

THE FOSSIL ODONATE PHENACOLESTES, WITH A DISCUSSION OF THE
VENATION OF THE LEGION PODAGRION SELYS.

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PHENACOLESTES MATERIAL STUDIED.

In 1908, Professor T. D. A. Cockerell described (1908a) two species of fossil Odonata from Station 14, Florissant, Colo., as *Phenacolestes mirandus* and *Ph.(?) parallelus*. A little later (1908b) he added a note based on an additional fragment which he referred to the latter species, and in another place (1908c) he gave a figure showing the body as well as the wings, the previous accounts having referred to the wings only. In connection with the original description he quotes from a letter from Professor Needham who almost implies that *Ph. mirandus* is to be placed in de Selys' legion Podagrion of the Agrioninæ (1908a, p. 63).

In the latter part of 1910, Professor Cockerell wrote to me that he had found more wings of *Phenacolestes*, and requested me to study them, in view of some differences of opinion as to its relationship to modern dragonflies.

When I accepted this offer, Professor Cockerell sent me four

specimens of these fossil wings which, for reference here, I have numbered as follows:

No. 1. Labelled "*Phenacolestes mirandus* Ckll. Florissant," in Professor Cockerell's handwriting; 27 mm. long from base to apex.

No. 2. Labelled "*Phenacolestes mirandus* Ckll. Florissant Sta. 12 B (G. N. Rohwer)," in the same hand. Apparently a hind wing. Distorted, length from base to apex as it lies on the stone 26 mm.

Nos. 3 and 4. Unlabelled. [These are the two impressions of the same wing, and were collected by Geo. N. Rohwer. T. D. A. Cockerell.] Apparently a front wing. Length of No. 3 from base to apex 28 mm.; of No. 4 (apex lost) from base to distal end of stigma 25 mm.

They are figured from enlarged photographs on Plate XIV as figures 1-4.

The beautiful preservation of these wings has rendered possible the drawing up of almost as full a description of the venation as for any living species.

Professor Cockerell has very kindly presented specimen No. 3 to the Academy of Natural Sciences of Philadelphia; the other three specimens will be returned to him.

Thanks to the kindness of Dr. F. A. Bather, through the good offices of Mr. C. J. Gahan, I have also studied two fossils of this insect in the British Museum of Natural History, when in London in August, 1912. One of these, catalogued as "No. I 8423," is the paratype of Professor Cockerell's original description of *Phenacolestes mirandus*. The other, "No. I 15,049," is labelled in Professor Cockerell's handwriting "*Phenacolestes mirandus* Ckll. Florissant Sta. 13 B (S. A. Rohwer)." No. I 8423 measures 20.5 mm. in length from the wing-base to the proximal end of the stigma; the distal part of the stigma and the tip of the wing are lacking; the nodus is 9 mm. from the base. No. I 15,049 has lost the stigma and apex of the wing from the distal end of M_2 forward (cephalad and distad) and the extreme hind margin between the apices of M_2 and Cu_1 ; its length along the costa as preserved is 23 mm., the nodus is 10 mm. from base.

Use has also been made of an excellent photograph, for which I thank Professor Cockerell and Dr. Max M. Ellis, of the University of Colorado, of an almost perfect wing from the same locality as that of the second specimen quoted in the preceding paragraph. This photograph is reproduced as figure 5 on Plate XIV accompanying this paper; it will be designated as No. 5 in these pages and apparently represents a front wing.

The following account is based, therefore, on six wings in seven impressions.

Throughout this paper the Comstock-Needham nomenclature for the wing-veins has been employed. In the previous literature on the living members of the legion Podagrion the Selysian terms have been used. The equivalents of the two systems are therefore appended here.

De Selys: Costa	=	C.-N.: Costa, C.
Subcosta	=	Subcosta, Sc.
Median vein	=	R ₁ .
Principal sector	=	M ₁ .
Ultra-nodal sector	=	M _{1a} .
Nodal sector	=	M ₂ .
Subnodal sector	=	R _s (+ the bridge, if it be present). ¹
Median sector	=	M ₃ .
Short sector	=	M ₄ .
First (or superior) sector of the triangle	=	Cu ₁ .
Second (or inferior) sector of the triangle	=	Cu ₂ and Anal (A).
Basal postcostal nervule	=	Cubito-anal cross-vein or c-a.

THE PRINCIPAL CHARACTERS OF PHENACOLESTES (Plate XIV, figs. 1-5).

1. Nodus at one-third of the wing-length.
2. More than two antenodals. (Four in at least two (Nos. 2, 3, 4) of these specimens, five in No. 5 and in the two cited from Brit. Mus.)
3. Postnodals 17-19.
4. Stigma having its proximal edge oblique.
5. Cells of the wing generally, posterior to M₁, not greatly elongated at right angles to long axis of wing.
6. The veins generally, posterior to M₁, have but a slight caudal curvature shortly before they approach the hind margin of the wing.
7. Between M₁ and M_{1a} is only one row of cells throughout to wing-margin. (In No. 5, increased to two rows at five cells' distance from the margin.)
8. Between M_{1a} and M₂ is one row of cells, increasing to two and then three rows, and so continuing to wing-margin.

¹ Throughout this paper "Rs" has been used as the equivalent of de Selys' "subnodal sector."

9. M_2 separates from M_1 at five-thirteenths ($= .38$) of the distance from nodus to stigma. (In No. 5, however, the distance is only .28, in No. I 8423 B. M. it is .26.)
10. Between M_2 and R_s is one row of cells increasing to two and then three rows, and so continuing to the margin.
11. R_s separates from M_{1+2} at the subnodus. (Nos. 3, 4, 5, and B. M. I 15,049 show this clearly; B. M. I 8423 apparently agrees with them; No. 1 has the point of separation slightly proximal to the subnodus, while in No. 2 this part is indistinguishable.)
12. Between R_s and M_3 is one row of cells, increasing to two and then to three rows of cells.
13. Arculus slightly proximal to the second antenodal.²
14. M_3 separating from M_{1+2} at six-tenths' to three-fourths' way from arculus to subnodus.
15. Between M_3 and M_4 are (a) at least two cross-veins proximal to the level of the subnodus,³ and (b) at the wing-margin are 4-5 rows of cells.
16. Quadrilateral with (a) its proximal and distal sides strongly diverging caudad and (b) its distal side more than one-and one-half times as long as its proximal side.
17. Between M_4 and Cu_1 are (a) seven antenodal cells (*sensu Selysii*) and (b) at the wing-margin four to five rows of cells.
18. Cubito-anal cross-veins one, which is situated between the levels of the first and second antenodals.
19. Between Cu_1 and Cu_2 at the wing-margin are about two rows of cells (three rows in B. M. No. I 15,049).
20. Area posterior to Cu_2 without distinct branches, but with three to four rows of cells.
21. Anal vein separating from the hind wing-margin (a) proximad to the level of the arculus and (b) proximad to the level of the cubito-anal cross-vein.
22. Anal cross-veins, proximal to the level of the distal end of the quadrilateral, *one*.

Compared with Professor Cockerell's original description of *Phenacolestes mirandus* (1908a, p. 61), the present material shows the following differences:

Antenodal cross-veins⁴ four in *some* specimens instead of five.

Basal space (*i.e.*, cell M_{1-4}) 4 mm. long, instead of nearly 5 mm.

² For B. M. No. I 8423 I have even noted, "Arculus very slightly more distal than midway between the two normal antenodals."

³ The second, or distal, of these is actually at the subnodus in the two British Museum specimens.

⁴ Prof. Cockerell speaks of antenodal and postnodal *sectors* meaning these cross-veins. This word is not in accordance with the usage of other authors on the Odonata. R_3 in the same description should be R_s .

Quadrangle with its upper side distinctly shorter than the lower side.

M₃ separating from M₁₊₂ at 3.5–4 mm. from the arculus, 2.5–1 mm. from level of nodus.

Postnodal cross-veins⁴ 17–19, instead of 21.

Stigma bounding $3\frac{1}{2}$ or $4\frac{1}{2}$ cells above, preservation imperfect in most of these specimens.

M₁ and M₂ separating at as much as 10.75 mm. from arculus, instead of 9.67 mm.

Beyond the quadrangle, *i.e.*, between M₄ and Cu₁, are seventeen single cells (Nos. 3 and 4), or sixteen (No. 5), then two rows increasing; hence very different from Prof. Cockerell's statement, p. 62, which does not seem to agree with his figure (13 of Plate V).

There is but one row of cells between M₁ and M_{1a} throughout, thus agreeing with the description of *Ph.(?) parallelus* (*l.c.*, p. 62) in distinction from *Ph. mirandus*.

Two specimens, Nos. 1 and 3, are sufficiently preserved to enable a count of the cells between M₂ and R_s to be made. From the margin proximad these are, in No. 1, 7 marginal cells, then 3 rows for 3–4 cells, then 2 rows for 6 cells, then 1 row (which is consequently met at 10–11 cells in from the margin), this single row comprising about 15 cells to the origin of R_s, three of these 15 being basad of the origin of M₂. Corresponding figures for specimen No. 3 are 5 (?) marginal cells, then 3 rows for 4 cells, then 2 rows for 3 cells, then 1 row (which is consequently met at 8 cells in from the margin), this single row comprising about 20 cells to the origin of R_s, $5\frac{1}{2}$ of these 20 being basad of the origin of M₂. In B. M. No. I 8423, this single row consists apparently of 15 cells, 4 of which are basad of the origin of M₂. In B. M. No. I 15,049, this single row consists of 15 or 16 cells, 3 and the greater part of the fourth of which are basad of the origin of M₂; No. 5 appears to be very similar. None of these arrangements is identical with that described for *Ph. mirandus*, where, however, the single row of cells is met at 11 cells in from the margin.

Prof. Cockerell gives two formulæ for *Ph. mirandus* and *Ph.(?) parallelus*, respectively (*l.c.*, p. 62), these formulæ being obtained by taking "a section of the wing down from the basal part of the stigma to Cu₂, and count[ing] the numbers of rows of cells successively met between the longitudinal veins commencing with that between R₁ and M₁." The numbers of cells so obtained will depend on the exact position of the line of section, but Prof. Cockerell does not specify this. Choosing, as the two points fixing this line, the

inferior proximal angle of the stigma and the point where Cu₂ meets the hind wing-margin, the following formulæ for the present material were obtained:

No. 1: 1, 1, 2, 1, 2, 2, 3, 2.

No. 2: (too imperfect).

No. 3: 1, 1, 2, 1, 2, 2, 3, 2.

No. 4: 1, 1, 2, 1, 2, 2, 3, 2.

No. 5: 1, 1, 2, 2, 2, 2, 3, 2.

No. I 15,049: 1, 1, 2, 2, 2, 2, 3, 2.

We have here two different formulæ, neither of which agree with either of Prof. Cockerell's formulæ.

Guided by the amount of variation in venational details of one and the same living species of Agrioninæ, I am of the opinion that the differences shown by the present material, *inter se* and from Prof. Cockerell's data, do not justify the specific separation of the specimens before me from *Ph. mirandus*.

All of the present material show more or less distinctly the dark band across the wing, described by Prof. Cockerell; it is best illustrated in our figure 5.

Phenacolestes agrees with the venational characters of the legion Podagrion, as stated by de Selys in 1886,⁵ with the one exception that the wings are *not* "pétiolées beaucoup plus loin que la nervule basale postcostale." I think that there can be no doubt that its nearest living allies are to be found in this group. I have therefore made comparisons with a number of genera of this legion, especially American, with the results set forth below. As I have had only five of the fossil wings and photographs of one other before me and am unable to determine whether all of them are of the fore or hind pairs, I have not thought it necessary to employ any great number of specimens of the living species for these comparisons.

COMPARISON OF THE FOSSIL DYSAGRION (PACKARDII, FREDERICII) WITH PHENACOLESTES.

According to the figures and descriptions of this Eocene genus, from the Green River shales of Wyoming, given by Scudder,⁶ *Dysagrion* and *Phenacolestes* agree in the characters above numbered 2, 3, 4, 5, 7,⁷ 10, 11,⁸ 14, 15*b*, 16*a* and *b*, 20, 21*a* and *b*, and 22, and

⁵ *Mem. Couron. Acad. Belg.*, XXXVIII, p. 30.

⁶ *Tertiary Insects of North America*, 1890, pl. 6, figs. 3, 9, 14 and pp. 128-133.

⁷ In *D. packardii*, but not in *D. fredericii*.

⁸ As Scudder has pointed out, p. 129, however, the subnodus is bent proximad (instead of distad as is the case in *Phenacolestes*).

differ in the following characters, the difference shown by *Dysagrion* being stated:

1. Nodus at .37 of the wing-length.
6. The veins generally, posterior to M_1 , have a slighter caudal curvature as they approach the hind margin.
7. Between M_1 and M_{1a} are two rows of cells beginning under the stigma (*D. fredericii*, not *D. packardii*).
8. Between M_{1a} and M_2 is one row of cells increasing to two, three, and finally five rows.
9. M_2 separates from M_1 at .15⁹ of the distance from nodus to stigma.
12. Between R_s and M_3 is one row of cells increasing to two, three, and eventually eight rows.
13. Arculus apparently at the second antenodal.
- 15a. Between M_3 and M_4 is apparently only one cross-vein proximal to the level of the subnodus.
17. Between M_4 and Cu_1 are (a) 8–10 antenodal cells (the quadrilateral is much shorter than in *Phenacolestes*) and (b) at the wing-margin only one row of cells.
18. Cubito-anal cross-veins two in *D. fredericii*, one of them proximal, the other distal, to the arculus; none shown in *D. packardii*.
19. Between Cu_1 and Cu_2 at wing-margin one (*D. packardii*) or three (*D. fredericii*) rows of cells.

COMPARISON OF THE FOSSIL MELANAGRION (UMBRATUM) WITH PHENACOLESTES.

According to the figures and description of this Miocene genus from Florissant, Colo., given by Scudder,¹⁰ *Melanagrion* and *Phenacolestes* agree in the characters above numbered 5, 7, 8,¹¹ 9, 10,¹¹ 13, 14, 15a, 16a and b, 18, and differ in the following characters, the difference shown by *Melanagrion* being stated:

1. Nodus at .3 (?) of the wing-length.
2. Only two antenodals.
3. More than 26 postnodals (27, Scudder).
4. Stigma having both proximal and distal ends much less oblique.
6. The veins generally, posterior to M_1 , have a slighter caudal curvature as they approach the hind margin.
11. R_s separates from M_{1+2} slightly proximal to the subnodus.

⁹ This is taken by measurement from Scudder's figure, although he says that the "nodal sector arises from the principal . . . scarcely more than one-fifth way to the pterostigma" (p. 129), and in another place (p. 128) "at scarcely one-fifth the distance from the nodus to the pterostigma." Whether figure or text be correct, both differ from the condition in *Phenacolestes*.

¹⁰ Scudder, *Tertiary Insects of North America*, 1890, pl. 13, figs. 12, 14, p. 136, described this form as a *Lithagrion*. It was made the type of a new genus, *Melanagrion*, by Prof. Cockerell in *Bull. Amer. Mus. Nat. Hist.*, XXXIII, p. 138, 1907.

¹¹ At the extreme margin there are four rows in *Melanagrion*.

12. Between R_s and M_3 is one row of cells increasing to two rows.
- 15b. Between M_3 and M_4 at the wing-margin are only three rows of cells.
17. Between M_4 and Cu_1 are (a) about three antenodal cells and (b) at the margin one row of cells.
19. Between Cu_1 and Cu_2 at the wing-margin appear to be but one row of cells.
20. Area posterior to Cu_2 with no more than two rows of cells.
21. Anal vein separating from the hind wing-margin (a) distad (fig. 12) or proximad (fig. 14) to the level of the arculus and (b) at the level of the cubito-anal cross-vein (fig. 14, cross-vein not shown in fig. 12).¹²
22. No anal cross-veins, according to both figures.

COMPARISON OF THE FOSSIL LITHAGRION (HYALINUM) WITH
PHENACOLESTES.

According to the figure and description of this Miocene genus from Florissant, Colo., given by Scudder¹³ and some notes on more recently found specimens kindly communicated by Prof. Cockerell, *Lithagrion* and *Phenacolestes* agree in the characters above numbered 1, 3, 5, 7, 8, 9, 10 (probably), 11, 14, 15a, 16a and b, 18, and differ in the following characters, the differences shown by *Lithagrion* being stated:

2. Probably only two antenodals.¹⁴
4. Stigma having its proximal edge very much less oblique.
6. The veins generally, posterior to M_1 , have a slighter caudal curvature as they approach the wing-margin.
12. Between R_s and M_3 is only one row of cells to the wing-margin.
13. Arculus at the second antenodal.¹⁵
- 15b. Between M_3 and M_4 at the wing-margin are only two or three rows of cells.
17. Between M_4 and Cu_1 are (a) three antenodal cells and (b) one row of cells increasing to two rows only at the extreme margin.
19. Between Cu_1 and Cu_2 at the wing-margin is only one row of cells.
20. Area posterior to Cu_2 with only one row of cells.
21. Anal vein separating from the hind margin of the wing distad to the levels (a) of the arculus and (b) of the cubito-anal cross-vein.
22. Anal cross-veins proximal to the level of the distal end of the quadrilateral apparently none.

¹² Scudder's description, p. 136, says, "The wings are petiolated very nearly up to the first postcostal nervule, which is placed shortly before the base of the quadrilateral."

¹³ *Tertiary Insects of North America*, 1890, pl. 13, fig. 4, and pp. 128, 134-136.

¹⁴ Scudder's figure, *l.c.*, shows but one, at the arculus. Compare Prof. Cockerell's statements on this point in *Bull. Amer. Mus. Nat. Hist.*, XXXIII, p. 137 (1907); XXXIV, p. 63 (1908); *Amer. Journ. Sci.*, XXVI, p. 69 (1908).

¹⁵ A sketch kindly sent by Prof. Cockerell shows the arculus a little distal to the second antenodal.

COMPARISON OF THAUMATONEURA (INOPINATA AND PELLUCIDA)
WITH PHENACOLESTES.

(*Th. inopinata* ♂ ♀, *Th. pellucida* ♂, Costa Rica).

These two genera *agree* in the characters above numbered 2, 11, 14 (except as noted below), and 21a. As regards character 11, the separation point of R_s in *Thaumtoneura* varies and may be a little proximal to, at, or a little distal to, the subnodus.

The two genera *differ* in characters given below; after each number the difference shown by *Thaumtoneura* is stated:

1. Nodus at about one-fifth of the wing-length.
3. Postnodals very numerous, about 70.
4. Proximal edge of stigma more oblique.
5. Cells more elongated at right angles to long axis of wing.
6. Stronger caudal curvatures of the veins generally as they approach the hind margin of wing.
7. The one row of cells between M_1 and M_{1a} increases to about 10 rows at the wing-margin.
8. The one row of cells between M_{1a} and M_2 increases to 6+ rows at the wing-margin.
9. M_2 separates from M_1 at nearly one-half way from nodus to stigma and at a less acute angle.
10. Between M_2 and R_s at the wing-margin are 6-7+ rows of cells.
12. Between R_s and M_3 at the wing-margin are 7-8+ rows of cells.
13. Arculus at the second antenodal.
14. M_3 separates from M_{1+2} at a less acute angle.
15. Between M_3 and M_4 , (a) no cross-veins proximal to the level of the subnodus, (b) at the wing-margin 10+ rows of cells.
16. Quadrilateral with (a) its proximal and distal sides subparallel and (b) subequal.
17. Between M_4 and Cu_1 are (a) 3-6 antenodal cells and (b) at the wing-margin 8+ rows of cells.
18. Cubito-anal cross-veins *two*, one proximal to the level of the first antenodal cross-vein, the other below the middle of the quadrilateral.
19. Between Cu_1 and Cu_2 at wing-margin are about 12 rows of cells.
20. Area posterior to Cu_2 much larger, Cu_2 with many branches.
- 21b. Anal vein separates from the hind margin of the wing distad to the level of the proximal cubito-anal cross-vein.
22. Anal cross-veins proximal to the level of the distal end of the quadrilateral 3-5.

RELATIONSHIPS OF THAUMATONEURA.

Some words may be added here as to the retention of *Thaumtoneura* in this group after the diverging opinions of Professors Needham and Foerster. The late Mr. McLachlan, on describing *Thaumato-*

neura (1897), referred it to the Calopteryginae. In 1902, I placed it in the legion Podagrion of the Agrioninae.¹⁶ In 1903, Professor Needham associated it with the Anormostigmatini (= legion Pseudostigma of Selys), stating that "it has all the essential venational characters of this group, and surely these are sufficiently distinctive."¹⁷ A comparison of *Thaumatoneura* with these essential venational characters¹⁸ gives the following result.

Thaumatoneura agrees with the Anormostigmatini in that R_s separates from M_{1+2} at or very close to the subnodus and the part of the wing beyond the nodus is greatly enlarged. On the other hand, *Thaumatoneura* differs from the Anormostigmatini in that, while the stigma is not braced, it is not diffuse or lost; the matching of cross-veins is not so marked; the longest vein between M_1 and M_2 , which, in the preceding pages, we have assumed to be M_{1a} , does not parallel M_2 more than it parallels M_1 and lies almost midway between M_1 and M_2 ; it has shorter supplementary sectors between itself and M_1 and also between itself and M_2 ; these latter tend to be longer and better developed than those anterior to M_{1a} , and in this *Thaumatoneura* resembles *Paraphlebia* and differs from the Anormostigmatini. This tendency to the development of more rows of cells between M_{1a} and M_2 than between M_1 and M_{1a} is emphasized in *Philogenia carrillica*, *P. terraba*, *Heteragrion tricellulare*, *H. erythrogastrum* and *Argiolestes icteromelas* which have no supplementary sectors between M_1 and M_{1a} , but two between M_{1a} and M_2 ; all these are Podagrionines. Even in more reduced venations of the same group, as in *Allopodagrion* there are no supplementary sectors between M_1 and M_{1a} , but still one between M_{1a} and M_2 . On the other hand, even in Anormostigmatini with the most reduced venation, e.g., *Mecistogaster*, there is a longer supplementary sector between M_1 and M_{1a} than between M_{1a} and M_2 . Professor Needham himself has pointed out some further differences of *Thaumatoneura* from *Megaloprepus*, and still others may be added. Thus the nodus and quadrilateral (quadrangle) are no more approximated in *Thaumatoneura* than in many other undoubted members of the legion Podagrion (See Table I, p. 250, *postea*). *Thaumatoneura* possesses more supplementary sectors between M_2 and R_s and between R_s and M_3 . I believe, therefore, that *Thaumatoneura* shows more resemblances to the legion Podagrion than to the legion Pseudostigma, but it does not

¹⁶ 1902, pp. 29-32. *Biol. Centr. Amer. Neur.*, p. 58.

¹⁷ *Genealogic Study*, pp. 748-749, footnote.

¹⁸ Needham, *l.c.*, p. 748.

seem impossible that the Anormostigmatini may have descended from some form like *Thaumatoneura*.

Professor Foerster considers *Thaumatoneura* as a connecting form between the Calopteryginae and the legion Podagrion, "which is better left with the Calopteryginae." "Bei *Thaumatoneura* ist der äussere Ast des Sector inferior trianguli convex nach vorn gebogen wie bei allen echten Calopterygiden. Bei allen Agrioninen ist er dagegen schwach convex nach hinten."¹⁹ Many Calopteryginae (Selys) have not Cu₂ convex anteriorly, of course, such as *Micromerus*, *Rhinocypha biforata* and other species, *Libellago*, etc., but perhaps these are not "echt." On the other hand, such Agrionines as *Megaloprepus*, *Microstigma*, and *Paraphlebia* also have Cu₂ convex anteriorly, while a tendency in the same direction is observable in *Argiolestes* and even in *Hyponeura*, so that I cannot see that any strong argument for the Calopterygine affinities of *Thaumatoneura* can be drawn from this character.

COMPARISON OF PHILOGENIA (TERRABA, CARRILICA) WITH
PHENACOLESTES.

(*Ph. terraba* ♂, *Ph. carrillica* ♂ ♀, Costa Rica.)

These two genera agree in the characters above numbered 4, 5, 6, 7, 10,²⁰ 11 (*carrillica*, not *terraba*), 12,²⁰ 14, 16, 18.

These two genera differ in characters given below; after each number the difference shown by *Philogenia* is stated.

1. Nodus at one-fourth of the wing-length.
2. Only two antenodals.
3. Postnodals 22-30.
8. Between M_{1a} and M₂ is at first but one row of cells which, more distad, is increased to two and then to three rows by the presence of two distinct curvilinear (*i.e.*, not broken) supplementary sectors, the posterior of which arises proximad to the anterior; each of these three rows increases to a double row before reaching the wing-margin at an individually variable distance therefrom.
9. M₂ separating from M₁ at one-third of the distance from nodus to stigma.
11. R_s separating from M₁₊₂ a little distad to the subnodus (*terraba*, not *carrillica*).
13. Arculus slightly distal to the second antenodal.

¹⁹ *Jahrb. Nassau. Ver. f. Naturk. in Wiesbaden*, 62, p. 214, 1909.

²⁰ At the very margin itself, each of the three rows in *Philogenia* tends to divide into two rows, but each of these last extends inward only 2-3 cells from the margin.

15. Between M_3 and M_4 is (a) one cross-vein proximal to the level of the subnodus and (b) at the wing-margin are two or three rows of cells.
17. Between M_4 and Cu_1 are (a) 2-3 antenodal cells and (b) at the wing-margin one row of cells.
19. Between Cu_1 and Cu_2 at the wing-margin is one row of cells.
20. Area posterior to Cu_2 less developed, having only one row of cells.
21. Anal vein separating from the hind wing-margin at the mid-level of the quadrilateral, hence distad both to (a) the level of the arculus and (b) that of the cubito-anal cross-vein.
22. No anal cross-vein proximal to the level of the distal end of the quadrilateral, but there is a cross-vein continuing the vein which forms the distal end of the quadrilateral to the wing-margin; this cross-vein is absent in *Phenacolestes*, *Thaumato-neura* and *Paraphlebia*.

Note.—The wing figured by Prof. Needham (*Genealogic Study*, Pl. 53, fig. 4) as that of "*Philogenia* sp.?" is not *Philogenia*, but *Megapodagrion* Selys *sens. lat.* (*Allopodagrion* Foerster).

COMPARISON OF MEGAPODAGRION (NEBULOSUM²¹) WITH
PHENACOLESTES.

(*M. nebulosum* 2 ♂, Bolivia.)

These two forms *agree* in the characters above numbered 1, 3, 5, 7, 10, 11, 14, 16, 18, 21a, 22.

These two forms *differ* in the characters given below; after each number the difference shown by the *Megapodagrion* is stated.

2. Only two antenodals.
4. Stigma having its proximal edge less oblique.
6. The longitudinal veins show less curvature.
8. Between M_{1a} and M_2 at the wing-margin are two rows of cells.
9. M_2 separates from M_1 at .45 to .41 of the distance from nodus to stigma.
12. Between R_s and M_3 at the wing-margin is only one row of cells.
13. Arculus at the second antenodal.
15. Between M_3 and M_4 is (a) only one cross-vein proximal to the level of the subnodus and (b) at the wing-margin are two rows of cells.
17. Between M_4 and Cu_1 are (a) 3-5 antenodal cells and (b) at the wing-margin only one row of cells.
19. Between Cu_1 and Cu_2 at the wing-margin is only one row of cells.
20. Area posterior to Cu_2 with only one row of cells.

²¹ *Megapodagrion nebulosum* Selys is referable to the recently proposed genus *Allopodagrion* of Förster, *Wien. Ent. Zeit.*, XXIX, p. 51, 1910.

21b. Anal vein separating from the hind margin of the wing at or slightly distad to the cubito-anal cross-vein.

Note.—The wing figured by Prof. Needham (*Genealogic Study*, pl. 53, fig. 4) as that of "*Philogenia* sp.?" is really that of a *Megapodagrion* Selys *sens. lat.*, *Allopodagrion* Foerster.

COMPARISON OF PARAPHLEBIA (ZOE AND ABROGATA) WITH
PHENACOLESTES.

(*P. zoe* ♂ ♀ Mexico, *P. abrogata* ♂ Guatemala.)

These two genera agree in the characters above numbered 4, 5, 10 (*abrogata* only), 12 (*abrogata* only), and 15b (*abrogata* only).

These two genera differ in the characters given below; after each number the difference shown by *Paraphlebia* is stated.

1. Nodus at one-fifth of the wing-length.
2. Only two antenodals.
3. Postnodals 40 ±.
6. Stronger caudal curvatures of the longitudinal veins generally as they approach the hind margin of the wing, although less strongly curved than in *Thaumatonereura*.
7. The one row of cells between M_1 and M_{1a} increases to 3 rows (*abrogata*) or 4–6 rows (*zoe*) at the wing-margin.
8. The one row of cells between M_{1a} and M_2 increases to 3 rows (*abrogata*) or 4–6 rows (*zoe*) at the wing-margin.
9. M_2 separates from M_1 at one-half (*abrogata*) or thirteen-thirtieths (= .43) of the distance from nodus to stigma (*zoe*).
10. Between M_2 and R_s at the wing-margin are 3–6 rows of cells (*zoe*).
11. R_s separates from M_{1+2} distad to the subnodus.
12. Between R_s and M_3 at the wing-margin are 3–6 rows of cells (*zoe*).
13. Arculus at or even slightly distal to the second antenodal.
14. M_3 separating from M_{1+2} at or distad to the subnodus.
15. Between M_3 and M_4 (a) are no cross-veins proximal to the level of the subnodus (*zoe*, *abrogata*), and (b) at the wing-margin are 5–7 rows (front wings, *zoe*) or 6–11 rows (hind wings, *zoe*) of cells.
16. Quadrilateral with (a) its proximal and distal sides subparallel or slightly diverging caudad, and (b) its distal side hardly more than one and one-half times as long as the proximal side.
17. Between M_4 and Cu_1 is (a) one, or less than one, antenodal cell, and (b) at the wing-margin are 3 (*abrogata*) or 3–6 (*zoe*) rows of cells.
18. Cubito-anal cross-veins two, one between the levels of the first and second antenodals, but nearer to that of the first, the other nearly below the middle (or distal to the middle) of the quadrilateral.

19. Between Cu_1 and Cu_2 at the wing-margin are 10–14 rows of cells in *zoe*, seven (front wings) or five (hind wings) rows in *abrogata*.
20. Area posterior to Cu_2 less developed and with only two (*abrogata*, *zoe* ♀) or three (*zoe* ♂) rows of cells.²²
21. Anal vein separating from the hind wing-margin (*a*) distad to the level of the arculus and (*b*) nearly at the level of the second (distal) cubito-anal cross-vein.
22. Anal cross-veins, proximal to the level of the distal end of the quadrilateral, *two* (one in the front wings of the single female *zoe*).

COMPARISON OF DIMERAGRION N. GEN. (PERCUBITALE N. SP.) WITH PHENACOLESTES.

(*D. percubitale* 14 ♂, 6 ♀, British Guiana, Plate XIV, fig. 6.)

These two genera *agree* in the characters above numbered 1, 5, 7,²³ 8, 9, 12,²⁴ 16*a*, 16*b*.

These two genera *differ* in characters given below; after each number the difference shown by *Dimeragrion* is stated.

2. Two antenodals.²⁵
3. Postnodals 20–27 (front wing), 16–24 (hind wing), fewer in the females than in the males.
4. Stigma having its proximal edge more oblique.
6. The veins generally, posterior to M_1 , have a slighter caudal curvature, or are almost straight, as they approach the hind margin of the wing.
10. Between M_2 and R_s is but one row of cells which at a distance of usually two²⁶ cells from the wing-margin increases to two rows.
11. R_s separates from M_{1+2} at the first postnodal, or a little proximad thereto, or between the first and second postnodals.
13. Arculus at or very slightly distal to the second antenodal.
14. M_3 separates from M_{1+2} a little proximad to the subnodus, at least at seven-eighths' distance from arculus to subnodus.²⁷

²² The hind wings of some individuals, ♂ ♀, of *P. duodecima* have only one row of cells here.

²³ Two rows of cells between M_1 and M_{1a} for short distances proximad to the level of the stigma have occasionally been noted in *Dimeragrion*, viz.: for three cells in one front wing each of two males and for two cells in the other front wing of one of these same two males.

²⁴ Each of the three rows of cells in the terminal part of the area R_s increases to two rows at the wing-margin in one front and one hind wing of the same male.

²⁵ A third antenodal placed between the usual two and confined to the costal space exists in the right hind wing only of one male.

²⁶ This increase to two rows has been noted as beginning at three cells from the margin in 2 front wings and 2 hind wings; at four cells in 3 front wings, 1 hind wing; at five cells in 2 front wings, 1 hind wing; at six cells in 2 front wings, 2 hind wings; at seven cells in 1 hind wing. All the individuals, seven in number, showing these variations are males.

²⁷ In one wing only it separated at the subnodus.

15. Between M_{1-3} and M_4 are (a) no cross-veins proximal to the level of the subnodus, and (b) between M_3 and M_4 is only one row of cells to the wing-margin.
17. Between M_4 and Cu_1 are (a) two to three antenodal cells (*sensu Selysi*) and (b) only one²⁸ row of cells to the wing-margin.
18. Cubito-anal cross-veins between the levels of the two antenodals varying from one to four, most frequently two; often an additional cross-vein proximal to the level of the first antenodal.²⁹
19. Between Cu_1 and Cu_2 is only one row of cells to the wing-margin.
20. Area posterior to Cu_2 with only one row of cells.
21. Anal vein separating from the hind wing-margin (a) distad to the level of the arculus and (b) distad to the level of the cubito-anal cross-vein or veins.
22. Anal cross-veins, proximal to the level of the distal end of the quadrilateral, one, situated a little proximad to the oblique vein which continues the distal side of the quadrilateral caudad, or at that oblique vein.

COMPARISON OF HETERAGRION (TRICELLULARE) WITH
PHENACOLESTES.

(*H. tricellulare* ♂, Guatemala.)³⁰

These two forms *agree* in the characters above numbered 5, 7, 8, 16, 18, 21a.

These two forms *differ* in characters given below; after each number the difference shown by the *Heteragrion* is stated.

1. Nodus at one-fourth of the wing-length.
2. Only two antenodals.
3. Postnodals 21-25.
4. Proximal edge of pterostigma more oblique, but the difference is less marked than in *Thaumato-neura*.
6. Longitudinal veins hardly curved at all caudad on approaching the wing-margin.
9. M_2 separates from M_1 at three-sevenths (= .43) of the distance from nodus to stigma.
10. Between M_2 and R_s at the wing-margin is but one row of cells.
11. R_s separates from M_{1+2} far distad (e.g., five to six cells) to the subnodus.
12. Between R_s and M_3 at the wing-margin is but one row of cells.
13. Arculus at the second antenodal.
14. M_3 separating from M_{1+2} at or barely proximad to the subnodus.
15. Between M_3 and M_4 are (a) no cross-veins proximal to the level of the subnodus, as results from No. 14, and (b) at the wing-margin only one row of cells.

²⁸ Two rows exist in both hind wings of each of two females and in one hind wing of one male.

²⁹ For details see the specific description of *Dimeragrion percubitale*, *postea*, p. 269.

³⁰ The wing of *Heteragrion flavovittatum* has been figured by Needham (*Geneal. Study*, pl. 53, fig. 6).

17. Between M_4 and Cu_1 are (a) three antenodal cells³¹ and (b) at the wing-margin only one row of cells.
19. Between Cu_1 and Cu_2 at the wing-margin only one row of cells.
20. Area posterior to Cu_2 less developed, having only one row of cells.
- 21b. Anal vein separating from the hind wing-margin at or distad to the cubito-anal cross-vein.
22. Anal cross-vein as stated above for *Philogenia*.

COMPARISON OF MESAGRION, HETEROPODAGRION, AND NEURAGRION
WITH PHENACOLESTES.

Of three other American genera of the legion Podagrion, *Mesagrion* Selys, *Heteropodagrion* Selys and *Neuragrion* Karsch, each represented by a single species, the first from Bogota, the second from Quito, the third from Ecuador without more definite locality, I have seen no material.

According to the description of de Selys (1886), *Mesagrion* agrees with *Phenacolestes* in characters above numbered 3, 7 (probably), 8, 12, and 16a, and differs from *Phenacolestes* in the following characters:

2. Only two antenodal cross-veins.
10. Between M_2 and R_s only one row of cells.
11. R_s separates from M_{1+2} distad to the subnodus.
14. M_3 separates from M_{1+2} a little distad to the subnodus.
- 15b (Probably one row of cells between M_3 and M_4).
- 17a. Between M_4 and Cu_1 are two antenodal cells and b (probably one row of cells at the wing-margin).
18. Cubito-anal cross-veins one, situated proximad to the level of the first antenodal cross-vein.
19. (Probably one row of cells between Cu_1 and Cu_2).
21. Anal vein separating from the hind margin of the wing (a) distad to the level of the arculus, and (b) distad to the level of the cubito-anal cross-vein.

According to de Selys' description (1886), *Heteropodagrion* agrees with *Phenacolestes* in characters above numbered 7 (probably), 10, 12, 14, and 16a, and differs from *Phenacolestes* in Nos. 2, 11, 15b (probably), 17a (and b probably), 18, and 21 in the same particulars as *Mesagrion* is above stated to differ from *Phenacolestes*. *Heteropodagrion* further differs from *Phenacolestes* in the following characters:

3. Postnodals 20-23.
8. (Probably one³² row of cells between M_{1a} and M_2).

³¹ Other species of *Heteragrion* have but two or one antenodal cell (Selys, 1886, pp. 54, 55).

³² Dr. Karsch, in his description of *Neuragrion*, states that it has "zwei Schaltsectoren . . . zwischen dem Nodal- und Ultranodalsector," and, further on, that it agrees in this respect with *Heteropodagrion*, but de Selys' description of the latter is silent on this point (although not for the same area of *Mesagrion*) and, I think, implies the absence of "Schaltsectoren" here.

According to Karsch's description,³³ *Neuragrion* agrees with *Phenacolestes* in characters above numbered 2 (but for the hind wings only),³⁴ 8, 10, 12, 14 (in so far as "Der Mediansector entspringt aus dem Principalis vor der vom Nodus absteigenden Ader"), and 16a, and differs from *Phenacolestes* in the following characters:

2. Only two antenodals on the *front* wings.
3. Postnodals 20-21.
11. R_s separates from M_{1+2} near the first postnodal cross-vein.
13. Arculus distal to the normal second antenodal.
- 15b. Between M_3 and M_4 probably only one row of cells to margin.
- 17b. Between M_4 and Cu_1 probably only one row of cells to margin.
18. Cubito-anal cross-vein apparently proximal to ("vor," not "von"?) the level of the first antenodal.
19. Between Cu_1 and Cu_2 at wing-margin probably only one row of cells.
21. Anal vein separates from the hind wing-margin (a) at the level of the arculus and therefore (b) distad to the level of the cubito-anal cross-vein.

COMPARISON OF RHIPIDOLESTES (ACULEATA) WITH PHENACOLESTES.

(*Rhipidolestes aculeata* inhabits Formosa.)

According to the description and figure of Dr. Ris (1912), these two forms agree in the characters above numbered 1, 5, 6, 7, 8, 9, 10,³⁵ 12,³⁵ 15a, 16a (and perhaps 16b), 18, 19, and differ in the following characters possessed by *Rhipidolestes*:

2. Only two antenodals.
3. Postnodals about 22 (front wing) and 21 (hind wing).
4. Stigma, although having its proximal edge of about the same obliquity as in *Phenacolestes*, is shorter proximo-distally and its distal edge is less oblique.
11. R_s separates from M_{1+2} proximad to the subnodus at very nearly three-fourths' distance from arculus to subnodus.
13. Arculus at the second antenodal.
14. M_3 separates from M_{1+2} at mid-way from arculus to subnodus.
- 15b. Between M_3 and M_4 at the wing-margin are three rows of cells.
17. Between M_4 and Cu_1 are (a) three antenodal cells and (b) at the wing-margin three rows of cells.
20. Area posterior to Cu_2 with only one row of cells.

³³ *Societas Entomologica* VI, p. 105, 1891. *Neuragrion* was described from a single female.

³⁴ "Im Hinterflügel drei Antecubitalqueradern, deren mittlere auf den Subcostalraum beschränkt ist."

³⁵ Each of the three rows in the terminal parts of these M_2 and R_s areas may divide itself into two rows at two or three cells' distance from the wing-margin.

21. Anal vein separating from the hind wing-margin (*a*) distad to the level of the arculus and (*b*) distad to the level of the cubito-anal cross-vein.
22. Anal cross-vein at the vein descending from the distal end of the quadrilateral.

COMPARISON OF *PODOPTERYX* (*ROSEONOTATUS*) WITH
PHENACOLESTES.³⁶

(*P. roseonotatus* ♂ type of Selys (from Aru), 1 ♂ 1 ♀ Queensland determined by Mr. Herbert Campion; all three in the British Museum.)

These two genera *agree* in the characters above numbered 5, 7, 8,³⁷ 10,³⁸ 11,³⁹ 12⁴⁰, 16, 17*b*, and 18.⁴¹

These two genera *differ* in the characters given below; after each number the difference shown by *Podopteryx* is stated.

1. Nodus at one-fourth of the wing-length.
2. More often only two antenodals.⁴²
3. Postnodals 32-35.
4. Stigma less oblique, shorter in its proximo-distal dimension in proportion to its antero-posterior dimension.
6. The veins generally, posterior to M₁, have a more pronounced caudal curvature as they approach the hind margin of the wing.
9. M₂ separates from M₁ at .37 to .43 of the distance from nodus to stigma.
13. Arculus at the second antenodal.⁴³

³⁶ I am indebted to Mr. Herbert Campion for first calling my attention to the desirability of comparing this genus with *Phenacolestes*.

³⁷ There are 7-8 rows at the extreme margin, however.

³⁸ There are 5-7 rows at the extreme margin, however.

³⁹ In both front wings of the Queensland male and in the left front wing of the female R_s is united with M₃ for from one-half to one cell distad of the subnodus.

⁴⁰ There are 5-6 rows at the extreme margin, however.

⁴¹ The right hind wing of the type male, the right front and left hind wings of the Queensland female have a second cubito-anal cross-vein proximal to the normal one and nearly mid-way between the levels of the first and second antenodals; the normal cubito-anal cross-vein is, in all, nearer to the level of the second antenodal. Prof. F. Foerster has also noted (Termesz. Fü. XXIII, p. 104, 1900) an instance of two cubito-anal cross-veins in *Podopteryx*.

⁴² The type male has three antenodals on all four wings, the third being distal to the other two and not reaching posteriorly beyond the subcosta. The two Queensland examples have only two antenodals on all the wings. The type male has also a subcostal cross-vein, proximal to the first antenodal, on both front wings and the right hind wing; this is lacking in the Queensland specimens.

⁴³ Slightly distal to the second antenodal on the two wings of the right side of the Queensland male. This is an appropriate place to record certain abnormalities of the type male, already mentioned by de Selys (1886); three of its wings have each a single medio-cubital cross-vein which, on the right front wing, is slightly proximal to the level of the normal first antenodal, but on the right hind wing and left front wing is slightly distal to the normal first antenodal. On the left hind wing there is merely a slight rudiment or vestige of such a cross-vein projecting forward as a stump from Cu slightly distad to the level of the first antenodal.

14. M_3 separates from M_{1+2} at .75 to .83 of the distance from arculus to subnodus.
15. Between M_3 and M_4 is (a) only one cross-vein proximal to the level of the subnodus and (b) one row of cells increasing to 9 to 11 rows at the wing-margin.
- 17a. Between M_4 and Cu_1 are 3+ to 5 antenodal cells (*sensu Selysi*).
19. Between Cu_1 and the *very much angulated* Cu_2 is one row of cells.
20. Area posterior to Cu_2 with many branches from that vein and four (front wings) or five (hind wings) rows of cells between it and the wing-margin.
21. Anal vein separates from the hind margin (a) at or slightly distad to the level of the arculus and therefore (b) much more distad to the level of the cubito-anal cross-vein.
22. More often no anal cross-veins.⁴⁴

COMPARISON OF ARGIOLESTES (ICTEROMELAS) WITH PHENACOLESTES.

(*A. icteromelas* ♂ ♀, Victoria, Australia.)

These two forms *agree* in the characters above numbered 1, 3, 5, 7, 8, 10, 11, 12, 14, 16, 18.

These two forms *differ* in the characters given below; after each number the difference shown by the *Argiolestes* is stated.

2. Only two antenodals.
4. Proximal edge of pterostigma nearly as in *Phenacolestes*, but the distal edge much more oblique.
6. Longitudinal veins posterior to M_1 with a stronger caudal curvature as they approach the margin.
9. M_2 separates from M_1 at four-tenths to one-half of the distance from nodus to stigma.
13. Arculus at or slightly distal to the second antenodal.
15. Between M_3 and M_4 is (a) one cross-vein proximal to the level of the subnodus, and (b) at the wing-margin are 8-10 (front wings) or 6-8 (hind wings) rows of cells.
17. Between M_4 and Cu_1 are (a) three (occasionally four) antenodal cells and (b) at the wing-margin are two to three rows of cells.
19. Between Cu_1 and Cu_2 at the wing-margin is only one row of cells.
20. Area posterior to Cu_2 with about two rows of cells.
21. Anal vein separating from the hind margin distad to the levels (a) of the arculus, and (b) of the cubito-anal cross-vein.
22. Anal cross-vein as stated above for *Philogenia*.

⁴⁴ There is an anal cross-vein proximal to the level of the distal end of the quadrilateral in the right front and right hind wings of the Queensland male and in the right front and left hind wings of the female. In the other eight wings, the first cross-vein in this part of the wing is at or slightly distal to the vein descending from the distal end of the quadrilateral and therefore should perhaps not be called an *anal* cross-vein, but a cross-vein posterior to Cu_2 . It has been marked Cu_{2a} by Mr. Williamson, 1913, p. 260.

COMPARISON OF CHLOROLESTES (FASCIATUS) WITH PHENACOLESTES.

(*Ch. fasciatus*, 2 ♂ Natal, 1 ♂ "Pirie Bush, S. Africa, A. N. Stenning 98-191"; all 3⁴⁵ in the British Museum.)

These two genera *agree* in the characters above numbered 5, 6, 7,⁴⁶ 8,⁴⁷ 9,⁴⁸ 10,⁴⁹ 15b, 16, 18,⁵⁰ and 22.

These two genera *differ* in the characters given below; after each number the difference shown by *Chlorolestes* is stated.

1. Nodus at four-fifteenths (= .27) of the wing-length.
2. Only two antenodals.⁵¹
3. Postnodals on the front wings 22-23, on the hind wings 17-20.
4. Stigma less oblique.
11. R_s separates one to two cells distad to the subnodus, but in all cases nearer to M_3 than to M_{1+2} .
12. Between R_s and M_3 is one row of cells which may increase to two rows at the extreme margin, symmetrically or asymmetrically.
13. Arculus at the second antenodal.
14. M_3 separating from M_{1+2} at the subnodus.
- 15a. Between M_3 and M_4 are no cross-veins proximal to the level of the subnodus, the first cross-vein being very nearly at, but still slightly distal to, the level of the subnodus.
17. Between M_4 and Cu_1 are (a) two to three antenodal cells (*sensu Selysii*) and (b) one row of cells to the wing-margin.
19. Between Cu_1 and Cu_2 is one row of cells to the wing-margin.
20. Area posterior to Cu_2 with only one row of cells.
21. Anal vein separating from the hind wing-margin at, or slightly distal to, the level of the middle of the lower side of the quadrilateral, therefore far distad (a) to the level of the arculus and (b) to that of the cubito-anal cross-vein.

VARIOUS OLD WORLD GENERA AND PHENACOLESTES.

The genus *Wahnesia* Förster, of New Guinea, has the area posterior to Cu_2 fairly well developed, but not to the extent that it is in *Phenacolestes*, but as this genus differs from *Phenacolestes* in a number of characters, such as Nos. 2, 9, 11, 13, 14, 21, 22, a more detailed comparison has not been made.

⁴⁵ These three males have a brown band for the full width of the wing from the origin of M_2 distad to half-way from this point to the proximal end of the stigma.

⁴⁶ Occasionally increasing to two rows at the extreme margin.

⁴⁷ Each one of the three rows may divide, however, into two rows at the extreme margin.

⁴⁸ M_2 separates from M_1 at .28 to .33 of the distance from nodus to stigma.

⁴⁹ At the extreme margin there are 5-7 rows, however; but compare p. 229, *antea*.

⁵⁰ The cubito-anal cross-vein is nearer to the level of the first than to that of the second antenodal.

⁵¹ One of the Natal males has on the right hind wing an additional antenodal proximal to the normal first and confined to the costal area.

None of the following Old World genera seem to offer any close approximations to *Phenacolestes* and therefore have not been studied further in this connection: *Neurolestes* Selys, *Nesolestes* Selys, *Podolestes* Selys and *Synlestes* Selys. It may be noted, however, that in *Neurolestes trinervis* Selys, from Old Calabar, the three antenodals are so arranged that the arcus is at the third antenodal on all four wings.

GENERAL DISCUSSION OF THE VALUE OF THE VENATIONAL CHARACTERS COMPARED IN THE PRECEDING GENERA FOR THE DETERMINATION OF RELATIONSHIPS.

Many of the ideas which have been expressed on the changes which have taken place in the venation of Odonate wings have been based on the comparative morphology of living representatives of the order or on considerations of mechanical advantage. It does not follow that these foundations are trustworthy or that there has always been mechanical improvement in the wings. Degeneration is just as probable as progressive development. The actual course of phylogeny cannot be deduced from these considerations or from the data of morphology. It seems therefore desirable to attempt to ascertain what paleontological evidence exists affording clues to the descent of these insects, by tracing the modifications which the wings exhibit from the Carboniferous period down to the present time.

The characters of *Phenacolestes* and other genera which have been compared in the preceding pages under the numbers 1 to 22 may for the most part be arranged into two groups:

A. Those characters which are concerned with the positions of the points of separation of longitudinal veins and the positions and number of certain cross-veins.

B. Those characters which are concerned with the number of rows of cells existing between the longitudinal veins and their branches.

Group A includes numbers 1, 2, 3, 4, 9, 11, 13, 14, 15a, 16, 17a, 18, 21, and 22.

1. *The Position of the Nodus*.—The Protodonata of the Carboniferous and the Permian possessed no nodus; their subcosta (whose apex in the Odonata usually coincides with the nodus) reached often beyond mid-length of the wing, its minimal extent being to four-tenths of the wing-length in *Meganeurula* (Handlirsch⁵²). The earliest of

⁵² *Foss. Ins.*, p. 309, Taf. XXXI, figs. 37, 38.

the known Odonata, from the Lias, have been segregated by Handlirsch as a suborder, distinct from the existing Zygoptera and Anisoptera, under the name Anisozygoptera.⁵³ These insects usually possessed a nodus which lay at about mid-length of the wing. Handlirsch considers⁵⁴ that, of the recent forms, the Gomphidæ and Calopterygidæ have unquestionably the closest relations to the Anisozygoptera and are probably direct descendants thereof. The Agrioninæ of Selys have usually been looked on as descendants of Calopterygid(or -gine)-like forms.⁵⁵ The position of the nodus in Calopteryginæ and in Agrioninæ, respectively, has been stated as follows:

"The position of the nodus varies in both the Calopteryginæ and the Agrioninæ, but in general it is farther from the base of the wing in the former than in the latter. Among the first-named it is probably nearest the base (one-third the wing-length) in *Amphipteryx* and in *Chalcopteryx*,⁵⁶ among the second group it is farthest from the base (more than one-third the wing-length) in *Archilestes*. No Calopteryginæ have the nodus as near to the base as one-fifth the wing-length, but many Agrioninæ have it in that position."⁵⁷

This statement was based on conditions existing in recent forms. Very little is known of fossil Zygoptera of periods earlier than the Eocene⁵⁸ when *Dysagrion* and fragments named *Podagrion abortivum* by Scudder appear. From the Jurassic, Handlirsch lists⁵⁹ *Euphæopsis multinervis* Hagen, in fair preservation, and four possible but indecipherable species of *Pseudoeuphæa*, all considered to be allied to the living *Epallage*, *Euphæa*, etc., i.e., Calopteryginæ of Selys. *Euphæopsis multinervis* had the nodus at .44 of the wing-length. Another fossil of the same age is *Steleopteron deichmülleri* placed by Handlirsch in a separate family Steleopteridæ, which is considered to possess

⁵³ *L.c.*, p. 463, August, 1906.

⁵⁴ *L.c.*, p. 464.

⁵⁵ Calvert, *Trans. Amer. Ent. Soc.*, XX, pp. 211, 212, 1893; Ris, *Zool. Jahrb.*, *Abth. Syst. Geog. Biol. Thiere*, IX, p. 623, 1896.

Cf. Needham, *Genealogic Study*, pp. 742, 748, 750, 1903; Handlirsch, *Foss. Ins.*, p. 472, 1906; Tillyard, *Proc. Linn. Soc. N. S. Wales*, XXXVI, p. 600, 1912; XXXVII, p. 406, 1913.

⁵⁶ In *Chalcopteryx* the nodus is at .37 (front wing) or .39 (hind wing) of the wing-length.

⁵⁷ Calvert, *Ent. Mo. Mag.*, (2), XIII, p. 31, 1902.

⁵⁸ Osborn, *The Age of Mammals*, 1910, p. 42, places the Green River shales in which these genera occur as equivalent to the Upper Ypresian, i.e., Middle Eocene.

⁵⁹ *Fossile Insekten*, pp. 595 et seq.

both Epallagid (Calopterygine) and Agrionine affinities. It had the nodus at only three-tenths of the wing-length.⁶⁰

No Cretaceous Zygoptera are listed by Handlirsch.

No ontogenetic data showing a proximal shifting in position of the nodus in any Zygopteron seem to have been published. If the evidence that may be drawn from the hypothetical descent of Agrioninae (Selys) from Calopteryginae (Selys) be left out of consideration, there yet appears to be good paleontological support, as sketched above, for the statement of Needham⁶¹ that shortening of the subcosta and retraction of the nodus toward the base of the wing is a developmental tendency away from the generalized condition of a long subcosta and a nodus remote from the wing-base. Yet it must be pointed that an upper Liassic fossil is known in which the subcosta ends at only .15 of the wing-length. This is *Protomyrmeleon brunonis* Geinitz, for which Handlirsch has erected the suborder Archi-Zygoptera and which he even suggests⁶² may have been a connecting link between the Protodonata and the Agrionidæ (=Agrioninae Selys). Should such an ancestry for the latter group ever be demonstrated, the retraction of the nodus in living Odonata could not have the same significance, as a sign of specialization, which Needham has given it. The alternative suggestion of Handlirsch, that *Protomyrmeleon* is simply an analogue to the Agrionidæ (Agrioninae Selys) whose descendants have become extinct, seems at present the more probable.

2. *The Number of Antenodal Cross-veins.*—*A priori* one might expect retraction of the nodus to be accompanied by a decrease in the number of antenodal cross-veins. No such proportional reduction exists, however. The two Calopterygine genera cited on p. 246 *anted* as having the most retracted nodus in that whole group, *Chalcopteryx*

⁶⁰ Still another Jurassic (Eichstädt) fossil is the *Agrion eichstättense* of Hagen, listed by Handlirsch as *Malmagrion eichstättense* (*Foss. Ins.*, p. 599). Hagen says of it (*Paleontographica*, X, p. 119, 1862): "Die Flügel sind 21 mm. lang, sehr schmal . . . Der Nodus liegt 6 mm. von der Basis. Das Geader ist nicht deutlich." His lithographic figure 5, Taf. XIV, agrees with these proportions.

Meunier (*Ann. Soc. Ent. France*, LXV, pl. 3, 1896) has given a figure labelled "Agrion? eichstättense Hagen type." It is photographic and represents an insect lying in the same position as that of Hagen's figure and of the same natural size. From Meunier's figure the position of the nodus cannot be recognized. In his text Meunier says, p. 131, "*Agrion eichstättense* Hagen. No. 150. Type de cet auteur. *Paleontographica*, t. x, p. 118 à 119, pl. XIV; Cassel, 1862." I cannot understand his expression a few lines farther in the same paragraph: "Cette échantillon a beaucoup d'analogie avec celui de Hagen."

⁶¹ *Genealogic Study*, p. 730.

⁶² *Foss. Ins.*, p. 472.

and *Amphipteryx*, have respectively 23–26 (front wing), 21–23 (hind wing), and 7–10 (front wing), 7–8 (hind wing) antenodals. The paleontological evidence (with the exception of *Protomyrmeleon*, which has but one antenodal), including *Steleopteron*, is favorable to the view that reduction in the number of antenodals is a more recent acquisition. The preceding paper by Mr. Campion⁶³ discusses in a suggestive way the apparent evidence for such reduction afforded by recent Agrioninæ.

3. *The Number of Postnodal Cross-veins*.—Prof. Needham has concluded⁶⁴ that one of the developmental tendencies of the Odonata is: “Antenodal and postnodal cross-veins becoming reduced in number, stronger, more regular, sometimes matched in position or differentiated among themselves.” In the Zygoptera this tendency is more evident in the antenodals than in the postnodals, the latter never becoming so few, absolutely, or relatively to the antenodals, as in certain Anisoptera, e.g., *Pachydiplax* (front wing: antenodals 6, postnodals 6) or *Miathyria simplex* (front wing: antenodals 7, postnodals 5).

In the Protodonata, owing to the great extension of the subcosta toward the apex of the wing, although there was no nodus, the potential postnodals were less numerous than the actual antenodals, assuming that the nodus of the Odonata developed at, or but little proximad to, the apex of the subcosta. With retraction of the nodus a greater number of postnodals in the costal space became possible. Numerous cases of subsequent reduction in the number doubtless occurred independently of each other, but the paleontological data are not sufficiently abundant to demonstrate progressive reduction in any one line of descent, however likely this may appear from the standpoint of mechanical advantage or of economy of vein-forming material.

4. *The Pterostigma*.—The stigma is an Odonate feature not possessed by the Protodonata. In those Anisozygoptera, which are considered by Handlirsch⁶⁵ to be ancestral to the Calopterygidae, viz., the Tarsophlebiidæ, the stigma was fairly oblique and in one species at least braced at its proximal end.⁶⁶

In *Euphæopsis*, of the Jurassic, the stigma is not oblique; in

⁶³ The Antenodal Reticulation of the Wings of Agrionine Dragonflies. This volume of these PROCEEDINGS, *antea*, pp. 220–224.

⁶⁴ *Genealogic Study*, p. 730.

⁶⁵ *Foss. Ins.*, p. 468.

⁶⁶ *Tarsophlebia eximia* of the Jurassic; Handlirsch, *l.c.*, Taf. XLVII, fig. 1.

Steleopteron, also of the same age, its proximal edge is not as oblique as in *Tarsophlebia eximia* and unbraced while its distal edge is more oblique. So far as one may judge from Handlirsch's figures⁶⁷ of Liassic Odonata the stigma was not oblique, or but moderately so, and unbraced; the forms in which it is preserved, however, seem to have but little relationship to the insects discussed in this paper. The paleontological evidence, therefore, furnishes little encouragement to use the stigma as a means of determining relationships.⁶⁸ It is important to notice, however, from the accompanying Table I, that the position of the stigma in the wing varies but little in different genera and species, so that it constitutes a relatively fixed landmark.

9, 11. *The Points of Separation of M_2 from M_1 and of R_s from M_{1+2} .*—Prof. Needham has noted⁶⁹ a minor line of development within the Agrioninæ, "in which nodus and quadrangle become more and more approximate, and the veins M_2 , R_s , and M_3 migrate separately along vein M_1 from their accustomed places toward the stigma." This migration may be real or apparent. Retraction of the nodus with no change in position of the separation point of M_2 would result in a greater interval between nodus and M_2 and hence an apparent movement of the latter toward the stigma, but no real movement in respect to the wing as a whole. (Compare Table I, *Thaumato-neura*, *Rhipidolestes* and *Paraphlebia zoe* ♂.)

Real migration is where the separation-point of M_2 is transferred distad considered in relation to the total wing-length, and may or may not be accompanied by a change in the position of the nodus. (Compare Table I, *Perilestes* and *Dysagrion*, and *Perilestes*, *Argiolestes icteromelas* ♀ and *Melanagrion*.) These remarks will also apply to characters 11 (the separation-point of R_s , including its bridge where it exists, from M_{1+2}), 14 (the separation-point of M_3 from M_{1+2}), 15a (the number of cross-veins proximal to the level of the subnodus between M_3 and M_4) and 17a (the number of antenodal cells between M_4 and Cu_1). In the preceding pp. 228–244, the statements for these characters have been made with reference, not to the wing-length, but to certain more or less varying landmarks, as the arculus, nodus, or stigma; this course has been in conformity with the established custom of descriptive writers.

⁶⁷ *L.c.*, Taf. XLII.

⁶⁸ Cf. Needham, *Genealogic Study*, pp. 710 at top and 730 at bottom.

⁶⁹ *L.c.*, p. 749.

TABLE I.

*Positions of Certain Wing-details in Decimal Parts of Wing-length for
Certain Odonata.*

The measurements have been made from a single wing only in each species (front wing in living species).

GENUS AND SPECIES. (Recent, except where otherwise marked.)	Nodus. (1) ⁷⁰	Proximal costal angle of Stigma. (4)	Separation-point of M ₂ from M ₁ . (9)	Separation-point of R _s from M ₁ +2. (11)	Arculus. (13)	Separation-point of M ₃ from M ₁ +2. (14)	Distal anterior angle of quadrilateral. (16)	Separation-point of A from hind margin. (21)
<i>Protomyrmeleon brunonis</i> (Lias).....	.15	.88	.48	.21	(None)	.71.53		
<i>Tarsophlebia eximia</i> (Jurassic).....	.45	.87	.47	.38	.14	.33	.15	
<i>Euphaeopsis multinervis</i> (Jurassic).....	.44	.83	.45	.3	.08	.15	.13	.02
<i>Steleopteron deichmülleri</i> (Jurassic).....	.30	.88	.40	.25	.10	.23	.15	.16
<i>Dysagrion packardii</i> (Eocene).....	.39	.87	.46	.39	.15	.30	.17	.07
<i>Phenacolestes mirandus</i> (Miocene) spmn. No. 3.....	.33	.83	.52	.35	.13	.29	.18	.10
<i>Phenacolestes mirandus</i> (Miocene) spmn. No. 5.....	.34	.84	.49	.34	.14	.26	.20	.11
<i>Thaumato-neura inopinata</i> ♂.....	.18	.90	.51	.20	.08	.17	.12	.06
“ <i>pellucida</i> ♂.....	.18	.88	.51	.19	.08	.16	.12	.06
<i>Melanagrion umbratum</i> (Miocene).....	.29	.83	.48	.29	.16	.25	.27	.15
<i>Rhipidolestes aculeata</i> ♂.....	.29	.93	.51	.29	.18	.25	.22	.20
<i>Argiolestes icteromelas</i> ♂.....	.30	.89	.57	.31	.17	.28	.22	.18
“ “ ♀.....	.28	.89	.55	.32	.16	.28	.21	.18
<i>Allopodagrion nebulosum</i> ♂.....	.29	.90	.53	.31	.18	.27	.21	.16
<i>Lithagrion hyalinum</i> (Miocene).....	.34	.88	.50	.34	.20	.28	.24	.23
<i>Philogenia carrillica</i> ♂.....	.23	.91	.43	.26	.16	.23	.20	.18
“ “ ♀.....	.24	.90	.47	.26	.16	.24	.21	.20
“ <i>terraba</i> ♂.....	.25	.91	.44	.26	.16	.23	.20	.19
<i>Paraphlebia zoe</i> ♂.....	.19	.93	.51	.24	.12	.20	.19	.17
“ “ ♀.....	.19	.95	.54	.23	.13	.20	.19	.18
“ <i>abrogata</i> ♂.....	.20	.92	.55	.24	.14	.22	.22	.21
<i>Dimeragrion percubitale</i> ♂.....	.25	.81	.46	.28	.16	.25	.19	.18
<i>Heteragrion tricellulare</i> ♂.....	.23	.91	.50	.38	.16	.25	.20	.15
<i>Perilestes fragilis?</i> ♂.....	.28	.88	.66	.49	.21	.36	.25	.72
Summary:								
Maximum.....	.45	.95	.66	.49	.21	.36	.27	.23
Minimum.....	.15	.81	.40	.19	.08	.15	.12	.02
Range.....	.30	.14	.26	.30	.13	.21	.15	.21

⁷⁰ The number in parenthesis at the top of each vertical column is that under which that character has been treated throughout this paper.

⁷¹ In *Protomyrmeleon brunonis* M₃ separates from R_s.

⁷² A not developed as a vein separate from the hind margin.

The paleontological evidence with reference to the separation-points of M_2 , R_s and M_3 is that the Liassic fossils (with the exception of *Protomyrmeleon*) had M_2 separating at the subnodus, and R_s (including its bridge) and M_3 proximad to the nodus;⁷³ none of these fossils which have the nodal region preserved are considered by Handlirsch to be ancestral to Zygoptera, however. For many of the Jurassic remains⁷⁴ the same statement as to the positions of these separation-points holds true, including *Tarsophlebia eximia* and *Euphaeopsis multinervis*; *Steleopteron* had R_s and M_3 arising well proximad to the nodus, M_2 only a short distance distad to the nodus; *Palaeophlebia synlestoides*, which Brauer, Redtenbacher and Ganglbauer assigned to the legion Podagrion of Selys⁷⁵ but which Handlirsch regards as an Anisozygopter of doubtful position,⁷⁶ is imperfectly preserved, but seems to have had the origins of both R_s and M_2 distinctly distal to the nodus, while that of M_3 was probably proximal to the nodus. *Paleophlebia* came from the Dogger, or lower Jurassic, of Siberia, and is therefore older than the other Jurassic fossils just referred to, all of which are Malm or Upper Jura. The paleontological evidence is consequently not altogether satisfactory and at least admits of the possibility of the separation-points of these three veins having fluctuated proximad or distad from time to time. Prof. Needham's statement as to their migration, quoted above, has not that evidence from other sources than comparative morphology which is necessary to enable us to use these characters with perfect confidence.

13. *The position of the arculus* has been relatively stable, so that there is little reason for attaching any special phylogenetic value to it.

14. *The Point of Separation of M_3 from M_{1+2} .*—(See the discussion above under Nos. 9, 11.)

15a. *The Number of Cross-veins, Proximal to the Level of the Subnodus, between M_3 and M_4 .*—This character is closely dependent on No. 14, for the more proximal is the separation-point of M_3 from M_{1+2} , the greater is the area available for these cross-veins. In the genera here compared the greatest number of cross-veins, two, is found in *Phenacolestes*, *Lithagrion*, and *Melanagrion*, all of which have a more proximal origin of M_3 . The reverse case is not necessarily true, as *Philogenia*, *Allopodagrion*, and *Dysagrion*, with an equally proximal

⁷³ Handlirsch, *Foss. Ins.*, Taf. XLII.

⁷⁴ *L.c.*, Taf. XLVII.

⁷⁵ *Mem. Acad. Imp. Sci. St. Petersb.*, (7), XXXVI, p. 6, 1889.

⁷⁶ *Foss. Ins.*, p. 584.

origin of M_3 (see Table I), have but one such cross-vein. *Tarsophlebia eximia* had five in its hind wing (these veins are not preserved in the front wing) and *Steleopteron* had two.

16. *The Obliquity of the Quadrilateral*.—The shape of the quadrilateral becomes more oblique with the greater divergence of its proximal and distal sides. Prof. Needham has assumed⁷⁷ that a nearly rectangular quadrilateral, in which opposite sides are parallel to each other, is the more primitive form and that from it at least two kinds of oblique quadrilaterals have arisen. There seems to be no published ontogenetic evidence in favor of this view and the only paleontological evidence not contradicting it is limited to that puzzling Liassic form, *Protomyrmeleon*, in which, if Handlirsch's interpretation of the venation be correct,⁷⁸ R and M are still distinct from the base distad, and there is no trace of a beginning arculus.

On the other hand, all the Jurassic fossils, which are not clearly Anisoptera, show an *oblique* quadrilateral with its posterior distal angle acute.⁷⁹ This holds true not only for those fossils referred by Handlirsch to the Zygoptera like *Euphæopsis* and *Steleopteron*, or for forms regarded by him as ancestral to Zygoptera, as *Tarsophlebia* (and including a Liassic fragment, *T. westwoodi*⁸⁰), but also for other Anisozygoptera not apparently forefathers of the Zygoptera, as *Stenophlebia*, *Isophlebia*, and *Anisophlebia*. *Dysagrion* of the Eocene had an oblique quadrilateral, and in fact not one of the published descriptions and figures of Tertiary Zygoptera listed by Handlirsch⁸¹ shows a rectangular quadrilateral; all have it oblique.

It therefore seems necessary to regard the oblique quadrilateral as the more primitive and the rectangular as a later appearance.

⁷⁷ *Genealogic Study*, p. 717, fig. 11, p. 731. See also Williamson, 1913, p. 259, and figs. 1 and 2 on p. 260.

⁷⁸ *Foss. Ins.*, Taf. XLII, fig. 14.

⁷⁹ *L.c.*, Taf. XLVII. Hagen, indeed (*Paleontographica*, X, Taf. VIII, f. 8), shows the quadrilateral of the Jurassic *Euphæa longiventris* as rectangular. In his description, p. 123, he says, "Noch undeutlicher ist der übrige Theil des Geäders . . . das Viereck ist gleichfalls undeutlich," and he gives no details of its shape. Meunier's photographic reproductions (*Arch. Mus. Teyler*, 2, VI, pl. XXVI, figs. 81, 82, cf. p. 127), not of Hagen's type, but of other specimens in the Munich Museum, show the shape of the quadrilateral as indecipherable. Handlirsch (*Fossil Ins.*, p. 580) places *Euphæa longiventris* Hagen as a synonym of *Tarsophlebia eximia* Hagen and remarks, "Bezüglich Hagens *Euphæa longiventris* [longiventris] habe ich zu bemerken, dass der von ihm t. 13 f. 8 abgebildete Flügel allerdings von jenem der *Tarsophlebia* wesentlich abweicht. Aus der Beschreibung ergibt sich jedoch, dass die basale Partie des Flügels an dem Fossile kaum zu entziffern ist, so dass wir diese Reconstruction als werthlos betrachten können."

⁸⁰ *Foss. Ins.*, Taf. XLII, fig. 6.

⁸¹ *L.c.*, pp. 896-899, 1357.

17a. *The Number of Antenodal Cells between M_4 and Cu_1 .*—This character is in general dependent on the degree of retraction of the nodus, as the more the nodus approaches the base of the wing the smaller is the area available for these cells. This correlation, although not absolute and exact in the genera here compared, holds in a rough way. We may therefore regard reduction in the number of antenodal cells as a specialization. There appear to have been 12 on the front wing, 13 on the hind wing of *Tarsophlebia eximia* (counting only a single row—there are two rows in part of this area), almost three in *Steleopteron*. A reduction in the number of antenodal cells may occur independently of retraction of the nodus, however, by the greater development of the quadrilateral distad. (Compare Table I, *Thaumatooneura* and *Paraphlebia*, also pp. 233, 237 *anted.*)

18. *The Number of Cubito-anal Cross-veins.*—These veins are usually small and weak in the Zygoptera, and they have not been preserved well in the fossils, so that few data on their development in point of geologic time are available. Perhaps the same kind of evidence which Mr. Champion has secured⁸² for the reduction of the antenodals might be obtained for these cross-veins also. It is conceivable that the ancestral Zygopteron might have had a moderate number and that some of its descendants might have acquired more, others fewer. While recognizing the paucity of evidence, I am inclined to view reduction in their number as specialization, in harmony with the reduction of antenodals.

21. *Petiolation of the Wing.*—When the anal vein (A) separates from the hind margin of the wing at some distance from the base, a stalk-like appearance of the wing-base is produced, especially on the hind margin, to which the term “pétiolée” was long ago applied by de Selys. Petiolation involves a reduction of the anal area and is specifically mentioned by Prof. Needham⁸³ as a fundamental developmental tendency in the Agrionidæ (= Agrioninæ Selys). It is not visible in *Protomyrmeleon* (Lias); in *Tarsophlebia*, *Stenophlebia*, *Isophlebia*, or *Anisophlebia* (Jura). It seems to have been well-marked in *Steleopteron*, while the shape of the wing-outline certainly suggests it in *Euphæopsis*, although here A may have remained distinct from the hind margin.⁸⁴ It seems justifiable to assume that the farther distad petiolation has progressed, the more specialized the insect.

⁸² These PROCEEDINGS, p. 223, *anted.*

⁸³ *Genealogic Study*, p. 748. Cf. Ris, 1912, p. 45; Tillyard, 1913, p. 444.

⁸⁴ Handlirsch, *Foss. Ins.*, Taf. XLVII.

22. *The Number of Anal Cross-veins*.—Progressive petiolation reduces the area available for anal cross-veins, but not always to the extent one might expect. Thus of American genera discussed in this paper which have the petiolation extending distad to the arculus, *Paraphlebia* has 2, *Philogenia* 0, *Dimeragrion* 1 or 0, *Lithagrion* 0 anal cross-veins. Calopteryginae (Selys) have on the whole more anal cross-veins than do the Agrioninae Selys. If the latter are descendants of some of the former and if *Tarsophlebia* stands in an ancestral position to the Zygoptera, then we may consider reduction in number of the anal cross-veins as a specialization. *Protomyrmeleon*, *Tarsophlebia*, *Isophlebia*, and *Anisophlebia* each had not less than four anal cross-veins, some of them many more. In *Euphæopsis* they are not preserved, in *Steleopteron* they appear to have been present only distad to the level of the outer (distal) end of the quadrilateral.

B. The characters included under group B on p. 245, *antèd*, are Nos. 7, 8, 10, 12, 15*b*, 17*b*, 19, and 20. In the comparisons made in the early pages of this paper, these characters have been stated in terms of numbers of rows of cells found between the branches of the great veins. They may be stated also by specifying the number of interposed, or supplementary, sectors in each area, and have usually been so stated in the taxonomic literature. It is easy to translate one method of statement into the other, as one row of cells implies no supplementary sector, two rows of cells one supplementary sector, three rows two sectors, etc. The individual variation to which they are subject increases as the hind margin of the wing is approached.

The Protodonate wing of the Carboniferous and the Permian was richly veined with many supplementary sectors. So also were the Odonate wings of the Lias, excepting *Protomyrmeleon*; if Handlirsch's interpretation of its venation be correct,⁸⁵ there was but one row of cells between each of the branches of the main veins, except between R_s and M_3 (two rows increasing to three), M_3 and M_4 (two rows), M_4 and Cu_1 (two rows), and posterior to A (two rows).

Turning to the Odonata of the Jura,⁸⁶ we find richly veined wings in the Anisozygoptera (*Tarsophlebia*, *Stenophlebia*, *Isophlebia*, *Anisophlebia*), and in *Euphæopsis*; *Steleopteron* has one row of cells between M_1 and M_{1a} , M_{1a} and M_2 , M_2 and R_s , M_3 and M_4 , and between the veins posterior to Cu_1 , three rows between R_s and M_3 , two rows between M_4 and Cu_1 .

⁸⁵ *Foss. Ins.*, Taf. XLII, fig. 14.

⁸⁶ Handlirsch, *Foss. Ins.*, Taf. XLVII.

If Handlirsch be correct in his conjecture⁸⁷ that the Protodonata have descended from such genera of the Dictyoneuridæ (Palæodictyoptera) as *Stenodictya*, the dense venation of the former evolved from the equally dense, but more irregular, network of the latter. The Odonata then carried reduction in the network to a greater degree than in the Protodonata and reduction in the rows of cells of the areas now under discussion would, therefore, be a specialization. We must then recognize that as early as the Lias such reduction was carried in *Protomyrmeleon* to a greater degree than is shown by many living genera and a similar statement must be made for *Steleopteron* of the Jura. That any of these reduced venations were capable of giving rise to more exuberantly veined descendants would be denied by many phylogenists, but the actual proof of such a denial is not at hand for the Odonata. We have, therefore, only the general tendency to guide us when we assume that reduction in density of venation in the characters of group B means specialization. On the other hand, we must suppose that such richly veined forms of the present day as *Thaumatoneura*, *Calopteryx*, *Thore*, and *Neurothemis* have either preserved the dense venation of, perhaps Mesozoic, ancestors or that they have acquired their density by hypertrophy in the course of generations.⁸⁸ Here, as elsewhere in this discussion, the possibility of further light from ontogenetic studies is very evident.

Summarizing the results of this discussion, we conclude that later phylogenetic status is denoted by the following conditions in the characters of the genera compared in this paper:

1. Retraction of the nodus toward the wing-base.
2. Reduction in the number of antenodals.
- (3. Reduction in the number of postnodals.)
- (7. Reduction in the number of rows of cells between M_1 and M_{1a} .)
- (8. Reduction in the number of rows of cells between M_{1a} and M_2 .)
9. More distal position of origin of M_2 .
- (10. Reduction in the number of rows of cells between M_2 and R_s .)
11. More distal position of origin of R_s .
- (12. Reduction in the number of rows of cells between R_s and M_3 .)
14. More distal position of origin of M_3 .
- 15a. Reduction in number of cross-veins proximal to the subnodus between M_3 and M_4 .

⁸⁷ *L.c.*, p. 305.

⁸⁸ The latter alternative is apparently that held by Dr. Ris for the analogous cases of *Pantala* and *Tramea*. 1912, p. 46.

- (15*b*. Reduction in the number of rows of cells between M_3 and M_4 .)
- 16. Rectangular quadrilateral.
- 17*a*. Reduction in the number of antenodal cells between M_4 and Cu_1 .
- (17*b*. Reduction in the number of rows of cells between M_4 and Cu_1 .)
- (18. Reduction in the number of cubito-anal cross-veins.)
- (19. Reduction in the number of rows of cells between Cu_1 and Cu_2 .)
- (20. Reduction in the number of rows of cells posterior to Cu_2 .)
- 21. More distal petiolation of the wing.
- (22. Reduction in the number of anal cross-veins.)

I have endeavored to indicate that the paleontological evidence is not as strong for some of these statements, by enclosing them in parentheses, as for those left unenclosed. There is no ontogenetic evidence as yet.

These conclusions and the data on which they are based merely permit us to determine the probable course, or direction, of change in certain features of the venation. They do not enable us to decide as to the relative order in which the different features changed, whether, for example in the ancestors of living Podagrionine genera, M_3 assumed a position at or distad to the subnodus at an earlier, or at a later, period than the reduction of the number of rows of cells in the area posterior to Cu_2 occurred, although, given a character, we can say which genera should come first and which should follow in our phylogenetic list in respect to the modifications of that character. In the imperfection of our knowledge, we are largely guided, therefore, by motives of convenience in selecting the primary characters on which a classification of the members of this group is to be based. Having regard to all these considerations, the following scheme for a phylogenetic grouping of the genera of Selys' legion Podagrion is presented.

SYNOPSIS OF VENATIONAL CHARACTERS OF GENERA OF THE LEGION PODAGRION.

Legion Podagrion Selys 1862.

M_3 separating from M_{1+2} nearer to the nodus than to the arculus. Pterostigma normal, *i.e.*, consisting of but a single cell. Cu_2 present. Supplementary sectors present, at least between M_{1a} and M_2 , except in *Perilestes*.

A.— M_3 separating from M_{1+2} proximad to the subnodus, at six-tenths or more of the distance from arculus to subnodus (half-way in *Rhipidolestes*).

- B.—Antenodals more than two on all the wings, or on the hind wings only (*Neuragrion*). (See also the parenthesis following rubric BB.)
- C.—Area posterior to Cu₂ with three or more rows of cells, A separating from the hind margin proximad to the level of the arculus, R_s beginning at the subnodus.
- D.—Quadrilateral oblique at distal end.
- E.—Supplementary sectors between M₄ and Cu₁ absent; between M_{1a} and M₂ five, between R_s and M₃ eight rows of cells, respectively.....*Dysagrion* Scudder, 1878 (Eocene, Wyoming).
- EE.—Supplementary sectors between M₄ and Cu₁ three or four; between M_{1a} and M₂ three, between R_s and M₃ three rows of cells respectively.....
Phenacolestes Cockerell, 1906 (Miocene, Colorado).
- DD.—Quadrilateral almost rectangular at both proximal and distal ends; many supplementary sectors from M₁ to hind margin.....
Thaumatoneura M'Lachlan, 1897 (Central America).
- CC.—Area posterior to Cu₂ with only one row of cells, A separating from hind margin at or distad to the level of the arculus.
- F.—R_s beginning at subnodus, supplementary sectors from M_{1a} to M₄, two or more cubito-anal cross-veins.....
Neurolestes Selys, 1882 (West Africa).
- FF.—R_s beginning distad to the subnodus, supplementary sectors from M_{1a} to M₃, one cubito-anal cross-vein.....
Neuragrion Karsch, 1891 (Ecuador).
- BB.—Antenodals two only (more than two have been noted in occasional specimens of *Podopteryx*, a genus included under this rubric).
- G.—R_s beginning proximad to the subnodus.
- H.—Area posterior to Cu₂ with two rows of cells, A separating from the hind margin proximad to the level of the arculus, supplementary sectors from M_{1a} to M₄.....
Melanagrion Cockerell, 1907 (Miocene, Colorado).
- HH.—Area posterior to Cu₂ with one row of cells, A separating from hind margin distad to the level of the arculus, supplementary sectors from M_{1a} to Cu₂.....
Rhipidolestes Ris, 1912 (Formosa).
- GG.—R_s beginning at the subnodus.
- J.—Area posterior to Cu₂ with 4–5 rows of cells, A separating from the hind margin at or distad to the level of the arculus, supplementary sectors from M_{1a} to Cu₁.....
Podopteryx Selys, 1871 (Aru, Queensland).
- JJ.—Area posterior to Cu₂ with 2 rows of cells, otherwise as in *Podopteryx*.....
Argiolestes Selys, 1862, sens. strict.⁸⁹ (Australian region).

⁸⁹ As here limited includes only the groups 1C and 2 of Selys' Revision of 1886, p. 81. See the remarks of Martin on the variability of the points of departure of M₃ and R_s in *Argiolestes*, *Boll. Soc. Ent. Ital.*, lx, p. 201, 1909.

- JJJ.—Area posterior to Cu_2 with one row of cells.
- K.—Old World Genera.⁹⁰
- L.—A separating from the hind margin proximad to the level of the arculus (some *Podolestes* fall here—see below under OO).
- M.—Supplementary sectors from M_1 to M_3 and between M_4 and Cu_2 , none between M_3 and M_4
Rhinagrion nom. n. for *Amphilestes* Selys, 1862⁹¹ (Malaysia).
- MM.—Supplementary sectors (two each) from M_{1a} to R_s , one between M_3 and M_4
Mesopodagrion McLachlan, 1896 (Thibet, West China).
- LL.—A separating from the hind margin distad to the level of the arculus.
- N.—Quadrilateral with its anterior side more than half as long as its posterior side, Cu_1 only slightly arched forward on leaving the quadrilateral.
- O.—Arculus distinctly distal to the second antenodal, supplementary sectors (two each) from M_{1a} to M_4*Nesolestes* Selys, 1891 (Madagascar).
- OO.—Arculus at, or but slightly distal to, the second antenodal, supplementary sectors (one or two each) from M_{1a} to M_4
Podolestes Selys, 1862 (Labuan, Sumatra).
- NN.—Quadrilateral with its anterior side half, or less than half, as long as the posterior side; Cu_1 strongly arched forward on leaving the quadrilateral, supplementary sectors (one each) from M_1 or M_{1a} to R_s or M_3
Synlestes Selys, 1869 (Australia).
- KK.—New World Genera.
- P.—A separating from the hind margin proximad to the level of the arculus, supplementary sectors from M_{1a} to R_s and between M_3 and M_4 .
- Q.—Area M_{1a} to M_2 with three rows of cells, two unbroken supplementary sectors between M_2 and R_s*Megapodagrion* Selys, 1885, sens. strict. (Brazil).
- QQ.—Area M_{1a} to M_2 with two rows of cells, one zigzag supplementary sector between M_2 and R_s*Allopodagrion* Foerster, 1910 (Northern South America).

⁹⁰ Although the first two subdivisions, K and KK, under rubric JJJ are geographical, not structural, for convenience' sake, the structural features under K and KK are sufficiently detailed to enable the identification of a form of unknown habitat to be made.

⁹¹ The name *Amphilestes* Selys is preoccupied by *Amphilestes* Owen (*Encyc. Brit.*, 8th edit., XVII, p. 157, 1859) for a fossil mammal. *Rhinagrion* is suggested by de Selys' emphasis of one of the characters of his *Amphilestes* as "Tête robuste, à épistome saillant."

- PP.—A separating from the hind margin distad to the level of the arculus.
- R.—Nodus more nearly at one-third of the wing-length, no supplementary sectors between R_s and M_3*Lithagrion* Scudder, 1882 (Miocene, Colorado).
- RR.—Nodus more nearly at one-fourth of the wing-length, at least two supplementary sectors between R_s and M_3 . (Supplementary sectors from M_{1a} to M_4 or Cu_1).....*Philogenia* Selys, 1862, except *P. terraba* Calv. (Costa Rica to Brazil).
- GGG.— R_s beginning distad to the subnodus, A separating from the hind margin distad to the level of the arculus.
- S.—Area posterior to Cu_2 with usually two or more rows of cells, supplementary sectors from M_1 to Cu_2 or to hind margin, two cubito-anal cross-veins, the second under the quadrilateral.....*Paraphlebia hyalina* Brauer, 1871 (Mexico).
- SS.—Area posterior to Cu_2 with one row of cells, no supplementary sectors posterior to M_4 .
- T.—Supplementary sectors from M_{1a} to M_4 , one cubito-anal cross-vein.
- U.—Antenodal cells between M_4 and Cu_1 two or three (otherwise as above under RR).....*Philogenia terraba*⁹² Calvert, 1907 (Costa Rica).
- UU.—Antenodal cells between M_4 and Cu_1 one; quadrilateral very long, reaching to the level of the nodus.....*Allolestes* Selys, 1869 (Seychelles).
- TT.—Supplementary sectors from M_{1a} to M_3 (often none between M_2 and R_s), usually more than one cubito-anal cross-vein.....*Dimeragrion* new genus (Guiana).⁹³
- TTT.—Supplementary sectors between M_2 and R_s and (two long ones) between R_s and M_3 , one cubito-anal cross-vein.....*Heteropodagrion* Selys, 1885 (Ecuador).

⁹² In spite of the fact that *Philogenia terraba* falls here, instead of under RR with the rest of the genus *Philogenia*, the only difference which separates it is the slight one of the more distal position of the separation-point of R_s from M_1+2 , and I think this does not entitle *terraba* to a different generic name.

⁹³ The genus *Neuragrion* Karsch was described from a single female and has been placed under rubric FF above. If additional specimens should prove to have only two antenodals, the genus would fall under TT and would differ from *Dimeragrion* presumably, at least, in possessing only one cubito-anal cross-vein.

- TTTT.—Supplementary sector one between M_{1a} and M_2 , one cubito-anal cross-vein, quadrilateral not reaching the level of the nodus.....
Protolestes Foerster, 1899 (Madagascar).
- AA.— M_3 separating from M_{1+2} at the subnodus, only two antenodals, R_s beginning distad to subnodus.
- V.—Area posterior to Cu_2 with usually two or more⁹⁴ rows of cells, A separating from the hind margin distad to the level of the arculus.
- W.—Supplementary sectors from M_1 to Cu_2 or to hind margin; two cubito-anal cross-veins, the second under the quadrilateral.....*Paraphlebia* Hagen, 1861 (Mexico, Guatemala).
- WW.—Supplementary sectors from M_{1a} to Cu_1 or to hind margin; one cubito-anal cross-vein.....*Wahnesia* Foerster, 1900 (New Guinea)⁹⁵
- VV.—Area posterior to Cu_2 with one row of cells, one cubito-anal cross-vein.
- X.—Supplementary sectors from M_{1a} to M_4 , A separating from hind margin at or distad to arculus.....*Chlorolestes* Selys, 1862 (South Africa).
- XX.—Supplementary sectors confined to area M_{1a} to M_2 , A separating from hind margin proximad to, at, or distad to, the level of the arculus.....*Heteragrion* Selys, 1862 (Mexico to Argentina).⁹⁶
- AAA.— M_3 separating from M_{1+2} distad to the subnodus, only two antenodals, R_s beginning distad to the subnodus, A separating from the hind margin distad to the level of the arculus (or not developed as separate from the hind margin in *Perilestes*).
- Y.—Area posterior to Cu_2 with two or three rows of cells.
- Z.—Supplementary sectors from M_1 to Cu_2 or to hind margin, other characters as above under W.....*Paraphlebia* (see W).

⁹⁴ Both sexes of *Paraphlebia duodecima* Calv. have only one row of cells posterior to Cu_2 on the hind wings, but two or more rows on the front wings.

⁹⁵ This is group 1B of *Argiolestes* in Selys' Revision of 1886, p. 81.

⁹⁶ In his Synopsis of 1862, p. 31, de Selys suggested the separation of *H. petiolatum* as a separate subgenus under the name of *Oxystigma*, chiefly distinguished from *Heteragrion* by the long quadrilateral reaching almost to the level of the nodus, the pterostigma extremely, pointed proximally and only one antenodal cell (between M_4 and Cu_1), but he did not adopt this suggestion in his Revision of 1886. The name *Oxystigma* does not appear in Kirby's Catalogue.

- ZZ.—Supplementary sectors from M_{1a} to Cu_1
Metagrion n. gen.⁹⁷ (New Guinea).
 YY.—Area posterior to Cu_2 with one row of cells, no supplementary sector posterior to M_3 .
 a.—Quadrilateral not touching the hind margin of the wing, supplementary sectors between M_{1a} and M_2 and between R_s and M_3
Mesagrion Selys, 1885 (Colombia).
 aa.—Quadrilateral touching the hind margin of the wing, no supplementary sectors except a rudiment between M_2 and R_s or between R_s and M_3 , arculus well distal to the second antenodal.....
Perilestes Selys, 1862
 (Costa Rica, Guiana, Brazil).

In view of the observations on the imperfection of our knowledge, made on p. 256, in introducing the preceding Synopsis, it seems useful to offer also this

OUTLINE OF AN ALTERNATIVE GROUPING OF THE GENERA OF THE
 LEGION PODAGRION.

- A.—Area posterior to Cu_2 with more than one row of cells.
 B.—A separating from the hind margin proximad to the level of the arculus, M_3 separating from M_{1+2} proximad to the subnodus.
 C.— R_s beginning proximad to the subnodus, two antenodals, supplementary sectors M_{1a} to M_4 , two rows of cells posterior to Cu_2*Melanagrion*.
 CC.— R_s beginning at the subnodus, more than two antenodals.....*Dysagrion*, *Phenacolestes*, *Thaumatoneura*.
 BB.—A separating from the hind margin at, or distad to, the level of the arculus, normally two antenodals.
 D.— M_3 separating from M_{1+2} proximad to the subnodus.
 E.— R_s beginning at the subnodus.....*Podopteryx*, *Argiolestes*.
 EE.— R_s beginning distad to the subnodus.....
Paraphlebia hyalina.
 DD.— M_3 separating from M_{1+2} at, or distad to, the level of the subnodus.....*Paraphlebia*, *Wahnesia*, *Metagrion*.
 AA.—Area posterior to Cu_2 with only one row of cells.
 F.—A separating from the hind margin proximad to the level of the arculus.

⁹⁷ Type: *Argiolestes postnodalis* Selys. This genus is group 1A of Selys' Revision of 1886, p. 81.

- G.— M_3 separating from M_{1+2} proximad to the subnodus, R_s at the subnodus.....
Rhinagrion, *Mesopodagrion*, *Megapodagrion*,
Allopodagrion, *Podolestes*.
- GG.— M_3 separating from M_{1+2} at the subnodus, R_s distad to the subnodus.....*Heteragrion*.
- FF.—A separating from the hind margin at, or distad to, the level of the arculus (or not developed as a vein distinct from the hind margin in *Perilestes*).
- H.— M_3 separating from M_{1+2} proximad to the subnodus.
- J.— R_s beginning proximad to subnodus.....
Rhipidolestes.
- JJ.— R_s beginning at the subnodus.....
Neurolestes (3 antenodals), *Lithagrion*,
Philogenia, *Nesolestes*, *Podolestes*, *Synlestes*.
- JJJ.— R_s beginning distad to the subnodus.....
Neuragrion (3 antenodals on hind wings),
Philogenia terraba, *Allolestes*, *Dimeragrion*,
Heteropodagrion, *Protolestes*.
- HH.— M_3 separating from M_{1+2} at the subnodus.....
Chlorolestes, *Heteragrion*.
- HHH.— M_3 separating from M_{1+2} distad to the subnodus.....*Mesagrion*, *Perilestes*.

The preceding Synopsis, pp. 256–261, will enable one using this Alternative Grouping to distinguish from each other the genera listed under each final rubric.

A comparison of Synopsis and Alternative Grouping will show that, in spite of a number of differences in the order in which the genera appear in the two schemes, both begin with and both end with nearly the same forms, which may therefore be regarded as, respectively, the oldest and the youngest members, phylogenetically, of the legion Podagrion.

THE RELATIONSHIPS OF PHENACOLESTES.

If the conclusions reached on pp. 255–256 be correct,

Dysagrion of the Eocene of Wyoming, the oldest member of the legion Podagrion now known, cannot have been an ancestor of any of the three known Miocene genera from Colorado, *Phenacolestes*, *Lithagrion*, and *Melanagrion*, because it lacked supplementary sectors between M_4 and Cu_1 . *Melanagrion* indeed possesses one more primitive feature than is found in any of the other three of these extinct genera, viz., R_s begins proximad to the subnodus.

Phenacolestes has preserved more primitive characters than has

its contemporary *Lithagrion*, as may be seen by a comparison of those numbered 2, (4?), 12, 15*b*, 17*a* and *b*, 19, 20, 21*a* and *b*, and 22, on pp. 227 and 232, *anted*.

Phenacolestes is more primitive than its contemporary *Melanagrion* in characters Nos. 1, 2, 12, 15*b*, 17*a* and *b*, 19, 20, 21*b* and 22, but less primitive in characters Nos. 3, (4?), and 11. See pp. 227 and 231, *anted*.

Phenacolestes may have been the ancestor of the New World genera *Megapodagrion*, *Allopodagrion*, and *Perilestes* and of the African *Chlorolestes*, unless it shall be shown that the less oblique pterostigma possessed by all four of these living genera cannot have been acquired from the form which existed in *Phenacolestes*. Of these four, *Megapodagrion* is most like *Phenacolestes*. But *Megapodagrion* and the other three genera may equally well have descended from *Melanagrion*, with which they agree more closely in the shape of the pterostigma, although *Melanagrion* is figured as having no anal cross-veins, a not very weighty objection in this connection.

Phenacolestes might be considered ancestral to *Heteropodagrion* and *Heteragrion*, were it not that these two have, in at least some species, a greater number of postnodals.

Phenacolestes was apparently not the ancestor of:

Neuragrion, which has more postnodals, and the cubito-anal cross-vein in a different position, *i.e.*, proximal to the level of the first antenodal;

Mesagrion, for the second reason just given for *Neuragrion*;

Thaumatoneura, *Paraphlebia*, or *Dimeragrion*, which have more than one cubito-anal cross-vein and denser venation in the wing generally (*Thaumatoneura*), or between Cu_1 and Cu_2 (*Paraphlebia*), or as shown in the greater numbers of postnodals (all three);

Philogenia, which has more postnodals and rather denser venation between M_{1a} and M_2 ;

Rhipidolestes, which has M_3 separating from M_{1+2} more proximad, R_s beginning proximad to subnodus, and more postnodals;

Podopteryx, which has a denser venation between M_3 and M_4 and posterior to Cu_2 , and more postnodals;

Argiolestes, which has a denser venation between M_3 and M_4 .

Comparisons with genera of the Old World having more reduced venations are useless, as the equally possible descent from other extinct genera than *Phenacolestes* arises again.

Whether *Megapodagrion* and its near ally *Allopodagrion* are to be looked on as descendants of *Phenacolestes* or of *Melanagrion*,

it is of interest to point out that they are not in their present geographical distribution the nearest Podagrionine genera to Colorado, as none of their species are known from a more northern locality than Colombia ("Bogota"). In the intervening territory are found *Thaumatoneura*, *Paraphlebia*, *Philogenia*, *Heteragrion*, and *Perilestes*, and of these four genera the most northern known representatives are *Paraphlebia zoe* and *hyalina* and *Heteragrion chrysops* of the State of Vera Cruz, Mexico.⁹⁸

Professor Cockerell has suggested in correspondence that although the genera allied to *Phenacolestes* are now Neotropical, they are of northern origin or had northern ancestors. Considering how widespread are the living genera of the legion Podagrion, it seems inconceivable that their forerunners in the Miocene did not inhabit many other regions than Colorado. The fact that we know them only from Florissant seems to the writer very negative and insufficient evidence on which to found a conjecture as to the place of origin of this group.

ON THE SUBFAMILY DYSAGRIONINÆ COCKERELL.

Preceding his original description of *Phenacolestes mirandus*, Professor Cockerell proposes a new subfamily of Agrionidæ (*sensu strictiori*), under the name Dysagrioninæ, which he defines as follows.⁹⁹

"Antenodals 2.....Subfamily Agrioninæ.
Antenodals 4 or more.....Subfamily Dysagrioninæ."

The number of antenodals is hardly a character of sufficient importance by itself to establish a subfamily, owing to its variability, and at least three genera come between Professor Cockerell's two divisions. Thus in *Thaumatoneura* M'Lachn., the number of antenodals varies from 3 to 5, and *Neurolestes* Selys of Africa and *Neuragrion* Karsch of Ecuador have *three* antenodals.¹⁰⁰ It is not without bearing on the present topic that all three of these living genera, as well as *Phenacolestes*, are of Selys' legion Podagrion, but if any new taxonomic arrangement, whether of "subfamilies" or of "legions," is to be made, the distinctive characters must be formulated in some other terms than those which Professor Cockerell has employed. The tenability of the subfamily Dysagrioninæ has also been discussed

⁹⁸ Calvert, *Biol. Centr. Amer. Neur.*, pp. 60, 61, 64, 1901.

⁹⁹ *Bull. Amer. Mus. Nat. Hist.*, XXIV, p. 60.

¹⁰⁰ Cf. Calvert, *Ent. Mo. Mag.*, XXXVIII [2-XIII], pp. 29-32, 1902, where also the characters of the Agrioninæ are discussed.

by Mr. Campion in his preceding paper on "The Antenodal Reticulation of the wings of Agrionine Dragonflies."¹⁰¹

ADDITIONAL DATA ON DIMERAGRION N. GEN.

In addition to the venational characters which have been given on pp. 238-239, *antèd*, the following are generic features from other parts of the body:

Second antennal joint one and one-half times as long as the first, the third longer than the first two together.

Ligula (median labial lobe) bilobed in its distal third, apices tapering but not very acute, separated by an interval whose width is about equal to its depth.

Tibial spines longer (often 2-3 times longer) than the intervals separating them, 7-8 in the anterior (outer) row, and 8-9 in the posterior (inner) row of the third tibia.

The generic name proposed is in allusion to the fact that there are two supplementary sectors only in two areas of the wing, viz., those between M_{1a} and M_2 and between R_s and M_3 .

Type, Dimeragrion percubitale n. sp.

Dimeragrion percubitale n. sp. Pl. XIV, figs. 6-8.

Adult ♂.—Vertex, genæ, and rear of the head black with some metallic green reflection not very brilliant. A yellowish streak between each antenna and the lateral ocellus of the same side. Traces of pruinosity on the rear of the head. Frons, nasus, and upper half of rhinarium dark metallic violet, well-defined from the black above and the pale yellow below, which latter forms a transverse band on the lower half of the rhinarium and basal half of the labrum, this band having almost parallel edges. Distal half of the labrum and the mandibles dark metallic violet. Submentum, mentum, and bases of the maxillæ luteous, the distal parts of these two pairs of appendages blackish. Antennæ black.

Prothorax black with a slight metallic green reflection.

Mesepisterna and mesepimera metallic green, lower part (more than half) of the former and the third fourth (counting from above) of the latter pruinose, or the latter without pruinosity. Metepisternum metallic green or metallic violet, a narrow pale (luteous?) stripe separating this color from that of the mesepimeron, or this pale stripe absent (still older males). Metepimeron and metasternum pale brown or luteous, some pruinosity on the latter.

¹⁰¹ These PROCEEDINGS, *antèd*, pp. 220-224.

Legs blackish, some pruinosity on coxæ, trochanters, and femora.

Wings uncolored, the venation described on p. 238. Stigma dark brown, surmounting 2+ to 4 cells, its proximal side very oblique, so that one or more postnodals are placed between it and the costa, and at least twice as long as the distal side. The relative lengths of the four sides of the stigma, beginning with the longest, are: posterior, proximal, anterior, distal. No brace-vein, *i.e.*, no thickened cross-vein in prolongation caudad of the proximal side.

Dorsum of abdominal segments 1 and 2 dark metallic green, of 3-10 black, except that in the middle of 3-5 or 6 the black is replaced by ill-defined dark brown. Sides of 1 and 2, a transverse basal ring on 3, sides inferiorly of 3-7, pale brown or luteous. The dorsal black of 3-6 is continued ventrad at the posterior ends of these segments, forming a transverse apical band on each. A transverse basal yellow ring on 4-7. Intersegmental articulations of 7-10 luteous, otherwise 8-10 are wholly black, 9 being also pruinose on the dorsum. Pruinose traces are also visible on the intersegmental articulation of 1-2 and on the sides and sternites of most of the segments. Hind margin of 10 entire.

Superior appendages longer than 10, a little shorter than 9, black, partly pruinose. Viewed in profile, the axis of each appendage is parallel to that of the abdomen, but the superior margin is strongly declined in the proximal fourth, less so in the remaining three-fourths; the inferior margin in the distal three-fourths of the appendage is produced ventrad into a strongly convex lamella which terminates at the blunt apex of the appendage; this lamella reaches its maximum at one-half to two-thirds of the appendage-length. On the dorsal surface of the appendage at the extreme base is a short transverse ridge, which in profile view appears as a tooth. In dorsal view, each superior appendage shows its superior margin as almost straight and decreasing in width throughout the proximal three-fourths, while the distal fourth is strongly curved toward its fellow of the opposite side; the ventral lamella is inclined inward and downward (*mesad* and *ventrad*), the short transverse basal ridge is at the *mesal* margin.

Inferior appendages about seven-eighths as long as the superiors, black. Each one, in profile view, conical, tapering more rapidly on the superior margin beyond two-fifths its length, so that at this point this margin shows an angle; distal third curved strongly upward (*dorsad*) and terminating in a slender very acute apex. In ventral view, each appendage is applied against its fellow for the proximal three-fifths of its length, beyond which it is continued along the outer

(ectal) edge as a blunt cylindrical process one-half to one-third as wide as the proximal part of the appendage; the abrupt contraction from the proximal part to the distal process is made by a right-angled "shoulder."

I have not been able to detect any differences either in these appendages or in the genitalia of the second abdominal segment of the males from the four different localities.

Young ♂.—Differs from the adult ♂ in the absence of pruinosity, in the paler hue of the yellow areas generally, in having pale yellow where the adult has luteous; metallic violet on the head paler, bases of the mandibles and a spot between each one and the adjacent eye yellow, metallic violet or metallic brown instead of metallic green on the thorax, an indistinct narrow yellowish stripe on each side of the mid-dorsal thoracic carina, a bright yellow line on the humeral suture, coxæ and trochanters pale yellow, pterostigma paler brown with a pale luteous line just within each bounding vein, dorsum of abdominal segments 1 and 2 metallic blue, of 3-7 dark brown, darker at the hind end of each where it is continued ventrad as in the adult, most of the ventral surfaces of 7-10 pale yellow, except at the hind ends of 7 and 8 which are blackish, proximal half of the inferior appendages yellowish ventrally.

♀. Differs from the adult ♂ as follows: Dark color on the nasus, rhinarium and labrum shining black instead of metallic violet. Sides of the first two (confluent with the transverse yellow band below), bases of the mandibles and an oblique band running from each eye upward (dorsad) and inward (mesad) on to the anterior surface of the frons to a variable distance (not correlated with amount of pruinosity on body), bright yellow. A narrow stripe on the humeral suture, a wider stripe on the first lateral suture and on the metepisternum bordering the second suture, yellowish. Pruinosity on the thorax in slight quantity on the sterna and metapleuron, or on the sterna only. Coxæ and trochanters yellow. Pterostigma as described for the young male, pruinose on the under surface. No pruinosity (or but a trace of it) on the dorsal side of abdominal segment 9, but present in slight traces on the sides inferiorly of 1-8 and in somewhat greater amount on the sternites of 1-8. Hind margin of 10 with a narrow mid-dorsal notch about one-fourth as deep as the length of the segment, from which runs a low median carina to the anterior end of the segment; ventral surface of this segment pale brown. Abdominal appendages about twice as long as segment 10, not as long as segment 9, straight, slender, tapering to an acute apex, black.

Genital valves (=external gonapophyses of 9) reaching almost, but not quite, to the level of the hind end of 10, brownish, ventral margin spinulose, the palps slender, reaching beyond the level of the hind end of 10, but not of that of the anal tubercle (=11), darker in color.

Of the two females from Tumatumari, one lacks all pruinosity on the body and the pterostigmata, the other has a small quantity on the rear of the head only; they appear to be the most immature of their sex in the present material.

Dimensions.—Abdomen ♂ 26.5–34, ♀ 24.5–25.5; hind wing ♂ 21.5–25, ♀ 20–22.5 mm.

Habitat.—British Guiana: Wismar, January 30 and 31, three males, three females; Rockstone, February 1, six males, one female; Tumatumari, February 5, one male, February 7, one female, February 11, one male, one female; Potoro Landing, February 10, three males. Collectors, L. A. and E. B. Williamson and B. J. Rainey, 1912.

Type.—A male from Wismar, January 30, abdomen 30.5, hind wing 22.5 mm. long, in the collection of Mr. E. B. Williamson, of Bluffton, Ind. The other material in the collections of Mr. Williamson and of the author.

Habits.—The Tumatumari female of February 11, the youngest of her sex of the present material bears this label by Mr. E. B. Williamson: "taken at top of trail 2½ mile past Tiger Creek trail on twig." A male from Potoro Landing, the smallest of his sex in all the present lot has this note by the same collector: "On ends of twigs wings expanded usually in shade."

Mr. Williamson has kindly furnished the following notes with reference to the habits: "At Wismar back from the river, across the railroad tracks and south of the eminence on which stands the manager's (Mr. Croombie's) house, is a brushy swampy woods, traversed by numerous small streams which head in small ravines with abrupt and rocky ends or pockets. These streams at the season I was there were small and frequently disappeared and hence were followed with some difficulty in their upper course. All were short and were intermingled in the lower (east) end of the woods where the ground was swampy and the footing treacherous. The Agrionines were found usually near the upper ends of the streams below the rocky pockets.

"At Rockstone the railroad track was followed back toward Wismar where two or three streams, small at this season, cross the track at intervals, flowing in a northerly direction. These streams were

followed in the direction of their flow till each was lost in the woods and it was impossible to trace its course further.

"The habits of the Agrionines at both locations (Wismar and Rockstone) were identical. They rested on the extreme tips of dead twigs, usually two or three feet from the ground, with outspread wings and rigidly horizontal bodies. The color and the position assumed gave the impression of alertness and self-reliance. The flight was swift, and because of light-conditions also, was difficult to follow. At rest they were fairly conspicuous. When one flew at my approach I stood still and began examining the possible destinations in the direction of its flight, and thus located it."

Variations.—The smallest males are from Potoro Landing, followed in order by those from Tumatumari, Wismar and Rockstone. The order of the females by size from the smallest is not the same, owing perhaps to there being but a single specimen of this sex from Rockstone, viz.: Tumatumari, Rockstone, Wismar.

The most remarkable variation in this species is in the number of cubito-anal cross-veins, which varies from 1 to 4 on the front wings and from 1 to 5 on the hind. Of the twenty specimens studied only three (all males) have the same number on all four wings, and of these three two have 2 cubito-anal cross-veins and the third three. Two other specimens (females) agree with each other in the number and arrangement of these veins on their four wings, leaving fifteen out of the twenty no two of which are exactly alike in this feature when all four wings are considered. The remarkable nature of this variation will be appreciated when it is recalled that in the great majority of the Agrioninæ of de Selys there is but a single cubito-anal cross-vein on each wing. The conditions found in the present material are summarized in the following

TABLE II.

Showing the Number of Wings of Twenty Individuals of Dimeragrion percubitale having the Specified Numbers of Cubito-anal Cross-veins.

(The numbers in parentheses are those of the wings in which the most proximal of these cross-veins is situated proximad to the level of the first antenodal.)

Right front wing.	Left front wing.	Right hind wing.	Left hind wing.
1 with 1 cu-a c-v	3 with 1 cu-a c-v	2 with 1 cu-a c-v	0 with 1 cu-a c-v
13 (1) " 2 " "	11 (1) " 2 " "	10 " 2 " "	8 " 2 " "
5 (1) " 3 " "	5 (4) " 3 " "	6 " 3 " "	8 (3) " 3 " "
1 " 4 " "	1 (1) " 4 " "	2 (1) " 4 " "	3 (2) " 4 " "
			1 (1) " 5 " "
20 (2)	20 (6)	20 (1)	20 (6)

It is rather curious, although at present insignificant, that the abnormality of having a cubito-anal cross-vein situated *proximal* to the level of the first antenodal should be more frequent on the left side in both the front and the hind wings.

The specific name proposed, *percubitale*, is in allusion to the unusual numbers of cubito-anal cross-veins.

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EXPLANATION OF PLATE XIV.

Figs. 1-5.—*Phenacolestes mirandus* Cockerell. Florissant, Colorado. From photographs. These are the specimens described *antea*, pp. 225-230.

Fig. 6.—*Dimeragrion percubitale* n. gen., n. sp. Wings of male, Rockstone, British Guiana, February 1, 1912. (From photograph by H. A. Walters.)

Figs. 7, 8.—*D. percubitale*, apex of abdomen of male type, Wismar, British Guiana, January 30, 1912. 7, dorsal view; 8, right side profile view. Camera drawings, Zeiss oc. 2, objective A with lower lens off. Scale alongside fig. 7 is that of one millimeter in tenths, for figures 7 and 8 only.



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