discovered, with well formed jugal lobe present. Margins of the wing are clearly evident except between the basal fourth of the hind margin and just below M_3 but the hindmarginal form is approximately defined by the apparent distal terminations of M_5 and Cu_1 . The length of the preserved portion of the wing, as shown in Fig. 4a is 8 mm.

Types. Holotype specimens from Site A at Mount Crosby, Mid-Triassic. Type to be deposited in the University of Queensland Geographical Museum as no. C.2327.

Remarks. A second specimen from the same horizon tentatively is considered to be a hindwing of the same species. It also is to be deposited in the same collection as no. C.2331. Its preserved length is 7 mm. This second specimen shares significant features with the designated type specimen. Such differences as exist, indicated in Fig. 4b, suggest the hindwing of an early lepidopteran. It differs in the presence of a small apical fork of R_1 . The *rm* crossvein, uncertain in the type, is well defined, as is also an oblique *im* vein. *Pcu* extends to margin and only one vannal vein is present.¹

First drawings of the above *Eocorona* fossils were made in 1943, but set aside. Interest in them was renewed after the discovery of three species of living Lophocoronidae by Common (1973). There were indications pointing to the Triassic as a probable time for the divergence of the Lepidoptera stem from other mecopteroids. I suggested this in 1945, but the view had been rejected by Riek (1955). As a result of

¹ Venational designations employed in this paper have been used by this author in many papers on the homoneurous moths of the family Hepialidae and were outlined in Tindale (1941). Due consideration was given then to the recommendations of Snodgrass (1935) about the postcubital (*Pcu*) and the vannal (*V*) veins in the anal area of the wing.

developments outlined in earlier paragraphs of this paper regarding *Eoses*, the new evidence afforded by *Eocorona* supports the view that by Triassic times some of the trends in development of the whole homoneurous stem of the Lepidoptera were foreshadowed. Thus it seemed proper to look even before the Mid-Triassic for the actual separation of the two orders Lepidoptera and Mecoptera.

In considering *Eocorona* with *Eoses* as ancestral Lepidoptera, some differences can be found. In the forewings of living Hepialidae, for example, there are only three main M branches with a fourth uniting with Cu, near the base of the wing, as was first noted by Tillyard. In *Eocorona* seemingly there is an additional M vein extending to the margin while it is a fifth one which links with Cu near the base (Figs. 4a and 4b). I have an alternative suggestion that M_3 has a bifurcation near the termen in which case there is no M_5 . I intend to publish this alternative view in a separate paper. The present interpretation serves to draw attention to some resemblances here and also in the looped vannal veins of the forewing, suggesting a possible link with the Permian *Microptysma* of Martynova (1959). Perhaps the venational characters which lead toward the Lepidoptera were already apparent at the very beginning of the Mesozoic.

In the looping up of the vannal veins of the forewing, *Eocorona* resembles both *Agathiphaga*, and to a lesser extent *Lophocorona*. Dr. I. F. B. Common (personal communication) noted that *Agathiphaga queenslandensis* possesses an M_4 much as in *Eocorona* and suggested that because of both this feature, and the indication that the apex of the wing comes between R_4 and R_5 , a link with the Agathiphagidae rather than with the Lophocoronidae might be favored. However he agreed that we are dealing with very primitive lepidopteran characters and these indications do not imply, necessarily, any close relationship. In the absence of parts other than the wings it is not possible, at present, to relate these fossils too closely to any existing family, or to modern classifications based on the structures of other body parts. Indications, based on their homoneurous venations, are that, if the wings are truly matched, they should be considered near ancestors to lines leading to the Dacnonypha of Hinton (1946) and the Monotrysia of Börner (1925), if these divisions have validity.

In comparing *Eocorona* with *Lophocorona*, while keeping *Eoses* in mind, it seems that in the Triassic there were vein modifications which have persisted up to the present day. Some important venational characteristics of present-day Homoneura were already established by that time.

Comparison of *Eocorona* with *Agathiphaga* yields interesting indications of a distant relationship, and also of some major differences. The long fork of R_4+R_5 in *Eocorona* seems to be a major difference, but the condition appears in living hepialids such as *Palpifer* (Fig. 8). In *Eocorona* also, the stalk of R_2+R_3 happens to be short and thus to differ from the length in other Homoneura, but this character is long in *Eoses* and so is comparable with the length in other hepialid genera (e.g., see *Fraus* and *Pharmacis*, and the same condition is seen in *Agathiphaga*). In *Archeptolus* (Fig. 5), which Mu-tuura (1971: 1133) considers to be the most primitive known of living Dacnonypha, there is a symmetrical branching of the R veins, as in *Eocorona*; the difference is that the stalk portions are longer than the forked ones. Davis (1975) did not comment on this feature when he linked *Archeptolus* with *Neopseustis* (Fig. 6) and with *Apoplania* (Fig. 7), in which there seems to be a specialization linked with some form of scent gland such as appears in the males of *Palpifer sexnotatus* (Fig. 8).

Crampton (1922: 288–229), basing conclusions on available material, suggested that from a pre-mecopteroid array came a line of development leading to Trichoptera and Lepidoptera. He was one of the first to perceive that these two lines paralleled each other very closely and would show common ancestry. Material in the present paper suggests that by Triassic times the early Lepidoptera were already in evidence. Necessity of considering only venational characters limits useful comparisons with other studies (e.g., Kristensen

1975) based on additional anatomical features. However the links he infers between the Lepidoptera, the Trichoptera, and the mecopteroid stem are not contradicted.

PART II. ORIGIN OF THE BUTTERFLY STEM

The origin of the Rhopalocera, today sometimes called the Papilionoidea, long has been a matter of doubt. Various studies have led to widely different conclusions. This group seems to be directly related to the heteroneurous Lepidoptera, but if their primitive forms have arisen from within that section of the Lepidoptera, their ancestors have yet to be determined to everyone's satisfaction.

The butterflies have been thought to be related to early Geometroidea. They seem, to some, closer to the Butterfly-moths of the superfamily Castnioidea, a group of day-flying species possessing, like them, clubbed antennae and bedecked in gay colors. Their roots can be suggested as linked with the Cossioidea, which, like them are concealed feeders in the larval stages. Other possible origins have been proposed. It is not the purpose of this paper to discuss the full history of such studies. Rather, I consider a small section of the entire problem, based on wing venations and the tracheal systems, as seen in pupae on the day of change into that resting stage, and during the development of the pharate adult.

Much of our knowledge of the origin of the mecopteroid orders of the Insecta has been deduced, of necessity, from the study of fossil wings, usually detached from other body parts. Sound conclusions make it desirable that all structures be given consideration, but wing veins have always received major attention and it may be of some value to look closely at evidence relating to their development in living forms, and to pay particular attention to the tracheae during the first hours after the change to the pupal state, while the tissues are still translucent.

Some work was done on first day tracheal systems in several species of butterflies in Brisbane, Queensland, between 1942 and 1944 and notes were discussed with Dr. F. E. Zeuner, in London, in June of 1944, in light of his then newly published paper (Zeuner, 1943).

Tracheal systems of the developing wings of several typical members of superfamilies of Rhopalocera are shown in Figs. 9-17. On them the tracheae are labelled so that, in general, only discussion of particular points are necessary.

Wing Tracheae in Pupae

In the superfamily Hesperioidea tracheal patterns perhaps retain the greatest number of primitive characters. As represented by the Australian Regent Skipper, *Euschemon*

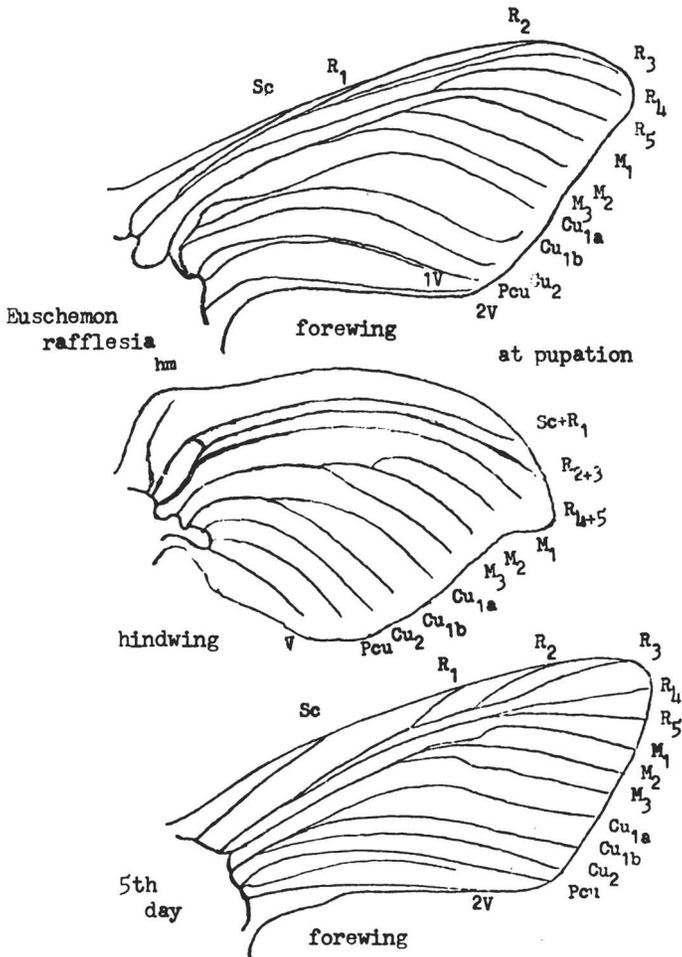
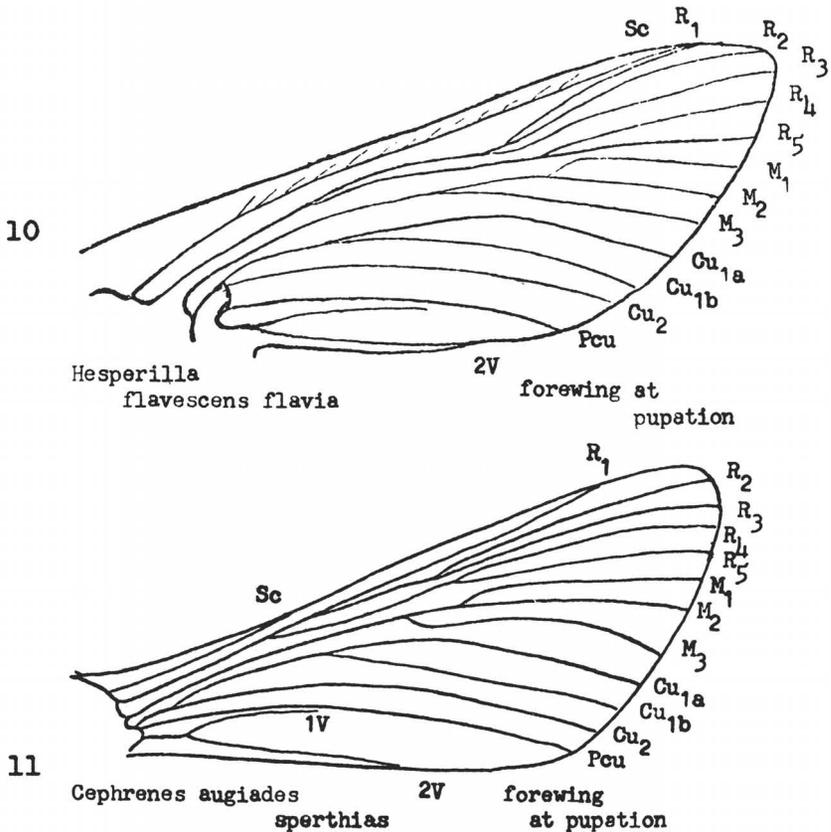


FIG. 9. *Euschemon rafflesia* (W. S. Macleay) 1826. **9a & b**, fore- and hindwing showing tracheal patterns, in life, of newly formed pupa. **9c**, forewing with pupal tracheation on fifth day of pupation.

r. rafflesia (W. S. Macleay) 1826 (Fig. 9a, b), the newly formed pupa, examined at the moment of pupal ecdysis displays a three-branched M series in both wings. In the forewing there are five R vein precursors present; R₂ and R₃ are combined for part of their lengths as a stem separate from that uniting R₄ and R₅, the junction between these two stems being near the base of the developing wing. In the vannal area Pcu and IV show close approximation towards the wing margin; 2V is present as a strong trachea.

As is characteristic of all heteroneurous Lepidoptera, in the hindwing, the number of R vein precursors is reduced, but there are some hitherto unexplained features in the radial system of *Euschemon*. Hindwing tracheae Sc and R₁ are conjoined almost from their base. This may be the indication of an early specialization in *Euschemon*. A more primitive condition with Sc and R₁ stems separate is seen in the Pierioidea. In



FIGS. 10-11. Upper, *Hesperilla flavescens flavia* Waterhouse, 1941, showing tracheation of forewing on first day of pupation. Lower, *Cephrenes augiades sperthias* (Felder), 1862, with forewing tracheation at pupation.

the newly formed hindwing of *Euschemon* R_2+R_3 and R_4+R_5 seem thus to be represented by separate tracheae. This is a revised interpretation since, according to Tillyard (1919), and to earlier writers on venation, Sc has been considered to be present as a separate trachea or vein, the others present being considered to be respectively R_1 and R_5 . The significance of this revision will be suggested in a later paragraph, after other wings have been discussed. In the hindwing only two post-cubital tracheae are evident, since either IV, or less likely Pcu has become obsolete, while 2V is present as a strong trachea.

In *Euschemon*, on the fifth day of pupation (Fig. 9c), the hindwing details are obscured, but those of the forewing are still clear. The reduction of IV of the forewing is now marked, and that of 2V also has begun. This is a condition in more evolved Hesperoids, as illustrated in the first day pupae of *Hesperilla flavescens flavia* Waterhouse, 1941 (Fig. 11), and *Cephrenes augiades sperthias* (Felder), 1862 (Fig. 12). There is a considerable difference in the relative lengths of the Sc trachea in these three species.

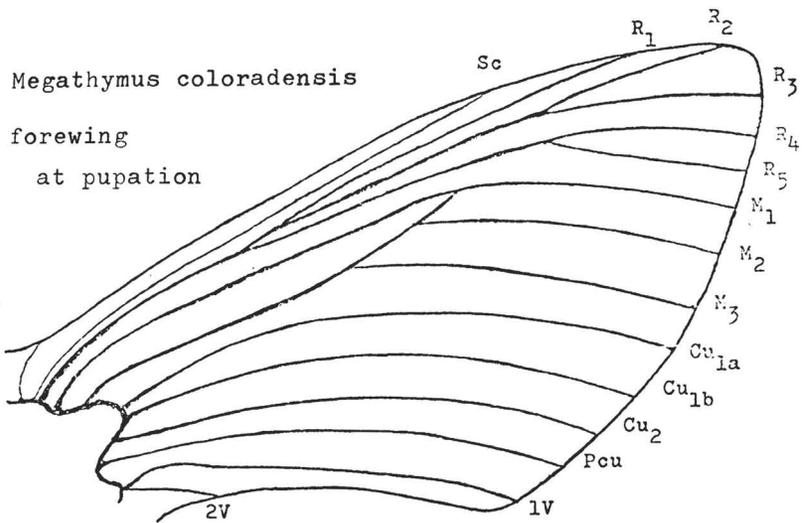


FIG. 12. *Megathymus coloradensis* Riley. Forewing tracheation, in life, on day of pupation.

Through the help of Mr. Ron S. Wielgus I examined first day pupae of *Megathymus coloradensis navajo* Skinner from Maricopa Co., Arizona. As shown in Fig. 12 there are resemblances to *Euschemon* in features of the forewing, as examined within the first four hours of pupal ecdysis. Trachea Cu_{1a} is separate from M from the base. However in one specimen it had already become approximated to M from the base to about one-third of its length, suggesting a change of direction as development proceeded. The full expression of the tracheae in the anal portion of the wing indicates a lesser degree of specialization than in any other butterfly family.

The Papilionoidea, as represented by newly formed pupae of the Orchard Butterfly, *Papilio aegaeus aegaeus* Donovan, 1805, from Mount Tamborine, Queensland (Fig. 13) show some primitive features in the tracheal system. The fork between R₂+R₃ and R₄+R₅ in the forewing is similar to that in *Euschemon* and occurs well down toward the base of the wing, while the second forking at which these vein precursors separate lies near the middle of the developing wing. This may be a very old feature. The forewing shows Cu₂ as a separate trunk, while Pcu is a strong trachea. Reduction of IV and 2V has occurred and IV does not reach wing margin.

In the hindwing of *Papilio aegaeus* hm trachea is lost, a definite absence as compared with the condition in the Hesperioidea where it is a strong trachea. Sc, R₁ and R₅ are united in a single basal stem and R₅ appears to be a single branch; signs are present of a fourth M; this disappears near the middle of the wing. All three cubital tracheae arise from a common stem and only two post-cubital tracheae are in evidence; these are considered to be respectively Pcu and IV. It is likely that in *Papilio aegaeus* adults, 2V is lost, as foreshadowed here in the pupal wing.

In the Common Australian Bean Blue, *Zizina otis labradus* (Godart), 1819, shown in Fig. 14 representing the Riodinoidea, the forewing of the first day pupa shows the same split, back between the stems (R₂+R₃) and (R₄+R₅), that is evident in the Papilionoidea and the Hesperioidea. The R₅ trachea is well developed in the midwing area, but loops down to touch M₁ before turning away again to run parallel to R₄. Near the margin it fades into minute branchlets. The apparent migration of M₁ to a position on the R stem in the adult wing thus is foreshadowed, and the position of the vein M₁

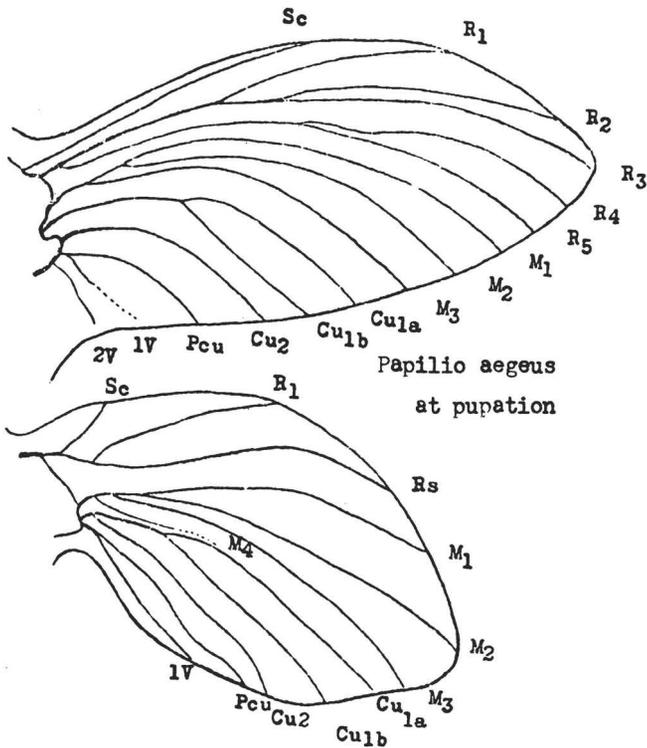


FIG. 13. *Papilio aegaeus* Donovan, 1805. Wing tracheation, in life, in newly formed pupa.

usually high up on the R_4+R_5 stem is explained by the day-old pupal condition. Another seeming specialization of the radial venation of the lycaenid adult, apparent in the early pupal tracheation, is the fusion of Sc and R_1 which is usual in the adult. An additional complication appears later in pupal life with the junction of the combined Sc+ R_1 usually shown as R_1 , and R_2 . In Australian species the independent condition of R_1 and R_2 is seen in *Candalides*, while progressive union may be traced through adults of *Nacaduba*, where R_1 and R_2 touch and then separate again, to *Theclinessthes* in which fusion is continued to the wing margin.

All the cubital and vannal tracheae are present in the early *Zizina* pupa, but Cu_2 sometimes does not reach the wing margin and shows signs of weakening, while 2V is hard to see and seemingly is on the way to disappearing. Thus it seems clear that Cu_2 is the vein that disappears in the adult wing, while Pcu remains as a strong vein and vannal veins are wanting. The pupal hindwing has not been studied in *Zizina*.

In the Pierioidea as represented by the Lemon Migrant, *Catopsilia pomona pomona* (Fabricius), 1775, the tracheation of the newly formed pupa, as shown in Fig. 15, shows some very primitive characters, along with some marked specializations. In the forewing the R tracheae are as in *Papilio*, as also Sc. Only two, instead of three M tracheae are present. As first demonstrated by Zeuner (1943), probably it is M_2 which has disappeared. However in *Dismorphia*, the most primitive of the Pierids, if it is one, M_2 is said to be present. In the advanced pupa of *Catopsilia* it may appear in the forewing,

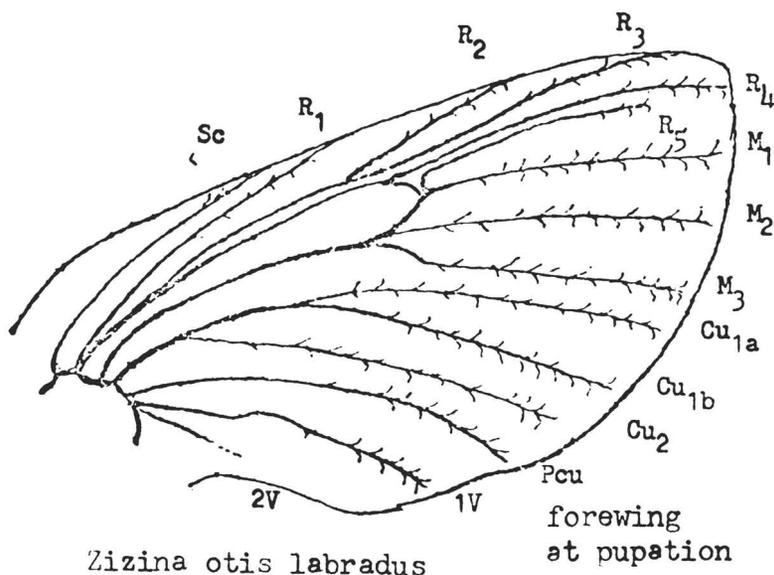


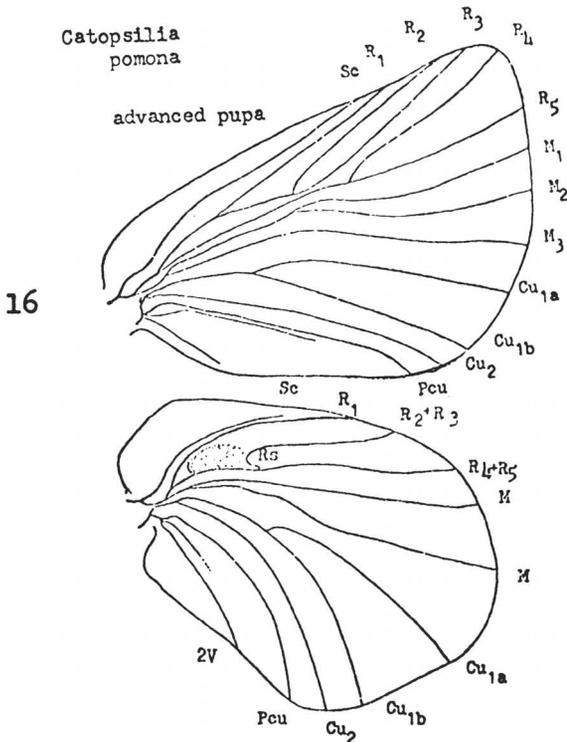
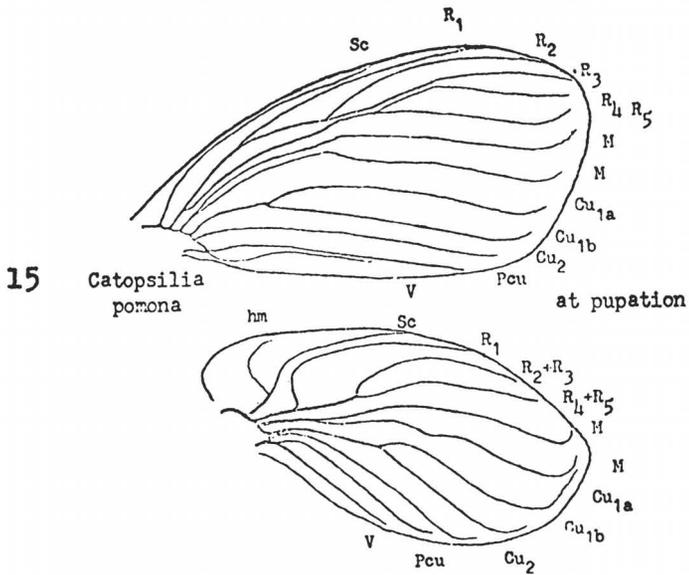
FIG. 14. *Zizina otis labradus* (Godart), 1819. Forewing tracheation on first day of pupation.

but not in the hindwing, and it fails to appear as a vein in the adult butterfly through a complex union with R.

In the hindwing of the newly formed *Catopsilia* pupa hm is a strong trachea which disappears later. R tracheae apparently show a primitive condition where R₁ is present and R₅ is a two-branched trachea. Both R₂ + R₃ and R₄ + R₅ are present, as in the early pupa of *Euschemon*. This condition persists into the late pupal stage. Cu₂ has its origin near the base of the wing as in the first day *Euschemon* pupa. Pcu is a strong trachea as in the forewing, and there is only a single vannal trachea; in the forewing it seems to be IV which is present while 2V is vestigial or absent; however the reverse may be the case in the hindwing. In the advanced pupa M₂ does appear in the forewing but not in the hindwing; in the latter a vestigial IV may be seen, but it does not reach the margin of the wing. Presence of these late tracheae help in determining the identification of the veins which have dropped out in the adult hindwing. The hm trachea of the first day pupa seems to disappear in a later stage.

In the Danaioidea, generally considered the most specialized of the superfamilies of the butterflies, as represented here by the Crow Butterfly, *Euploea core corinna* (W. S. Macleay), 1826, the fine branchlets of the first day tracheae are very well evident, as they are also in *Zizina*. As shown in Fig. 17 the R region is closely compressed along the costa; there is the same deep schism separating R₂ + R₃ from R₄ + R₅ as in all the other superfamilies so far considered. In the forewing also there is a midwing branching of M₃ which runs obliquely down to join Cu_{1a} before the middle, as if it were a vestige of an M₄ such as is found in archaic Lepidoptera. Cu₂ originates close to the base of the common Cu stem. Three post-cubital tracheae appear to be present, but IV appears to be vestigial.

In the hindwing of the first day *Euploea* pupa hm is present, R₅ is a simple trachea, Cu₂ is from the very base of the common stem and Pcu is a mere vestige, while both IV and 2V are strongly developed. Differences between the Pierioidea and the Dana-



FIGS. 15-16. *Catopsilia pomona* (Fabricius, 1775. Upper, wings showing tracheation on first day of pupation. Lower, the same showing tracheae at a late stage of pupal life.

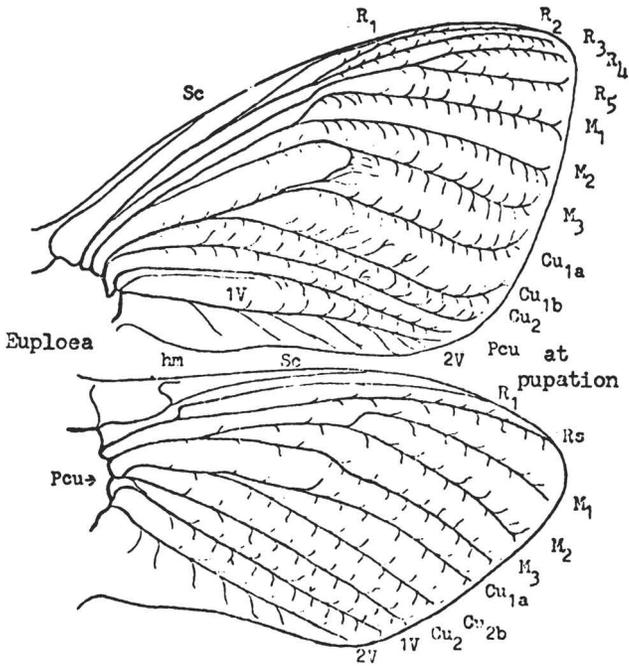


FIG. 17. *Euploea core corinna* (W. S. Macleay), 1826. Wings showing tracheae in life on first day of pupation.

ioidea in the vannal region of their developing wings suggest that in their common ancestor Pcu and both vannal veins were well developed. As is indicated in the discussion there may be another interpretation for the radial region of the hindwing as described in the above text and marked on Fig. 17.

An Archetype for the Butterflies

Bearing in mind the data derived from study of the tracheal systems and the rich information provided by Zeuner (1943) and his many predecessors I have taken what seem to me the most primitive characters displayed in each of the superfamilies and developed a possible archetype for the butterflies. It appears as a frenate lepidopteran with a venational pattern approximating that shown in Fig. 18.

No known lepidopteran possesses all the characters indicated in this reconstruction. If the concept bears resemblance to reality the butterflies must be considered a very archaic group with roots going back to the beginning of the development of the heteroneurous Lepidoptera, as distinct from the homoneurous ones.

Of living families of moths the concept seems suggestive of the Castnioidea, but may also bear comparison with the Cossioidea. It seems unlikely to be very directly linked with such advanced super-

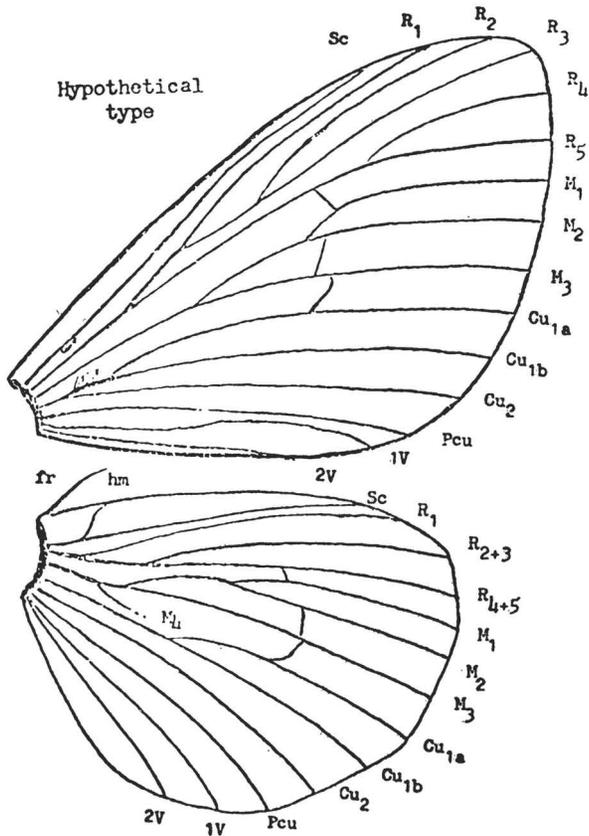


FIG. 18. Hypothetical archetype of the Rhopalocera or Butterflies.

families as the Geometroidea. Tillyard (1926: 455) sought a common ancestor near the Pyraloidea and the degraded Pterophoroidea. The presence of pilifers on the pupae of the butterflies, a character they share with the two above mentioned groups may suggest a link but the connections must be relatively remote. The most primitive of the Pyraloids seem to show some resemblances in the forewings but their hindwings are sufficiently different to suggest relationship only far down on the Lepidoptera stem.

The survival of a frenulum in the hesperioid *Euschemon* as well as its presence in the main line of the more primitive groups of the heteroneurous moths indicates a common frenate ancestor. This common ancestor must have possessed five main radial veins in its forewing. In the hindwing there was a reduction from a primary five to

a lesser number of radial veins. It has long been considered that all heteroneurous Lepidoptera possessed only two R veins in the hindwing, a clear dichotomy. However the attempt to explain the tracheal and venational patterns of *Catopsilia* and *Euschemon* has led to the conclusion that the ancestral butterfly may have retained three of the five radial veins in its hindwing instead of the two generally recognized as present in the heteroneurous moths. If this interpretation yields a true picture of the ancestor it would suggest the possibility of a fundamental separation somewhat greater than hitherto has been envisaged.

Accepting the idea of an ancestrally divided R_s , and combining it with the fact that the early pupal stages of the butterflies show a deeply divided (or split) condition in the forewing, separating the stem of R_2+R_3 from that of R_4+R_5 , we can conceive the condition as very archaic. Zeuner (1943: 300) had noticed this splitting back of the radials in this fashion as occurring in some heteroneurous families of the moths. At any rate this trait does not appear to be a character of the advanced families.

Perhaps the butterflies have from very early times moved along a different evolutionary path, one unsuspected by Comstock (1918:334). He may have come near the truth when he observed that in the Pieridae another trachea appeared to be attached to R but thought that trachea M in some unexplained manner had been transferred to R; he ascribed the condition to a supposed atrophy of the main stem of the media. His observations were made on the pupal hindwing of the Cabbage White, *Pieris rapae* (Linnaeus), 1758. Zeuner (1943) observed Comstock's error but did not follow up the implications of this fact. So far as the R_s of the hindwing is concerned the pierids are here presumed to have preserved a primitive condition, one common to the whole ancestral line of the butterflies. On the other hand they seem to have become specialized in the reduction of the media to a two-branched condition, a change that does not appear to have affected any other butterfly line. In *Euschemon* R_s can be seen as branched, as in the pierids, but there is a specialization in that R_1 joins with Sc just after the branching of R_s so that the three branched radial condition is less apparent.

In the tracheation of *Papilio* there is room for two different interpretations, in the hindwing, of the relationship between Sc and radials. The usual interpretation has been shown in Fig. 13, but it seems possible, in the light of the conditions prevailing in *Catopsilia* and *Euschemon* that Sc should be considered to be $Sc+R_1$, the trachea labelled as R_1 really is R_2+R_3 , and R_s should be regarded as R_4+R_5 . This interpretation seems to make the relationship clearer.

When we reexamine the hindwing of *Euploea* as shown in Fig. 17 it becomes easier to accept a similar change in the interpretation of the Sc and R situation since it is possible that the short trachea labelled as hm is really Sc while R_1 is separate from R_5 from the very base of the wing. In support of this interpretation, there is an otherwise unexplained small trachea at the base of the wing which perhaps is the real hm.

Thus it may seem that these limited studies of the early pupal tracheation, of *Euschemon* and *Catopsilia* in particular, may have revealed some vital clues, leading to a possible elucidation of the problem of the origin of the butterflies. Because Tillyard (1919) had to rely only on data provided by an advanced pupa (tenth day) he failed to see the earlier condition in *Euschemon*, which has been so informative. These data lead, in conjunction with data on the first day pupa of pierids to the conclusions set out here.

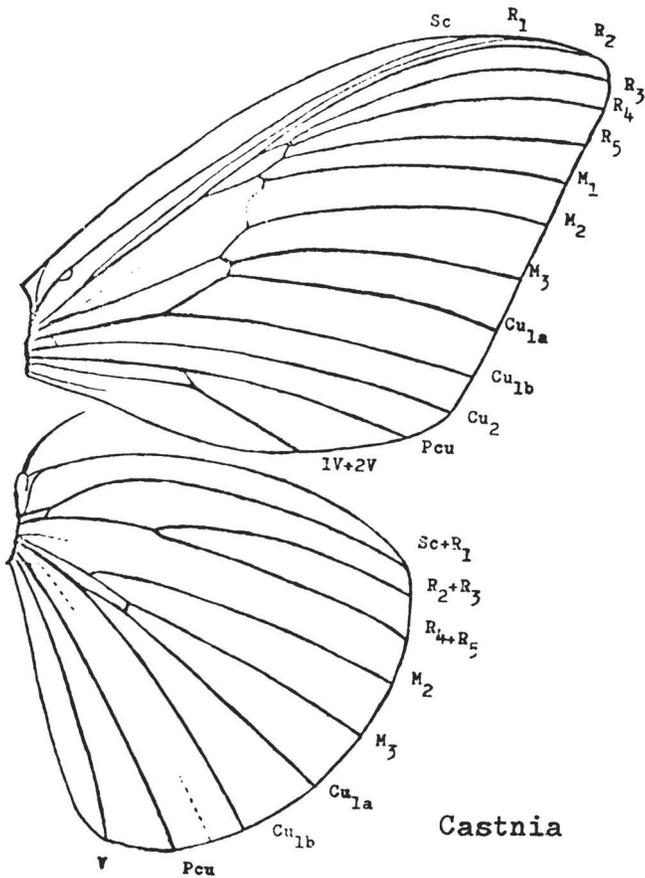
Fitting the hypothetical prototype (shown in Fig. 18) to present-day butterfly families necessitates taking note of certain lines of specialization. In the forewing these include the following trends:

- a) loss of the discoidal portions of the stem of the M veins;
- b) the obsolescence of the r-m crossvein by reduction so that M_1 has come to be directly connected to R_5 ;
- c) the reduction of Cu_2 so that it is represented by a basal loop with Pcu;
- d) the usual presence of only two, or even only one post-cubital vein, instead of three (usually it is 2V which is absent) although IV is often present (if only in the basal part of the wing, either looping up to join Pcu, or fading out in the distal part of the wing).

In the hindwing, specializations include the following:

- a) coalescence of Sc and R_1 to form a single vein;
- b) the union of R_4+R_5 with M_1 with loss of the r-m crossvein;
- c) the reduction, but only in the advanced pierids, of the M region by loss of M_2 ;
- d) the disappearance or modification of the r-m crossvein;
- e) the obsolescence of at least one post-cubital vein.

The above trends have progressed to different degrees in the superfamilies of the living butterflies. As Durden & Rose (1978) have shown by their discovery of Middle Eocene butterflies of species as far advanced as some living forms, it seems clear that many of the venational trends were determined already by the very beginning of the Tertiary period.



Castnia

FIG. 19. *Castnia licoides* Boisduval, 1875, from Bolivia, male venation.

The hypothetical archetype drawing bears sufficient resemblance to a member of the Butterfly-moth family Castniidae to suggest a rather closer relationship than had been previously considered. Several venational features support a view that they could have diverged directly from an early common stem.

Fig. 19 depicts the venation of a male Castniid, identified as *Castnia licoides* Boisduval, and taken near Cochabamba, Bolivia, in March 1975. The specimen was kindly given to me by Mr. Sharpe H. Osmondson of San Jose, California. In this *Castnia* the relatively complete venational pattern of the forewing, as theorized for the ancestral butterfly, is of interest. A principal difference is the retention of an ir

crossvein linking R_3 and R_4 . This appears to have disappeared from all the butterflies. Study of the Castniidae may enable us to obtain still earlier indications of the development of the butterflies. Study of the first day pupal tracheation of the Castniids is needed and such material is actively sought both in Australia and South America.

In the hindwing of *Castnia* there is a fusion of $Sc+R_1$, the same trend present in the true butterflies. R_2+R_3 and R_4+R_5 are also indicated as forming the radial veins. An apparent specialization is the obsolescence of M_1 . Tracheal studies may help in our understanding of this development.

ACKNOWLEDGMENTS

At the British Museum in August 1976 Dr. Paul E. S. Whalley showed me one of his then newly discovered Lower Cretaceous *Sabatinca*-like Lepidoptera from the Lebanon, and urged me to complete my study of the Triassic material I had in hand. Since this paper was completed he has published (Whalley, 1978) the Cretaceous lepidopteran as *Parasabatinca*, thus confirming the probabilities of a far earlier origin for the Lepidoptera stem.

Dr. Ian F. B. Common commented most helpfully on my preliminary notes on the fossil *Eocorona*. I have called the species *Iani* as a token of our appreciation of his important contributions both in the field and in our understanding of the primitive Lepidoptera.

Dr. Don R. Davis kindly read a draft of the paper for me and I appreciate his encouragement. The paper, in an intermediate state, was read at the meeting of the Lepidopterists' Society meeting in Boulder, Colorado, August 1977.

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