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Article XVIII.— THE FOSSIL AND RECENT BOMBYLIIDÆ COMPARED.

By T. D. A. Cockerell.

From the Miocene shales at Florissant, Colorado, we have obtained many fossil Bombyliidæ, all apparently representing extinct genera. The work has now reached a stage which permits a general review, with a discussion of the related living genera. The questions involved are not merely those of the taxonomy of the Bombyliidæ, but include matters of broader scope, concerning the nature of the evolution of new genera among insects. In my former works I was somewhat hindered by the lack of either figures or personal knowledge of several of the most interesting genera of living Bombyliidæ, and while descriptions were sufficient to show that they were not identical with the fossils, more precise information was greatly desired. When recently visiting the U. S. National Museum, I took advantage of the opportunity to examine and sketch parts of the venation of a number of the rarer genera. The diagrammatic sketches I made are published herewith, along with similar sketches of the fossil forms.

At the very outset, it is evident that the relationships between the groups of Bombyliidæ are complex, and no linear arrangement will express them. I will therefore follow, with modifications, the arrangement of Williston's key, which at least has the advantage of giving us a classification which is easy to use. The work is based almost entirely on the venation, as only the wings are adequately preserved in all the fossils. In place of the more usual type of key, I give one in which the contrasted categories bear the same number, with the difference of a letter added, as 1*a*, 1*b*, 1*c*.

1*a*. Præfurca long.....Anthracinæ.

Cyrtosia, which is a Bombyliine, has a remarkably long præfurca, and might be sought here; it is then easily known by the open discal cell.

Mythicomyia, on the character of the præfurca, will be sought here, but it is easily distinguished by the single submarginal cell. It appears to be related to *Glabellula*.

I give a figure of *Aldrichia ehrmanni* Coquillett, taken from the type. Williston's figure seems not quite accurate as to the end of the second vein.

I have never found any trace of an Anthracine in the Florissant shales; it seems probable that the subfamily was absent from Colorado in Miocene times, or at least during the earlier part of that long period. Anthracines have been reported from the Oligocene and Miocene of Europe, but little is known about them. Probably the group originated in the Old World, and on reaching America competed successfully with the endemic groups with

the result that many genera became extinct, and others are represented by rare and isolated species.

1*b*. Præfurca short. All the other groups.

2*a*. Three posterior cells.

3*a*. Discal cell open (confluent with second posterior). *Apolysis* Lw. (Spain, E. Europe, Asiatic Russia.)

3*b*. Discal cell closed.

4*a*. Two submarginal cells.

5*a*. First posterior cell closed; anal closed. *Pachysystropus* Ckll. (Florissant Miocene, two species).

5*b*. First posterior cell open.

6*a*. Anterior cross-vein well before middle of discal cell.

Geronites (n. gen.) **stigmalis** n. sp. (Fig. 9, discal cell.)

Length about 5 mm.; wing 5½; thorax not hairy; abdomen about as in *Geron*, very thinly hairy; legs with extremely fine short pubescence. As preserved, the insect is ferruginous; it was perhaps yellow or pale reddish in life. There is a stout proboscis, directed forwards, longer than head. Wings clear, with a dark region between the apical parts of the auxiliary and first veins, as in the living *Geron*.

Venation much as in *Geron*, but with the following peculiarities: second submarginal cell long; anterior cross-vein far before middle of discal cell; outer side of discal cell with a strong double curve (this is more or less evident in some species of *Geron*); second basal cell on discal twice as long as on third posterior. The end of the anal cell cannot be seen, but it is so wide in the middle that it is almost certainly open; in *Geron* it is closed.

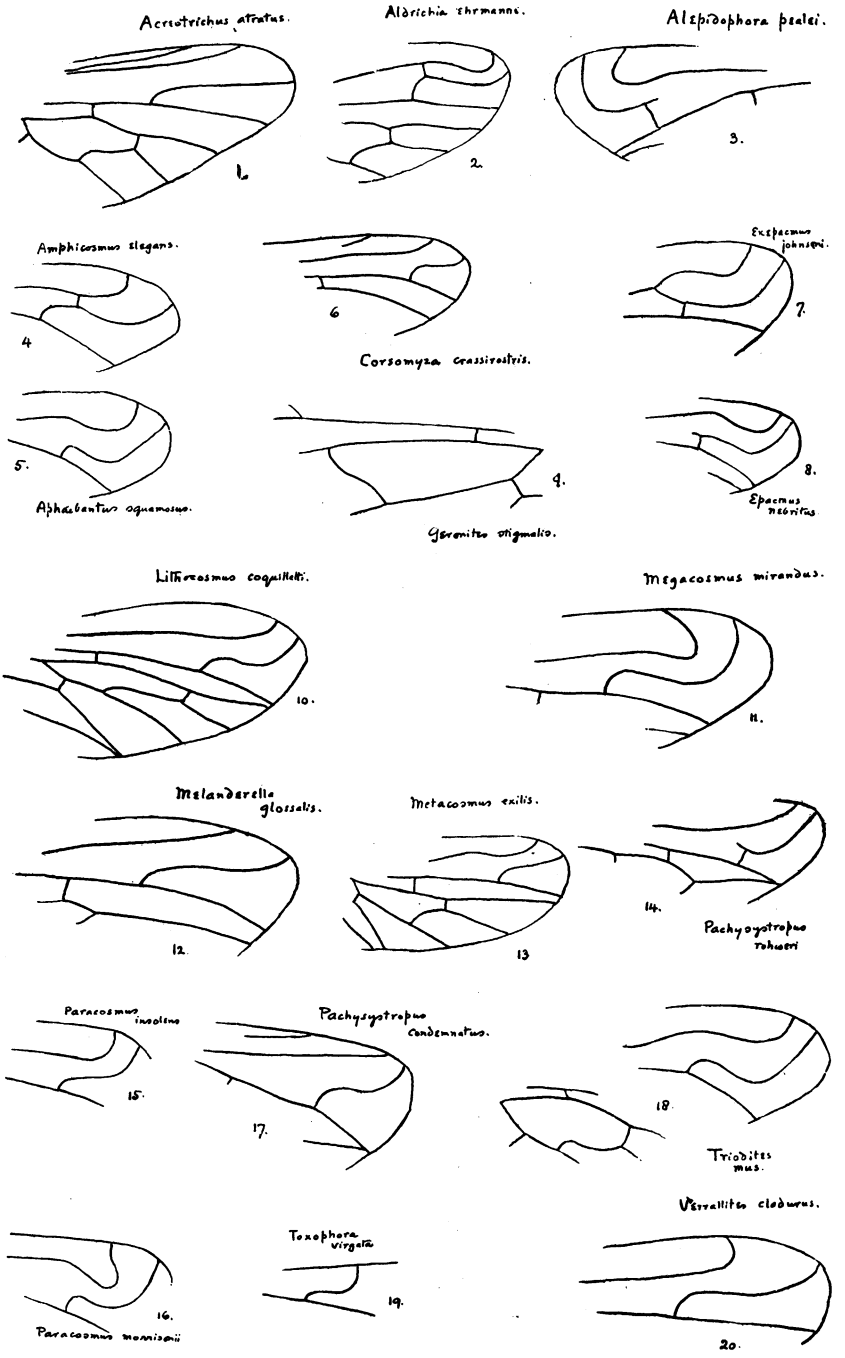
The following measurements are in microns: Second submarginal cell on first posterior 2048; first submarginal on first posterior, 1120; first submarginal on first basal, about 800; origin of præfurca basad of level of base of discal cell, about 560; length of anterior cross-vein, 144; first basal cell on discal, 560; first posterior on discal, 1170; second basal on discal, 320; second basal on third posterior, 160; width of anal at level of end of second basal, 480; end of first vein to end of second, 800.

Miocene shales of Florissant, station 14 (University of Colorado Expedition).

In Williston's table this runs straight to *Geron*, and I believe it is really an ancestral form of that genus, or related thereto.

6*b*. Anterior cross-vein at or a little beyond middle of discal cell; anal closed. *Geron* Meig., a genus which I have taken living at Florissant. It also occurs in the Old World, but there is only one Palæarctic species, whereas the Nearctic ones are numerous. The Nearctic species known to me have a more *Systropus*-like venation than the Old World *G. gibbosus*.

6*c*. Anterior cross-vein considerably beyond the middle of discal cell. Here fall the peculiar living Systropinæ, *Systropus* Wied and *Dolichomyia* Wied. They represent apparently a waning type, which has managed to remain widespread and relatively abundant in the genus *Systropus*, which so closely resembles certain Hymenoptera. The genus *Melanderella* Ckll. (*M. glossalis*


Acrotrichus atratus.
1.
Aldrichia thrmanns.
2.
Alcpidophora pealei.
3.
Amphicosmus elegans.
4
6
Corsomyza crassirostris.
Exopacmus johnsoni.
7.
5.
Aphaebantus squamosus.
9.
Geromitus stigmatis.
8.
Epacmus neonitus
Lithocosmus coquilletti.
10.
Megacosmus mirandus.
11.
Melanderella glossalis.
12.
Metacosmus exilis.
13
14.
Pachysyotropus rohweri
Paracosmus insolens
15.
Pachysyotropus condemnatus.
17.
18.
Triodites mus.
Verrallites cladurus.
Toxophora virgata
16.
Paracosmus monismii
19.
20.

Ckll.), from the Florissant shales, falls here, and is I think a relatively primitive ally of the Systropines, without the exaggerated characters seen in the living genera. It has a complete anal, only just closed on wing-margin. In the wide open first posterior cell, and the second basal much broader on the third posterior than on the discal, it resembles *Dolichomyia* rather than *Systropus;* but the base of the third posterior is straight.

A new specimen of *Melanderella glossalis*, found by Mr. S. A. Rohwer at station 14, Florissant, gives the following measurements in microns: First submarginal cell on first basal, 960; first submarginal on first posterior, 1009; second submarginal on first posterior, 1089; first basal on discal, 816; first posterior on discal, 528; discal on third posterior, 800; second basal on third posterior 224. The anterior cross-vein is a *little* oblique. The strong double curve in the outer side of discal cell is exactly as in *Systropus*.

4*b*. Three submarginal cells. *Toxophora* Meig.; type of subfamily Toxophorinæ. (Europe, Asia, Africa, America.)

2*b*. Four posterior cells.

7*a*. Discal cell confluent with third posterior; only one submarginal.

8*a*. Anterior cross-vein at extreme base of discal cell. *Empididеicus* Beck. (Algeria).

8*b*. Anterior cross-vein far beyond base of discal cell. *Cyrtosia* Perris. (Palæarctic).

Corsomyza Loew, from Baltic Amber, has an open discal cell according to Meunier's figure, kindly copied for me by Mr. S. A. Rohwer. The condition looks abnormal, however, the third posterior having a broad, obliquely truncate base. There are two submarginals, and the fly is certainly not allied to either of the modern genera just cited.

7*b*. Discal cell closed.

9*a*. Only one submarginal cell.

10*a*. Second basal confluent with discal. *Glabellula* Bezzi. (N. Europe and Siberia.) Type of new subfamily Glabellulinæ.[1] *Mythicomyia*, a similar humpbacked genus, appears to be related, but is not so specialized or modified.

10*b*. Discal cell normal..... *Platypygus* Lw. (Palæarctic).

9*b*. Two submarginal cells.

11*a*. First posterior cell closed. (*Parabombylius* and *Amictus* have this cell nearly closed.)

12*a*. Anterior cross-vein far beyond middle of discal cell. *Anisotamia* Macq. A Lomatine genus, perhaps only a subgenus of *Oncodocera*. *A. ruficornis* occurs in Egypt; other species are found in Mexico and Guatemala.

12*b*. Anterior cross-vein before middle of discal cell. Bombyliine genera such as *Bombylius* L. and *Systœchus* Lw.; I have found no trace of this now dominant type in the Florissant shales.

11*b*. First posterior cell open.

13*a*. Anal cell closed. (In *Lithocosmus* so nearly closed that the genus may be sought here.)

14*a*. Second vein at end strongly recurved, its inner angle with costa obtuse; anterior cross vein very oblique. *Oncodocera* Macq. (Lomatiine flies of the Neotropical region and southern part of the Nearctic; some very large.)

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[1] Becker (Genera Bombyliidarum, 1913) places *Glabellula, Platypygus, Cyrtosia* and *Empididеicus* in a subfamily Cyrtosiinæ.

14*b*. Second vein not thus recurved, but more turned upward at end in *Lithocosmus* than in the living genera.

15*a*. Upper branch of third vein strongly curved and bent upward; anterior cross-vein a little before middle of discal cell.

Lithocosmus Ckll. (Miocene of Florissant).

15*b*. Upper branch of third vein not thus curved; anterior cross-vein a little beyond middle of discal cell. *Phthiria* Meig. and *Acreotrichus* Macq., genera living in North America. I figure *Acreotrichus atratus* Coq., Sierra Madre; from the type.

Lithocosmus appears to be more specialized than *Phthiria*, and cannot well be ancestral to it.

13*b*. Anal cell open. Very numerous genera, belonging to Bombyliinæ, Lomatiinæ and Toxophorinæ, run to this place in the key; I do not attempt to deal with them all. Resemblances in venation seem here to be due at least in part to convergence.

16*a*. Upper basal corner of second submarginal cell sharply rectangular, with an accessory nervure pointing basad.

17*a*. Second vein recurved at end, its inner angle with costa extremely obtuse.

Alepidophora Ckll.; *A. pealei* Ckll. (Florissant Miocene).

17*b*. Second vein reaching costa at about a right angle. *Epacmus* O. S.; *E. nebritus* Coq. (California) is figured from type. Curiously the fossil genus appears to have a more specialized second vein than the recent one.

16*b*. Upper basal corner of second submarginal cell not rectangular.

18*a*. Inner angle formed by second vein with costa acute.

19*a*. Anal cell nearly closed; second posterior with a broad base.

20*a*. Anterior cross-vein conspicuously oblique, near end of discal cell. *Corsomyza* Lw. (Baltic Amber), if the discal cell in this genus is really closed.

20*b*. Anterior cross-vein a little before middle of discal cell.

Lithocosmus Ckll. (Miocene of Florissant).

19*b*. Anal cell evidently open; in *Desmatomyia* strongly narrowed apically, but the second posterior cell is narrowed almost to a point at base.

21*a*. First posterior cell greatly narrowed or almost closed at end; anterior cross-vein far beyond middle of discal cell, as in *Corsomyza*. *Amictus* Wied (a Toxophorine genus, well developed in Northern Africa, Southern Europe and Turkestan).

21*b*. First posterior cell widely or evidently open, though it may be much narrower at apex than at base, as in *Metacosmus*. Anterior cross-vein sometimes beyond middle, but not near to end of discal cell.

22*a*. Second posterior cell broader than long. *Psiatholasius* Beck. (a Bombyliine genus from Tunis).

22*b*. Second posterior cell longer than broad.

23*a*. Second posterior cell narrowed almost to a point basally.

Desmatomyia Willist. (*D. anomala* Willist., Colorado).

23*b*. Second posterior cell broad at base.

24*a*. Second vein straight, as in *Toxophora*. *Eclimus* Lw. (a Toxophorine genus, well developed in the Nearctic region, and sparingly in the countries around the Mediterranean).

24*b*. Second vein strongly curved or sinuous.

25*a*. Second vein with a single curve; vein separating discal from third posterior cell

straight. *Dischistus* Lw. (a Bombyliine genus, well developed in the Palæarctic Region).

25*b*. Second vein with a double curve; vein separating discal from third posterior cell strongly curved or arched.....*Metacosmus* Coq. (California).

18*b*. Inner angle formed by second vein with costa a right or obtuse angle.

26*a*. Anal cell extremely widely open, a little wider than the third posterior. *Verrallites* Ckll. (Miocene of Florissant; see Canadian Entomologist, July, 1913, p. 230).

26*b*. Anal cell not remarkable, but in *Lepidophora* only narrowly open.

27*a*. End of marginal cell level with beginning of second submarginal. *Legnotomyia* Bezzi, (a Bombyliine genus from Syria).

27*b*. End of marginal cell much beyond beginning of second submarginal.

28*a*. Anterior cross-vein at or before middle of discal cell.

29*a*. Discal cell very long and narrow. *Lepidophora* Westwood. (Neotropical and southern part of Nearctic Region.)

In *L. vetusta*, as figured by Williston, there is a band of pigment simulating the vein which goes from the second to the third vein in genera having three submarginal cells. It appears that the vein has disappeared, while the pigment has remained. *Lepidophora* certainly has two submarginals by the loss of a vein which is present in such other Toxophorines as *Cyllenia*, *Tomomyza* and *Toxophora*.

29*b*. Discal cell not long and narrow. *Aphœbantus* Lw., including *Triodites* O. S., (a Lomatiine genus, with one species in Algeria, and very many in California and adjacent regions).

28*b*. Anterior cross-vein much beyond middle of discal cell.

30*a*. Anterior cross-vein very oblique. *Lomatia* Meig. (type of Lomatiinæ; a genus well developed in the Palæarctic Region).

30*b*. Anterior cross-vein not very oblique. *Megacosmus* Ckll. (two species in Miocene of Florissant).

This fossil genus is very much like the living *Paracosmus* O. S., from California and Sonora. In the fossil genus the second vein is more recurved at end, and therefore more specialized, than in the recent one. The species of both genera differ among themselves in the details of the venation, and it is possible that future study will indicate that they are only subgenerically distinct. The species of *Megacosmus* are quite large flies, as the name indicates, while those of *Paracosmus* are small.

9*c*. Three submarginal cells.

31*a*. First posterior cell closed. *Pantarbes* O. S. (California, Arizona and Sonora) and *Triplasius* Lw. (California, Tunis, S. Africa).

31*b*. First posterior cell open.

32*a*. Base of upper apical submarginal cell apicad of base of lower apical s. m. cell; inner angle formed by second vein with costa an obtuse angle.
Amphicosmus Coq. (California and Mexico).

32*b*. Base of upper apical submarginal cell level with base of lower apical s. m. cell.

33*a*. Anterior cross-vein before middle of discal cell. *Ploas* Latr., (a Bombyliine genus well developed in the Palæarctic Region and in California).

33*b*. Anterior cross-vein beyond middle of discal cell. *Lordotus* Lw. (Western U. S. and Mexico. I have taken it in New Mexico; *L. junceus* Coq. (det. Coq.) at flowers of *Pectis papposa*, Mesilla Park, Sept. 17; *L. diversus* Coq. by Tularosa Creek).

32*c*. Base of upper apical submarginal cell far basad of lower apical s. m. cell, base of the latter sharply truncate.

34*a*. Inner angle of second vein with costa a right angle or greater; anterior cross-vein far beyond middle of discal cell. *Cyllenia* Latr. (a Toxophorine genus of the Palæarctic Region).

34*b*. Inner angle of second vein with costa an acute angle.
Tomomyza Wied. (a Palæarctic Toxophorine genus) and *Exepacmus* Coq. (California).

Conclusions.

The following conclusions are not stated at all dogmatically, but represent the impressions gained from this study.

(1.) The Bombyliidæ are a rather ancient group, showing very little forward evolution since the Miocene, but rather miscellaneous shuffling of characters; while many genera have become extinct, and others, as shown by the discontinuous distribution, appear to be or to have been on the wane.

(2.) There is much duplication of venational characters in different groups, but rarely upon *exactly* the same lines. This phenomenon is better called *duplication* than *convergence*.

(3.) In certain venational characters, the Miocene fossils are not rarely more specialized than their nearest living allies.

(4.) The Anthracinæ, and probably also the group of genera clustering around *Bombylius*, seem to have arisen in the Old World; they probably reached America toward the end of the Miocene, and thereupon became dominant, the Anthracinæ producing many species, while the earlier Bombyliid fauna of North America became very much reduced, and is now represented by mere fragments. This parallels the history of the fishes of the family Cyprinidæ, in relation to the Catostomidæ &c, though the parallel is not exact.

This study may also throw some light on the mechanics of wing-venation, but this is a large and difficult subject, and its consideration is deferred.

List of Figures († = fossil).

1. *Acreotrichus atratus*. From types. Sierra Madre.
2. *Aldrichia ehrmanni*. From type.
†3. *Alepidophora pealei*.
4. *Amphicosmus elegans*. From type.
5. *Aphœbantus squamosus*. From type. Almost the same as *Epacmus*, in regard to the parts shown.
†6. *Corsomyza crassirostris*.

7. *Exepacmus johnsoni.* From type.
8. *Epacmus nebritus.* From type.
†9. *Geronites stigmalis.* Discal cell.
†10. *Lithocosmus coquilletti.*
†11. *Megacosmus mirandus.*
†12. *Melanderella glossalis.*
13. *Metacosmus exilis.* From type.
†14. *Pachysystropus rohweri.*
15. *Paracosmus insolens.* From type. A very small species. Venation in general agrees with that of *Metacosmus exilis*, but differences in apical field as shown in figures.
16. *Paracosmus morrisoni.* San Diego, California (Coquillett).
†17. *Pachysystropus condemnatus.*
18. *Triodites mus.* Discal cell and apex of wing.
19. *Toxophora virgata.* End of discal cell. This is not like Williston's figure; but *T. pellucida* agrees with Williston's figure. A *T. pellucida* from Arizona has the barest rudiment of the stump of vein which if complete would separate second and third posterior cells.
†20. *Verrallites cladurus.*