

[From the Proceedings of the Linnean Society of New South Wales,  
1911, Vol. xxxvi., Part 2, July 26th.]

---

ON THE GENUS *CORDULEPHYA*.

By R. J. TILLYARD, M.A., F.E.S.

(Plates xi.-xii.)

The genus *Cordulephya* was first proposed and defined by de Selys in his "Synopsis des Cordulines," 1871,\* for the reception of the interesting little Australian species, *C. pygmaea* Selys. In that work he describes the male type only, from Melbourne. But, in his "Additions au Synopsis des Cordulines," 1874,† the same author adds a very short description of what is evidently a very immature female, in the British Museum, also from Melbourne.

Later on, Mr. Billingham discovered this insect in considerable numbers on the Goulburn River, at Alexandra, Vic., and sent a number to Europe. In 1905, when I began to study the Australian *Odonata*, this was one of the first insects which I took, the locality being Otford, Illawarra district, N.S.W. It appeared to be very rare there. But in 1907, very late in the season (April and May), I found it in great numbers at Lily Vale, only two miles from where I first took it. In the following years, I traced it to other localities, extending its range to the foot of the Blue Mountains, and also obtaining the larva and studying its life-history.

In January, 1910, while collecting at Medlow, Blue Mountains, I noticed several specimens of what I took to be this same insect. As I had a large series, I did not trouble to secure any, until it occurred to me that it was very peculiar that, at so great an elevation, it should be out on the wing in January, whilst lower

down along the coast it did not even begin to appear until late in February. I, therefore, secured a pair for comparison with my series of *C. pygmaea*. I was greatly surprised to find that these were a very distinct, though closely allied, species. So far, I have been unable to secure further specimens of the imago, but during a visit to Medlow, in November, 1910, I obtained two nearly full-fed larvæ. I have, therefore, practically complete material for a paper on this most interesting aberrant genus.

In this paper, I propose to follow the lines of my "Monograph of the genus *Synthemis*"\* in giving, besides full descriptions and life-histories of the two species concerned, a discussion of the position occupied by the genus in the subfamily *Cordulinae*, and an attempt to solve the difficult problem of placing it in its correct position in a linear classification. As with *Synthemis*, so with *Cordulephya*, it will be found that a knowledge of the life-history is an indispensable part of the data on which any conclusion should be based. Even if, as will be seen to be in some measure the case in this paper, the larval form does not fit in with our preconceived notions and expectations—derived from the study of wing-venation only—we must accept the facts as they are, and try still to solve the problem which our knowledge has only rendered more difficult.

As a careful comparison of the two species of the genus will throw a good deal of light on the question of classification, I propose to give descriptions and life-histories first. So that the comparison may be made more easily, I will place the descriptions side by side in tabular form.

#### Genus *CORDULEPHYA* de Selys.

The characters of the genus, as given by de Selys, are partly based on variable venational characters, and, therefore, need enlargement, not only to include the new species, which is essentially congeneric with the type *C. pygmaea*, but also to admit

\* Bull. Acad. Belgique. xxxi., 1871, p.315.

† *Ibid.* xxxvii., 1874, p.22.

\* These Proceedings, 1910, xxxv., p.312.

variations of the type-species itself. The locality (Melbourne) of the types is unfortunately at the extreme southern end of the range of the species. Hence the measurements given by de Selys disclose the fact that practically every other specimen from more northern localities is considerably larger than the type-specimens. More than this, variations in venational characters, used to define the genus, are not only due to difference in locality, but are an essential characteristic of the species; so that a long series, *taken from any given locality*, can be arranged to show a gradation from one extreme to the other. The chief variation lies in the form of the triangle of both wings. De Selys defines them as follows:— "Le triangle discoidal des ailes supérieures irrégulier, le côté supérieur brisé, ce côté formant un angle obtus dirigé vers la côte;" and, as he says nothing about the hindwing-triangle, it is, of course, to be assumed that the definition "regular" applies to it in this as in all other genera of the subfamily. An examination of a long series of *C. pygmaea*, however, discloses the fact that a *regular* triangle in the hindwing is rather the exception than the rule. In the majority of specimens, the superior (costal) side of this triangle is *distinctly broken* near the distal angle (Plate xii., figs. 3 and 4), and, in a few specimens, the break is even more than one-third of the whole length of the side from the distal angle. Another variable character is the position of the arculus-sectors at their base. De Selys defines them in the words (for the hindwing only) "l'arcus dont les secteurs naissent séparés." This is scarcely the case. In the forewing they are frequently *just separated*, and as frequently *just joined*. In the hindwing, however, they are usually *just joined*, and, in some specimens, *joined for a perceptible distance*. This may be clearly seen in the photograph of the wings given in Martin's "Cordulines,"\* though he does not comment upon it. [It should be here noted that the drawing of the wings of *C. pygmaea*, given by Needham in his "Critical Notes on the Classification of the

\* Coll. Zool. du baron Edm. de Selys-Longchamps, Fasc. xvii., *Cordulines*, Bruxelles, 1906.

*Cordulinae*,"\* and stated to be "after Martin," is entirely erroneous and misleading, both as regards the *complete* fusion of the arculus-sectors, and the position of the "break" in the costal side of the forewing-triangle. Such conditions as are shewn in this drawing do not, I venture to state, exist in a single specimen of *C. pygmaea* in any collection.]

In considering the new species, which I propose to name *Cordulephya montana*, we find a further modification necessary. De Selys says "Membranule nulle" for *C. pygmaea*. But, in *C. montana*, there is a small but quite clearly defined membranule. I, therefore, offer the following amended description of the genus. Basilar, median, and hypertrigonal spaces free. All triangles free, followed by a single row of post-trigonal cells for at least part of the discoidal area. Costal side of all triangles variable; that of forewings *always* broken, usually close to distal angle; that of hindwings sometimes complete, but more usually broken very close to distal angle. Sectors of arculus variable at their base, usually either *just separated* or *just joined*. Basal side of triangle of hindwings placed distally from arculus. Membranule small or obsolete. Anal border of hindwing of male not excavated, oblique, nearly straight, without a cross-nervule across the anal triangle; forming a very obtuse angle with the posterior margin of the wing. Female with no ovipositor. *Hindwing of both sexes very narrow at base, possessing a small and exceedingly reduced "anal loop" of from 2-4 cells only, with outer margin not strongly developed.*

The addition of the characters in italics is essential. They are, in my opinion, the most important of all for distinguishing this genus from all others in the subfamily.

Type of genus, *C. pygmaea* Selys.

The following is a detailed description of the two known species, arranged in tabular form to facilitate comparison. The description of *C. pygmaea* is taken from my own series, which accounts for the measurements being larger than those given by de Selys:—

\* Ann. Ent. Soc. America, i., No. 4, Dec., 1908.



## Head:—

<i>Vertex</i> .....	small, tubercled, metallic purplish-black.
<i>Antennae</i> .....	short, black.
<i>Front</i> .....	depressed medially, hairy, dark metallic purplish.
<i>Clypeus</i> .....	shining black, a narrow yellow band on anteclypeus.
<i>Labrum</i> .....	black.
<i>Labium</i> .....	yellow.

same as in *C. pygmaea*.

## Thorax:—

<i>Prothorax</i> .....	small, downy, blackish.
<i>Meso- and metathorax</i>	hairy above; black, with steely reflections on basal half; a fine yellow line along dorsal ridge; interalar ridge yellowish; a pair of orange-yellow antehumeral stripes placed well forward, rather broad and short, 2mm. long by 1mm. broad. Sides steely black with a broad lateral band of orange-yellow, and a yellow area close to abdomen, under hindwing-base. Scuta and scutella yellowish.

same as in *C. pygmaea*.generally similar to that of *C. pygmaea*, but with the antehumeral stripes less distinct, longer and narrower, and perceptibly curved inwards.*Legs* .....

long and slender; anterior tibia of male with a long narrow lamella underneath, and with an irregular armature of long and short spines (Plate xii., fig. 45); ditto of female without lamella, and with more regular armature. Colour black, coxæ and bases of profemora brown

as in *C. pygmaea*, but foreleg *much longer* in all its parts.

## Abdomen of Male:—

<i>Shape</i> .....	♂. long and narrow, 1-2 and 7-10 slightly enlarged.
<i>Auricles</i> .....	distinct, almost hooked (interior side concave); yellow with a touch of black at tips, which are rounded.
<i>Genitalia of 2</i> .....	deeply recessed within a large oval depression, the borders of which carry long grey hairs, most abundant at apical end. Seen in profile, the raised border completely hides the genitalia.
<i>Colouration</i> .....	orange-yellow and black as follows:— 1, yellow. 2-7, basal part yellow, apical part black, the two colours separated by a very straight transverse line, placed in 2-3 half-way, 4 slightly before half-way, 5-6 about one-third from base, 7 not quite half-way; in 3-7 the base of the preceding segment just overlaps the suture, so as to form a narrow black basal band continuous in colour. 8, black, with two basal yellow spots conjoined dorsally. 9-10 quite black.

♂. not so long for size of insect, slightly stouter, 1-2 and 7-10 somewhat more enlarged.

not so much hooked, interior side almost straight, tips slightly pointed inwards; yellow.

similar, but not so deeply recessed; the borders are slightly less raised, so that in the profile view a small part of the genitalia is seen protruding.

orange-yellow and black as follows:— 1, yellow shaded with brown. 2, basal half yellow, apical half black with a yellow central portion. 3, considerably over one-half from base yellow, rest black. 4, basal half yellow, rest black. 5, basal one-third yellow, rest black. 6, basal one-third yellow, rest black, but the division between the colours not distinct, the black encroaching on the yellow dorsally. 7, yellow for nearly two-thirds from base, rest black. 3-7 with the divisions between the colours neither so straight nor distinct as in *C. pygmaea*; black of previous segment slightly overlapping each suture. 8-10 as in *C. pygmaea*.

*Appendages* .....

*Superior* 1.5 mm., black, slightly hairy, nearly parallel, subcylindrical; tips bluntly pointed, usually converging slightly; a small dorsal spine at base, a more conspicuous tooth or projection beneath, about one-third from base.

*Inferior* 1.2 mm., black, fairly broad upcurved, slightly hollow above, tip squarely truncated; a flat hairy tubercle on 10 beneath.

(Plate xii., figs. 7, 8, 13).

**Abdomen of Female:***Shape* .....

stouter than in ♂, cylindrical.

*Colouration* .....

1-6 as in male, but in 6 the colour-division is not distinct. 7, with a basal yellow band encroaching dorsally on the black of next segment. 8, black, with two small basal yellow spots. 9-10, quite black.

*Genitalia* .....

No projecting ovipositor; underside of 8 not overlapping 9; marginal folds of 9 narrow, leaving the whole segment open and concave.

*Appendages* .....

0.6 mm., straight, black, downy, tips rounded, separated by a double rounded tubercle on 10 below and between them. (Plate xii., fig. 11).

**Types:—**

♂. Coll. MacLachlan.

♀. British Museum.

*Superior* 1.8 mm., black, hairy, converging, thicker near base than towards tips, which are slender, touching, and slightly upcurved; a small dorsal spine near bases and two small projections beneath, about one-third from base.

*Inferior* 1.1 mm., black, broad at base, hollow above, narrowing to tip, which is rounded and upcurved; a conspicuous double hairy tubercle on 10 beneath.

(Plate xii., figs. 9, 10, 14).

same as in *C. pygmaea*.

1-6 as in male. 7, basal half yellow, rest black. 8-10 quite black.

No projecting ovipositor; underside of 8 not overlapping 9; 9 with basal third only concave and uncovered, rest enclosed by a somewhat trifid fold.

0.8 mm., straight, black, hairy, tips well rounded; a large rather elongated tubercle projecting above and between them, and below it two smaller rounded tubercles, on 10. (Plate xii., fig. 12).

♂♀. (unique). Coll. Tillyard.

*Hab.*—*C. pygmaea* ranges from Melbourne up to the central coast of New South Wales. In Victoria it has been taken well inland at Alexandra, but in New South Wales all the recorded localities are within fifty miles of the coast. The following is a list of the localities:—Melbourne (♂♀ types), Alexandra (numerous examples taken by Mr. Billingham), Illawarra district, N.S.W., (Oxford, Lily Vale, Heathcote, a large number taken by myself), Sydney District, N.S.W., (Duck Creek, Auburn, fairly common), Nepean River and tributaries (Glenbrook, Menangle), Ourimbah (common). It emerges at the end of February, is most abundant during March and April, and may be taken right through May and June.

The only known locality for *C. montana* at present is Medlow, Blue Mountains, N.S.W., where I took the type-male and female on January 19th, 1910. From the appearance of the specimens, I should say that they had been on the wing considerably over a month (the border of the wing of the ♂ is slightly torn in one or two places). The fact that larvæ found on November 5th, 1910, were practically full-fed, leads me to give the middle or end of November as the probable date of emergence of this species. It probably does not continue on the wing beyond February.

*Life-History of C. pygmaea.*

On any warm still day in March or April, the female may be seen ovipositing in her favourite haunts. These are the little grass-fringed bays and corners that occur occasionally along the creeks in the hilly country round Sydney. The oviposition is carried out as follows. Suddenly, from the top of some bush or tree where she has been resting, the female will dart down to the water, and, in a most hurried and restless manner, begin to wash out the eggs, in large clusters, from the open vulva of segment 8, which is quite unprovided with any projecting ovipositor. This is done by continual wavings up and down of the abdomen, each downward stroke bringing it in contact with the water. During the whole time the flight of the female is so bewildering that it is difficult to follow, and so rapid is their motion that I have often seen the body of the insect poised with the wings practically

invisible. A swaying and almost pendulous-like motion backwards and forwards is kept up at the same time, so that the movements of the insect are almost impossible to follow. The only way to capture the female at such a time is to knock it, if possible into the water, and draw it into the bank with the net.

After ovipositing in this manner for a few minutes, visiting perhaps from fifty to one hundred yards of the borders of the stream, the female will suddenly rise with great swiftness, and disappear as quickly as it came.

A female, which I was fortunate enough to capture at Lily Vale, in May, 1907, immediately exuded an enormous cluster of eggs into a glass phial filled with water. There must have been nearly a hundred in the one mass, and she continued to exude large masses every few minutes. So that it seems that one of these females must, at a moderate estimate, lay several thousand eggs. These eggs are exceedingly interesting, for they are the only *Odonate* eggs known to me which possess a sculpture or surface-markings. Under a lens, they are seen to be irregularly pitted all over with shallow oval depressions, giving the whole egg a mottled appearance (Plate xi, fig. 6). Their colour is orange-brown; length 0.3, breadth 0.2 mm.; in shape a prolate spheroid. They are fastened together in a glutinous mass; each egg carries at one pole a small stem, and at the other a large gelatinous cap, as shown in the plate.

I kept some of these eggs in a Petri-dish for three weeks, during which time they gradually darkened in colour, becoming a deep brown. The eyes of the young larva could clearly be perceived, and they were evidently within a few days of hatching, when I lost them all from an attack of fungus.

Partly grown larvæ can be found from September to December, but the end of January and beginning of February are the best times to secure the full-fed nymph. At that time the only other *Odonate* nymphs which have not emerged are those of *Caliaeschna conspersa*, and the second brood of *Diplacodes hæmatodes*. These three inhabit different parts of the creek-bed; so that it seems that the larva of *Cordulephya* has been forced to accommodate itself to a very late period of emergence in order to escape the

rapacity of the large *Aeschnid* nymphs, which are common along the creek-borders earlier in the season, I have found that, in this respect, the larva of *Aeschna brevistyla* is the most to be feared, as it often frequents old sticks and trash on the creek-beds, and will even attack such large nymphs as those of *Hemicordulia tan* and *H. australis*.

The full-grown nymph of *Cordulephya pygmaea* is, in outward appearance, very similar to the nymph of *Hemicordulia australis*, though not so large. It is remarkable in possessing a labium unlike that of any known larva, and one which shews, in a very peculiar manner, both *Corduline* and *Libelluline* development. The following is a full description.

*Total length*, 14 mm.; *head*, 2 by 4 mm. wide; *thorax* 4 mm. wide; *abdomen* 5 mm. wide at broadest part (segment 6). *Legs* (measurements for femur, tibia, and tarsus respectively) fore, 3.5, 3, 1.7 mm.; middle, 4.3, 4, 1.9 mm.; hind, 5, 4.2, 2.1 mm. (these measurements coincide almost exactly with those for the imago).

*Head*: triangular in front, with eyes placed at extreme anterolateral angles; postocular areas fairly well rounded, with a conspicuous tuft of hairs on the outer margin; *ocelli* fairly conspicuous; *antennæ* long, 3 mm., slender, 7-jointed, first two joints shorter and thicker than the other five. *Labium: mentum* 4 mm. wide, narrowing rapidly to 2 mm. at basal joint; *median lobe* forming a very obtuse angle in middle; *mental setæ*, 11 on each side, longest about 1 mm., shortest 0.3 mm. *Lateral lobes* subtriangular, strongly built, outer margin 3 mm., inner margin 2.5 mm.; *lateral setæ*, 8, about 1 mm. long; *terminal hook* slender, 1 mm. *Distal border* with very remarkable indentations. Beginning from the terminal hook, on one lobe (usually the left) there is a small indentation followed by three very deep and narrow clefts, rounded at their bases, and isolating two long and narrow projections or teeth, which are also well rounded at their tips; the remainder of the border carries four much smaller rounded teeth with shallow angulated depressions between them; on the other lobe (usually the right), the first indentation is fairly deep, then follow two very deep indentations or clefts of the same shape as on the left, and next a fourth cleft only slightly deeper

than the first; the rest of the border carries three much smaller rounded teeth similar to those on the left. The margins of all these teeth are very finely crenulated, and at their tips they are furnished with from two to four short spines, of which the one nearest the terminal hook is the least, and the one farthest from it the greatest (when there are four, however, the fourth may be small also). The whole inner surface of the lateral lobes is irregularly spotted with small black warts and dots, and there is a row of tiny hairs along the inner margin. The lack of symmetry in this remarkable labium is, of course, only to be expected, to enable the two lobes in the position of rest to fit into one another [Plate xi., fig.3, outline of lateral lobe; fig.4, underview of head, shewing labium in position of rest, with lateral lobes placed so that the tip of each long tooth just rests in the opening of the opposite depression]. **Th o r a x** well built, with a sharply angulated, transverse, prothoracic ridge; sides of metathorax well rounded. *Wing-cases* 5 mm., reaching to beginning of sixth abdominal segment. *Legs* with a very few fine hairs on tibiae. **A b d o m e n** oval, well rounded above; underside slightly convex, with a longitudinal depression along each side. No dorsal spines. *Lateral spines* as follows—6, a very tiny spine on each side; 7, a fairly large and conspicuous curved spine; 8-9, still larger curved spines, quite 0.5 mm. long; 9 with anal border hollowed to enclose 10, which is very short. *Appendages*: superior short, broadly triangular; two lateral of same length but narrow and rather pointed; involucra of imaginal appendages somewhat shorter, lying between lateral and superior appendages. **C o l o u r** **P a t t e r n**: this varies a great deal, both in intensity and detail, according to the locality, and also in individual specimens. An average nymph may be described as having a dark brown abdomen, beautifully mottled all over with lighter brown; the head, thorax, legs, and wing-cases being light brown, with dark brown markings. The most conspicuous of these are: on the head, a dark transverse band between the eyes; on the legs, short patches of dark shading, three or four on femora and tibiae, two or three on tarsi; on the wing-cases a dark basal patch, a black slanting line on the nodus, followed by a large dark patch. On the

abdomen, the pale colouration consists of a fairly regular dorsal band, pale transverse basal lines on each segment, and a series of slanting semi-oval marks on each side of segments 4-8. For general appearance of this nymph, see Plate xi., fig.1 (*C. montana*), the chief difference being that, in *C. montana* the forelegs are much longer by comparison, for the size of the nymph.

The most beautifully marked nymphs are those which occur in the clear mountain-creeks, such as the creeks at Heathcote and Lily Vale, in the Illawarra district. In the more muddy creeks, such as Duck Creek, Auburn, the pattern of the nymphs is generally much less pronounced.

The habits of this nymph are very similar to those of the nymphs of *Hemicordulia*. It lives on the sandy bottom of the creek, lying hidden in the sheltered corners away from the main current of water. It never burrows nor buries itself in the sand; but relies for capturing its prey on its protective colouration—which suits its habitat remarkably well,—on its long and agile legs, and on its powerful labium. I have fed them on mosquito-larvæ, water-fleas, and small *Agrionid* nymphs, all of which they devour greedily. They can, however, go without food for fairly long periods, though I do not think that they can withstand any degree of drought.

When emerging, the nymph crawls up the bank of the creek, often very steep, or even overhanging, and then ascends the grass or reed-stems near by, often travelling a foot or more up the stem. In the aquarium, they find it very difficult to ascend a single reed-stem, but climb up mosquito-netting quite easily.

The imago, when newly emerged, has a very peculiar colouration, the eyes, pterostigma, and thorax being a kind of livid-grey. This colouration persists for some days, so that one can tell from it whether the insect is immature or not. The immature insects fly away into the bush, generally settling high up on the branches or trunks of trees, with their wings folded. The habits of the mature imago are very peculiar. It seldom flies for long at a time, and may usually be found settled upon a rock in the stream-bed, or on the trunk of a neighbouring tree, with its wings folded close along its back, just like an *Agrionid*. On a warm

day in late summer or early autumn, it is most interesting to watch these insects. At Lily Vale, in April, 1907, they were particularly numerous on the creek. Nearly every rock was tenanted by one or more males, the females being always excessively rare, and practically never seen except when ovipositing. Every few minutes a male would fly up, indulge in a short and very bewildering zig-zag flight, and then settle down on another rock. Often the males would disturb one another, and the two together, flying up, would indulge in the most fantastic evolutions, generally ending in a wild flight away into the trees. It is very seldom that a pair are seen together; I have several times seen a female dash rapidly down from the trees, as if to oviposit, and then be seized rapidly by a male, whereupon they would immediately fly off in the same wild zig-zag manner into the trees. Later in the day, and often throughout the day in late autumn, the males leave the creek, and seek out a sunny tree-trunk in some open glade of the bush. Here they will sit and sun themselves, occasionally making short flights, but always returning to the sunny patch on the tree-trunk. As the shadows lengthen in the afternoon, and the sunny patch gets smaller and moves slowly up the trunk, these insects follow it in the same manner that I have seen butterflies of the genus *Xenica* or *Heteronympha* behave; so that often several will be at rest close together, high up on the trunk. Finally, as the sun gets lower, they fly off one by one, and disappear into the forest.

#### *Life-History of C. montana.*

The few facts that I have been able to observe with regard to this species, shew that, on the whole, the life-history is very similar to that of *C. pygmaea*. The most important difference is that the eggs are laid during January (the type-female was captured while ovipositing), and that the larvæ are full-fed early in November; so that the imago is on the wing in December and January, instead of late in the season. Now this is a very interesting fact, because, on the Blue Mountains, at a high elevation, the local *Aeschnidæ* (of

which *Austroaeschna parvistigma*, var. *multipunctata*, is the commonest) appear *late* in the season, and their larvæ are not more than half-grown by the time that of *C. montana* is full-fed. Hence we have a striking instance of two closely allied species adapting themselves to circumstances, in two opposite ways, which achieve the same end; viz., along the coast, where the commonest *Aeschnid* emerges very early in the season (*Aeschna brevistyla* is on the wing from October to December) we have *C. pygmaea* emerging late; whereas on the mountains, where all\* the *Aeschnidæ* emerge late, we have *C. montana* emerging early. This may seem remarkable, in view of the fact that the mountain-climate is so much colder, and the season so much later. But if we consider the fact that the mountain-*Aeschnidæ* are on the wing right to the end of February, by which time the season for dragonflies is practically over, and the weather getting cold again, we shall see that the early emergence of *C. montana* was absolutely necessary to preserve the species.

I offer, for what it is worth, an interesting theory to account for this discrepancy. It is well known that our commonest species of the *Corduliinæ*, *Hemicordulia tau*, is distinctly double-brooded. They emerge in great numbers from September to November, and then again in February and March, or even April. The second brood, however, is not so constant as the first in point of abundance, being usually less numerous, though occasionally, for some unexplained cause, exceedingly abundant. Now, in the habits of its early stages, *Cordulephya* resembles *Hemicordulia* very closely. Assuming then that there was a time when the former was much more common than it is now, and that it originally occupied, in the Australian *Odonate* fauna, somewhat the same position that *Hemicordulia* does at present,

\* I ought to except *Æ. brevistyla*, which occurs *very sparingly* on the mountains, and is on the wing in December; but it is not at all common there.

we may suppose that the members of the genus were all double-brooded. Both the coastal and mountain-forms then, though they may not at that time have been specifically distinct, were faced with their own most formidable foes in the shape of numerous ravenous *Aeschnid* larvæ. On the coast, the swarms of larvæ of *Aeschna brevistyla* gradually exterminated the *early* brood of *C. pygmaea*, while, on the mountains, the late-developing larvæ of *Austroaeschna parvistigma* destroyed the second brood of *C. montana*. That this one circumstance, in itself, may have played a large part in the differentiation of the two species is very probable.

I find, on referring to my notes on *C. pygmaea*, that this theory is supported by the fact that, in October, 1907, I dredged, from the creek at Lily Vale, several very small larvæ of *C. pygmaea*, which were, however, *fully developed*. I did not know at the time to what species they belonged, but the fact that their wing-cases were so long, *reaching nearly to the end of the abdomen*, struck me as being so peculiar, that I made a note of it. On examining the labium, I determined the larvæ as those of *C. pygmaea*. Now I have never seen the imago out before February. It is not unreasonable, therefore, to suppose that many of the larvæ produced from the late brood, feed up rapidly, and are in a fair way to become a *first* brood for the next season. But here the enemy, the rapacious *Aeschna* larvæ, has to be reckoned with. Those that escape him, must hide away in obscure corners, and probably have to undergo a prolonged fast for many weeks, until the *Aeschna* larva has become full-fed and emerged. Supposing that the ecdyses take place as usual, we should then have the spectacle of a poor, miserably undersized larva, with huge wing-cases,—in fact, just such a one as those I took at Lily Vale. These larvæ most certainly did not emerge until the end of February, for I visited Lily Vale every month up to April, and saw no imagines until the beginning of March. Here also may be

found the explanation of the remarkable difference in size between the larvæ of *C. pygmaea* and *C. montana*, a difference quite unwarranted by the small difference of size in the imagines. For the larva of the latter, having no fear of *Aeschnid* larva, can feed up and develop rapidly, and so attain a much larger size.

The full-fed larva of *C. montana* (Plate xi., fig. 1) differs principally from that of *C. pygmaea* in the following points.

1. The great length of its forelegs. These are fore-shortened in the plate, as the insect sits with the femur and tibia bent up at an acute angle. The actual measurements are: femur, 4.7, tibia 4.8, tarsus 2.5 mm. For the middle leg, the corresponding measurements are 6, 5, 2.5 mm.; and for the hind leg, which is also extremely long, 7, 6, 3.2 mm.

2. In the labium (Plate xi., fig. 2) the dentition of the *right* lateral lobe is similar to that of the *left* in *C. pygmaea*, and *vice versa*. This is not important, however, as I have only examined two larvæ of *C. montana*, and the character may not be constant.

3. In the labium also, there is a peculiar development of *double* mental setæ, which I have not observed elsewhere. In the figure, for example, there are thirteen mental setæ on each side; but, on the right side, two pairs are grouped together so as to touch from their bases upwards. If these had coalesced, we should have had *eleven* setæ, the number found in *C. pygmaea*.

4. The greater size of the larva, whose total length is 17 mm., compared with 14 mm. for *C. pygmaea*, and correspondingly larger in all parts.

#### *Structure of the Larval Gizzard* (Plate xi., fig. 5).

This is essentially of the *Libellulid* type, with four fields shewing bilateral symmetry. A comparison with the gizzard of *Synthemis eustalacta* ("Monograph of the genus *Synthemis*," fig. 2, p. 326) shews two important differences.

1. In the two inner folds, the upper tooth is much larger, sharper and more prominent in *Cordulephyia* than in *Synthemis*.

2. In the two outer folds, the outer lateral edge of the tooth carries only three minor teeth or serrations, whereas in *Synthemis* there are four or five. In this latter respect, the gizzard of *Cordulephyia* differs from those of all other *Libellulidae*, which I have examined. I know of no other gizzard with less than four serrations, and some have as many as six or seven. (The figure in the plate is the gizzard of *C. montana* × 20).

As the form of the gizzard is practically constant throughout the *Libellulidae*, it is clear that these two differences, small as they are, shew that *Cordulephyia* and *Synthemis* are not closely allied,—a conclusion which a comparison of both larva and imago in every detail will manifestly strengthen. On the other hand, the gizzard of *Cordulephyia* resembles that of *Hemicordulia tan* very closely, though the latter, of larger size, possesses four serrations, instead of three, on the lateral edge of the single tooth in the outer fold.

*The Position of Cordulephyia in the Subfamily Corduliinae.*

The four main groups of the subfamily *Corduliinae*, have been already pointed out in two previous papers,\*

GROUP i. EUCORDULINA. *Larva* smooth, with large head and thorax, long legs, labium of *Libelluline* form, *i.e.*, with lateral lobes possessing shallow crenations along outer edge, with surface marked with small warts and dots, and with numerous mental and lateral setæ.

*Imago* usually of strong flight, with robust head and thorax, long legs, usually corduliform abdomen; wing-venation with large triangles and subtriangle (of forewing), usually crossed, complete or practically complete recession of hindwing-triangle, and elongated anal loop, shewing a definite longitudinal bisector.

\* "Monograph of the Genus "*Synthemis*," These Proceedings, 1910, xxxv., p.328.—"Further Notes on some rare Australian *Corduliinae*" These Proceedings, 1911, p.384.

GROUP ii. IDOCORDULINA. *Larva* smooth; with smaller head and thorax, short legs, very flat labium; labium with deep irregular incisions, no warts or dots, and few mental or lateral setæ.

*Imago* usually of weak flight, with smaller head and thorax, short legs, usually slender cylindrical abdomen; wing-venation with smaller free triangles and subtriangle, incomplete recession of hindwing-triangle, fairly short or quite short anal loop, shewing no longitudinal bisector.

GROUP iii. MACROMINA. *Larva* smooth, with nearly circular and very flattened abdomen, very long legs, head with a pyramidal frontal horn; labium with deep dentition of lateral lobes.

*Imago*: large insects of strong flight, and robust development; wing-venation with small triangles far removed from arculus, basilar space free, anal loop broad and compact.

GROUP iv. SYNTHEMINA. *Larva* very villose, with elongate-oval body, short legs, and divergent wing-cases, head square in front, with projecting eyes. *Imago*: insects of weak flight, and slender-build; wing-venation with dense or fairly dense reticulation, basilar space reticulated, hindwing-triangle usually not retracted to level of arculus, anal loop very broad and short, never as long as wide.

The genus *Cordulephyia* is obviously not at all closely related to either the *Macromina* or *Synthemina*. We should, therefore, consider whether it is closely enough allied to either the *Eucordulina* or *Idocordulina* to warrant its inclusion in one of them; or whether, perhaps, it shews a sufficiently independent development to deserve coordinate rank by itself. This is a very difficult problem, as it will be seen that the evidence is in many respects contradictory. It is, however, a problem of deep interest, and brings out some very interesting points in *Odonate* evolution. I propose to consider the evidence in detail afforded by the consideration of (i.) the early stages, (ii.) the form of the imago, (iii.) the wing-venation. (iv.) a comparison of the two known species of the genus.

i. *The early stages*.—A glance at the figure of the nymph of *Cordulephya montana* (Plate xi., fig. 1) will shew us, at once, its remarkable resemblance to the larvæ of the *Eucordulina*-group. In the shape of its head, the build of head and thorax, the general form of the abdomen, the long, spider-like legs, and the mottled colour-pattern, this nymph and that of *C. pygmaea* are exactly like those of *Hemicordulia*. They most closely approach the nymph of *H. australis*, from which they differ only in their slightly smaller size, their remarkable labium, and the absence of small dorsal hooks (the latter is purely a specific character, as it is absent in the larvæ of *H. tau* and *H. superba*). The form of the gizzard, too, is very close to *Hemicordulia*, especially in the relative sizes and shapes of the teeth on the inner folds.

We must now consider separately the remarkable labium of *Cordulephya*, which is, at first sight, so different from that of any known species. If we look at the outer border of the lateral lobe (Plate xi., figs. 2-3), we shall see that, although the upper half is very deeply indented, yet the lower half closely approximates to the form shewn in *Hemicordulia* and allied genera. In fact, if the deep incisions of the upper half were closed up by a wavy line, drawn so as to continue the shallow crenations of the lower half, we should then have a typical labium of the *Eucordulina*-group, with full development of lateral and mental setæ, warts and dots on lateral lobes, and sets of small spines on each shallow crenation. It is interesting to note (Plate xi., fig. 4) that the deep upper incisions are not made so as to fit closely into one another (this would be impossible unless the *whole* outer surface were also deeply incised), but that they lie, in the position of rest, just with their rounded tips resting in the tops of the opposite hollows. It is, I think, evident from fig. 4 that, as the labium is now constituted, the persistence of the deep incisions must be a disadvantage to the nymph, since the smaller prey can slip through the openings left by them. I conclude, therefore, that these deep incisions are an archaic character

which has persisted in *Cordulephya* alone, of all present-day *Libellulidæ*. [As such, they open to our view a most fascinating vista of the development of the *Anisopterid* labium along its two main lines, viz., the *Libellulid* and the *Aeschnid* forms.]

Turning now to the *Idocordulina*, we notice that the larva of *Cordulephya* shews not the slightest resemblance to the larva X, which we have taken as typical of that group. In this larva, the general form (large oval abdomen, very flat; short legs, small head and thorax), and the labial development (a widely and irregularly torn outer edge, no warts or dots, and few setæ), make it almost impossible to believe that *Cordulephya* is a member of this stock.

In its habits, the nymph of *Cordulephya* is altogether *Eucordulian*. A denizen of the secluded corners of streams, living quite uncovered on the sandy bottoms, it is able to move with considerable speed, and possesses a peculiar and fascinating mode of swimming, which may be aptly compared to the first regular strokes taken by a frog after diving,—fore-legs outstretched, and hind-legs taking slow and graceful strokes through the water. In these habits, and in its colour-pattern, it is so exactly similar to the larva of *Hemicordulia australis*, that I have held a few of each in my hand, and have been quite unable to distinguish them, except by looking at the labium.

Altogether, therefore, the evidence of the early stages is *very strongly in favour* of the inclusion of *Cordulephya* in the *Eucordulina*.

ii. *The Form of the Imago*.—Under this heading, I take the study of the imago, *apart from wing-venation*. As might be expected, the evidence, in most respects, reinforces that of the early stages. The robust head and thorax, and the remarkably long legs of the nymph are repeated in the imago, and shew unmistakably the *Eucordulian* connection. In *Cordulephya*, however, we do *not* find the corduliform abdo-

men usually associated with the *Eucordulina*. In this respect, *Cordulephyia* resembles the *Idocordulina*. It should be noted, however, that the abdomen of the larger species, *C. montana*, is not quite so cylindrical as that of *C. pygmaea*; so that the narrowing of the body may be merely concurrent with reduction in size.

iii. *The Wing-Venation*.—A study of the wing-venation of *Cordulephyia* (Plate xii., figs. 1-6) seems to shew not the slightest resemblance to the *Eucordulina*, but, on the other hand, exhibits many close resemblances to the *Idocordulina*. The impression is, of course, mainly gathered from the region of the triangles. Prof. J. B. Needham\* assumes that, in the ancestors of our *Anisoptera*, "fore and hind-wings were originally alike," and holds that *Cordulephyia* is a genus that has perpetuated this zygopterous character. From this basis, he traces the development of the *Corduliinae* by "differentiation of the fore and hind-wings, brought about by a number of minor shifts of parts, and chiefly by the broadening of the hind angle of the hind-wing and the development of an anal loop for its support." Now it is evident, since he takes *Cordulephyia* as an illustration of his primitive wing-type, that he would have us infer, that the fore and hindwings of the ancestors of the present-day *Corduliinae* were alike in being narrow and of a zygopterous character, and that the anal loop was a *cœnogenetic development* in the *Libellulidæ*. Neither the fossil record nor the study of the wings themselves bears this out. The oldest fossils referable to the *Protodonata* are not zygopterous but anisopterous, though, as might have been expected, there is no triangle or other highly specialised part, such as we associate with present-day *Anisoptera*. The essential tendency, which, in our *Zygoptera*, resulted in enormous reduction of the basal areas, and so led to the *petiolate* wing, is not indicated in the earliest fossils.

\* Ann. Ent. Soc. America, i., 4, 1908.

Again, taking the evidence of the wings themselves, the forewings of our *Anisoptera* bear unmistakable evidences of greater reduction than the hindwings, in the greater amount of bending undergone by the triangle, which is evident in the *Corduliinae*, but far more evident in most of the *Libellulinae*; and also in the distinctly *compressed* or slanting arrangement of the cells along or near the posterior margin.

The point I desire to emphasise is, that *all* the characters of our present-day *Anisoptera* were developed out of existing cell-material. Needham himself admits it in everything *except* the anal loop, and he has treated the development of the triangles in a very masterly manner. If his treatment of *Cordulephyia* is correct, we must assume that a remarkable *cœnogenetic* development of a whole host of anal cells in the hind-wing was begun, continued, and perfected during the development of the *Libellulidæ*, bringing about the principal differentiation between fore and hindwings. One has, however, only to look at the clear evidences of *stretching*, in a direction *across* the wing-length, undergone by the anal cells of any exceptionally broad-winged *Libellulid*, to see that the anal loop and the broad hindwing basal area is only a development of cells that were always present there, right back, through the aniso-zygopterid fossils, to the dawn of the order. Further back than that, we have evidence that many of the gigantic fossil insects of the Carboniferous age, which are now generally agreed to be the ancestors of our *Odonata* amongst other orders, possessed forewings that *overlapped* the hindwings. (See the figure of *Titanophasma fayoli* Brogniart in Sharp's "Cambridge Natural History of Insects," p. 276.)

I assume, therefore, contrary to Needham's hypothesis, that a moderately broad basal area of the hindwing was originally present in the older *Anisoptera*, and that in this area there were a large number of unarranged and readjustment, the different kinds of anal loops and supports now

found in the *Aeschnidæ* and *Libellulidæ* took their rise. As it is not the purpose of this paper to deal fully with this question, I will now proceed to consider the development of *Cordulephyia* from this new standpoint.

The *Eucordulian* relationship of *Cordulephyia* being so clearly indicated in its early stages, as well as by some of the imaginal characters, we have to seek an explanation of the remarkable character of the wing-venation, and its apparently *Idocordulian* connection, from the premises above stated. It is, I think, evident that *Cordulephyia*, instead of being, as Needham supposed, an archaic and generalised form, is a highly specialised and reduced form, descended from the same ancestors as the rest of the *Eucordulina*, after that group had become differentiated from the *Idocordulina*. In that case, the resemblance in wing-venation to the *Idocordulina* is purely a resemblance of convergence, brought about by extreme reduction. I give the following reasons in support of this statement:—

A. *The absence of generally recognised archaic characters in the venation.*—Notice particularly the freedom from supernumerary cross-veins, the strong formation of the bridge with no supplementary bridge-crossveins, and the convergence of  $M_4$  and  $Cu_1$  in the forewing; also the arculus-sectors, which shew some tendency towards fusion.

B. *The remarkable flight and habits of the imago.*—These seem to me to point to a high degree of specialisation, brought about by a strenuous fight against adverse conditions.

C. *A comparison of the wing-venation of the two species C. pygmaea and C. montana.*—This is most important. First of all, throughout Australia, wherever mountain-forms are found, they are almost certainly more archaic than the allied coastal forms. The admittedly archaic types, such as *Telephlebia*, *Petalura*, *Austroaeschna*, *Synthemis*, and *Synlestes* are either entirely confined to the mountains, or shew greater specialisation in their coastal representatives. The

explanation of this is simple, though it has not yet been worked out in detail. Along the coast, with its abundant rainfall and favourable conditions for *Odonate* life, the older indigenous *Odonata* of Australia have had to face a continuous invasion of new types. The main army of invaders passed into Australia *via* Torres Straits, and worked down along the Queensland coast into New South Wales, and even to Victoria. Besides these, evidence is accumulating that a smaller number crossed *via* Timor and Port Darwin, thence making eastward to reinforce the main stream of invaders in North Queensland. A few have worked down the North-Western coastline; about these little is known, but their effect on the autochthonous *Odonate* fauna of South-Western Australia has been very small indeed, compared with the effect of the main eastern invasion on those of Eastern Australia. Besides a large number of *Libellulinae* (of which subfamily a very large majority of the recorded Australian species can be shewn to be invaders), we may instance *Anax* and *Hemianax*, *Macromia*, and a number of highly reduced and specialised *Cænagrioninae*.

Now wherever these invaders have come into competition with the older forms, the latter have either succumbed, or have retreated into the mountain-fastnesses, where the conditions are more in their favour, or have remained and competed with the invader; the result being, in the last case, that the invaded, and very often the invader also, have become modified in a direction of greater specialisation, and nearly always by reduction. Many instances of this could be given, but two will suffice. Taking the *Synthemina*, we have the three genera *Synthemis*, *Metathemis*, and *Choristhemis*, of which the first is the least specialised, the other two showing a distinct advance on it. Now, in Western Australia, we have three species of *Synthemis*, none of the other two genera. In Eastern Australia (excluding Tasmania), we have only four species of *Synthemis*, three being confined to the mountains; four species of *Metathemis* found on the

mountains, and one on the coast also, but the mountain-form (*M. guttata*) is smaller than the corresponding coastal form (*M. guttata*, var. *pallida*); and finally two species of *Choristhenis*, both coastal forms only, and both distinctly more specialised than the other species. For the other example, I take *Synlestes weyersi*, a species that shews a remarkable gradation of venational forms. Specimens from the Blue Mountains are much larger and more densely reticulated than the coastal forms, and a series from different localities can be arranged to shew *progressive specialisation by reduction*, in a most perfect manner.

Comparing now the venation of *Cordulephya montana* and *C. pygmaea*, we see, at once, that the mountain-form (*C. montana*) is the *less reduced*. The point specially to be noticed here is, that all this evidence is in favour of the "quadrilateral" triangle of *Cordulephya* being "*not primitive, but secondarily derived from a three-sided one, and an extreme case of specialisation.*"\* (I quote the very words used by Needham on the four-sided triangle of *Pentathemis*). We may suppose that the two closely allied species now existing were, in the near past, one single species, with a range probably including that of the two, or of even greater extent. It is, moreover, extremely probable that this species had a *completely or almost completely* recessed hindwing-triangle. One portion of this species, located in the mountains, was not faced with such a strenuous task as the other portion, that along the coast. The latter, left to fight the invaders on its own ground, and, as it were, being placed in the forefront of the conflict, had either to be exterminated, or to conserve its resources so as to make a successful fight. The line of defence adopted is a well-known one, and had already been carried out more completely amongst the *Odonata*, by practically the whole of the *Cœnagrioninae*; viz., defence by reduction, conservation of force and material, and

\* *Loc. cit.*, p.276.

alteration of habits. Being unable to compete with the invaders along the *Libellulid* line of development, *Cordulephya* began a *cœnogenetic departure towards zygopterous lines*. This was confined to the imago, the larva being apparently well able to hold its own. This departure, aiming at reduction in size together with an alteration of habits of flight, necessitated a new line of development in wing-venation. The large triangles and anal area, so necessary to the soaring and skimming flight of *Libellulidae*, were no longer of value, and, to whatever degree these may have been developed in *Cordulephya*, they had now to be undone and altered to the new requirements. There set in, therefore, the *opposite tendencies* to those associated with the *Libellulidae* in general. Reduction in size meant *particularly* reduction in basal areas; as the hindwing became narrower, the anal loop (whether it was well-formed or not matters little here) became more and more reduced, until we see it represented now in *C. pygmaea* by two strong and well-formed cells; a *procession* instead of a *recession* of the hindwing-triangle began, accompanied by a reduction in actual size and an *ascent* of the upper cross-vein, re-forming the original "quadrilateral" triangle of the older *Libellulidae*. In all this, *C. pygmaea* far outran *C. montana*, as would have been expected. In *C. montana*, we see an intermediate stage, which is very strong evidence in favour of our view of the case. The hindwing-triangle is much *wider* than in *C. pygmaea*, and much less recessed. It appears that the triangle has been stretched or widened along the wing-length by the gradual narrowing of the basal areas, but that the basal side has not yet reached a position of stable equilibrium. *C. pygmaea* has solved the problem by shortening the triangle, and supporting it by a second cubital cross-vein placed well after the arculus. The forewing-triangle of *C. montana* is also much larger and wider than that of *C. pygmaea*, and the ascent of the upper cross-vein is less, so that the triangle of the former is more normally shaped. As regards the anal loop, the reduction

to three or four cells in *C. montana* shews us still a *well-defined anal loop*, especially in the female; from which we may infer that the original larger loop was also fairly well defined, as in other *Eucordulina*. Another interesting point is the reduction of the membranule. In *C. montana* ♀ it is still present in both wings; in *C. montana* ♂ it is absent from the forewing, and present, though much narrowed, in the hindwing. In *C. pygmaea*, both sexes, it is completely eliminated, being replaced in the hindwing by a small tuft of hairs (Plate xii., figs. 3-6). Finally, it should be noted that some of the parts under discussion are still variable, a long series of *C. pygmaea* shewing considerable differences in the position of the "break" of the costal side of the triangles. A few specimens have *normal* hindwing-triangles, and a nearly normal one in the forewing; but by far the greater number incline to the opposite extreme.

D. *Comparison of the two species apart from venation.*—Two points here are worthy of note. Firstly, *C. montana* has the more *corduliform* abdomen of the two. This shews that the species, before reduction, may have had a typically *Eucordulian* abdomen. I do not think the original abdomen was broadly corduliform, but a very good idea of its probable appearance may be gathered by comparing the abdomens of the *Synthemis*; the form in *Synthemis* corresponding to the original form for *Cordulephya*, that of *Metathemis* being similar to that of *C. montana*, and that of *Choristhemis* similar to that of *C. pygmaea*. Secondly, in the females of the two species, the vulvar lamina is more reduced in *C. pygmaea*, leaving the underside of segment 9 widely open, so that larger egg-masses can be more easily exuded. Bearing in mind the extreme rapidity and timidity of the movements of the female during oviposition, the advantage of this to *C. pygmaea* is evident.

E. *The comparative sizes of the larvæ.*—Though the imagines of *C. pygmaea* and *C. montana* do not differ very greatly

in size, yet the larva of the latter is remarkably large, both as compared with that of the former and with its own imago. In both species, the larvæ are large for the size of the imago. For instance, *Diplacodes haematodes* is a larger insect than *C. pygmaea*; the larva is, however, smaller. In the case of *C. montana*, it is hard to resist the conclusion that the imago must, at one time, have been a much larger insect. The reduction in size of the larvæ has not kept pace with that of the imagines, because the actual cænogenesis was confined to the *wings and abdomen* of the imagines only, (note the *Eucordulian* character of head, thorax and legs still remaining). This may also have been partly due to the existence of the two broods, which I have already explained. If the species were preserved by the complete sacrifice of one of two broods in the larval stage, there did not exist the further necessity for change that affected the imagines. But a certain amount of reduction of larval size must necessarily accompany the imaginal reduction; and this is still proceeding, without affecting the *Eucordulian* character of the larvæ.

iv. *A comparison of the two known Species of the Genus.*—This has already been discussed under headings C, D and E of iii., with a view to shewing that *Cordulephya* is specialised by reduction. The same argument is, of course, valid for its inclusion in the *Eucordulina*. It would, however, be greatly strengthened if we could point to one or more species that form intermediate links between *Cordulephya* and the main body of the *Eucordulina*. It would be too much to expect a complete series of forms linking the two together, but we might expect to find some Australian *Corduline*, as yet untouched by the main stream of invaders, which would give us an idea of what the ancestor of *Cordulephya* was like. Such a form, I venture to assert, may be seen in *Hesperocordulia berthoudi* Tillyard\*, a rare species found in South-Western Australia.

\* "Further Notes on some rare Australian *Cordulinae*" These Proceedings 1911, p.376.

Although this species is much larger than *Cordulephya*, its abdomen is scarcely more corduliform than that of *C. montana*; and it possesses a colour-pattern of thorax and abdomen which is remarkably similar to that of *Cordulephya*, the only difference being that the red of *Hesperocordulia* becomes dull orange in *Cordulephya*. If we consider the extreme peculiarity of the colour-pattern of these two insects, and that it is not even approached by any other known *Corduline*, we shall see that it constitutes a strong argument in favour of their close relationship. The ancestors of *Cordulephya*, before they came in contact with the eastern stream of invaders, must have been closely allied to *Hesperocordulia* as we find it now. Points of importance, here, in the wing-venation of *Hesperocordulia* are (i.) the fact that recession of the hindwing-triangle is not *absolutely* accomplished; (ii.) the fact that the anal loop has no apical extension; (iii.) the fact that the arculus-sectors are not fused. It is not necessary to suppose that the ancestor of *Cordulephya* had progressed even so far in a *Eucordulian* direction as *Hesperocordulia* now has. But even if it had, it would not yet have reached a *stable* position, for variation is still evident in that species. So much easier, therefore, would the start of the reduction-process be. Placing the wings of *Hesperocordulia berthoudi*, *Cordulephya montana* and *C. pygmaea* in order, side by side, we see

(i.) Three consecutive stages in the reduction of the triangles, by procession from the arculus and the ascent of the upper cross-vein.

(ii.) Three consecutive stages in the reduction of the anal loop, from ten cells to four or three, and then to two strong cells only.

(iii.) A tendency to strengthen the arculus by the beginnings of a fusion between the sectors.

I have already discussed\* the connection of *Hesperocordulia* with the *Eucordulina*, and have given reasons why it should be included in that group. We see, therefore, how it forms the connecting link between them and *Cordulephya*.

Reviewing the above evidence *in toto*, I conclude, (i.) that a *Eucordulian* connection for *Cordulephya* is proved; (ii.) that its apparently *Idocordulian* relationship in wing-venation is due to convergence by reduction; (iii.) that the *Eucordulian* connection is strong enough to justify us in including it in that group, rather than placing it in a separate group of its own.

NOTE A.—ON THE REDUCTION-PROCESS EXHIBITED BY CORDULEPHYA. —The important part played by cœnogenetic reduction in the formation of our present-day *Odonata* has been hitherto ignored, though there can be no doubt that it has played a far more effective part than any other form of specialisation. The result of ignoring it has been that a highly erroneous view of the phylogeny of the families of the *Odonata* is growing up. When their life-histories come to be written, I venture to state that such forms as many of the *Protoneura* (including *Selysioneura*, claimed by Foerster to be one of the most primitive of *Odonate* types), *Hemiphlebia*, *Nannophya*, *Agrionoptera*, and many others in which reduction can be traced, will be found to be *highly specialised by reduction*, and not truly archaic by comparison with other existing forms. We are so especially apt to think of Australia as the home of archaic forms, that we forget that Europe and Asia possess forms equally archaic. (*Cordulegaster* and *Palæophlebia* are probably as old as any now existing). We must not argue by analogy from the distribution of the higher animals, for the *Odonata* are a very ancient order, and reached a high degree of development long before Australia was as isolated as it now is. Nor have the

\* *Loc. cit.*, p. 381.

higher animals in Australia been subjected, in the same degree, to the strenuous competition with immigrants that the autochthonous Odonata have had to undergo.

As the *reduction-process along a new line of development*, which has been the main factor in evolving *Cordulephya*, is of the greatest importance, I propose the term *asthenogenesis* (Gr. ἀσθενής, weak) for it, in contrast to specialisation in development of parts to form *stronger* types, such as has been the main line of development of the *Libellulidae*. The latter may be termed *menogenesis* (Gr. μένος, strength). Thus, we should say that the *Anisoptera* as a whole are the *menogenetic* group, the *Zygoptera* the *asthenogenetic* group of *Odonata*. A race may follow a menogenetic line of development up to a certain standard, and then, like *Cordulephya*, adopt an asthenogenetic line. It is, of course, possible, though less likely, for the opposite to happen.

NOTE B.—ON THE “QUADRILATERAL” GENERA OF THE LIBELLULIDÆ.—It seems very open to doubt whether the four-sided triangle, at present found in some of the *Libellulid* genera, is in any case an archaic structure. It should be borne in mind that the *Anisopterid* triangle was formed at a period of intense energy and development amongst the *Odonata*, when the group probably occupied a far more dominant position amongst the *Insecta* than it does now. That being so, races that remained half-way, adopting neither the *anisopterous* nor the *zygopterous* tendency in full, must very soon have become extinct. The present-day “quadrilateral” *Libellulidæ* are all (except *Pentathemis*, an admittedly specialised form) small species in comparison with their nearest related forms. That being so, it is important to enquire how far asthenogenesis has affected them. If the larvæ are found to be highly developed, and the imagines, apart from the triangles, shew a general absence of archaic characters, the balance of evidence is surely in favour of their being *asthenogenetic* members of the more highly specialised groups. In

this connection, I suggest a comparison of the two species, *Nannophya* (*Nannodythemis*) *dalei* and *N. australis*, with *Cordulephya montana* and *C. pygmaea*. Exactly the same forces have been at work on the two species, and the relative states of the triangles and surrounding areas in the two pairs are remarkably similar. But *Nannophya* has not attained the splendid zig-zag flight of *Cordulephya*, owing to the persistence of the broader anal area of the hindwing. In *Nannophlebia* and *Tetrathemis*, however, the flight is very similar to that of *Cordulephya*, the basal areas being more reduced.

As regards *Neophya* and *Austrophya*, neither of these can now be claimed as being closely allied to *Cordulephya*. *Austrophya* is clearly an asthenogenetic member of the *Idocordulina*, possessing all the characteristics of that group. *Neophya* seems to me much more open to doubt. We should be content to await the discovery of its larva before pronouncing a judgment; but it is quite possible that some other African genus exists, which will connect it to a main group in the same way that *Hesperocordulia* connects *Cordulephya* to the *Eucordulina*.

---

EXPLANATION OF PLATES XI.-XII.

Plate xi.

- Fig. 1.—Full-fed nymph of *Cordulephya montana*, n.sp. (× 4).  
 Fig. 2.—Labium of same (× 11).  
 Fig. 3.—Outline of labium of nymph of *Cordulephya pygmaea* Selys (× 22).  
 Fig. 4.—Head of same, showing labium in position of rest (× 4).  
 Fig. 5.—Gizzard of same, showing chitinous folds with teeth (× 20).  
 Fig. 6.—Ovum of *Cordulephya pygmaea* Selys (× 45).

Plate xii.

- Fig. 1.—*Cordulephya pygmaea* Selys, ♂ (× 2½).  
 Fig. 2.—*Cordulephya montana*, n.sp., ♂ (× 2½).  
 Fig. 3.—Venation of basal portion of wings of *C. pygmaea*, ♀ (× 5).  
 h = basal tuft of hairs.

Fig. 4.—Venation of basal portion of wings of *C. pygmaea*, ♂ ( $\times 5$ ).  
*h* = basal tuft of hairs.

Fig. 5.—Venation of basal portion of wings of *C. montana*, ♂ ( $\times 5$ ).  
*m* = membranule.

Fig. 6.—Venation of basal portion of wings of *C. montana*, ♀ ( $\times 5$ ).  
*m* = membranule.

Fig. 7.—Appendages of *C. pygmaea*, ♂, dorsal view ( $\times 10$ ).

Fig. 8.— " " " " profile view ( $\times 10$ ).

Fig. 9.—Appendages of *C. montana*, ♂, dorsal view ( $\times 10$ ).

Fig. 10.— " " " " profile view ( $\times 10$ ).

Fig. 11.—Underside of segments 8-10 of *C. pygmaea*, ♀ ( $\times 10$ ).

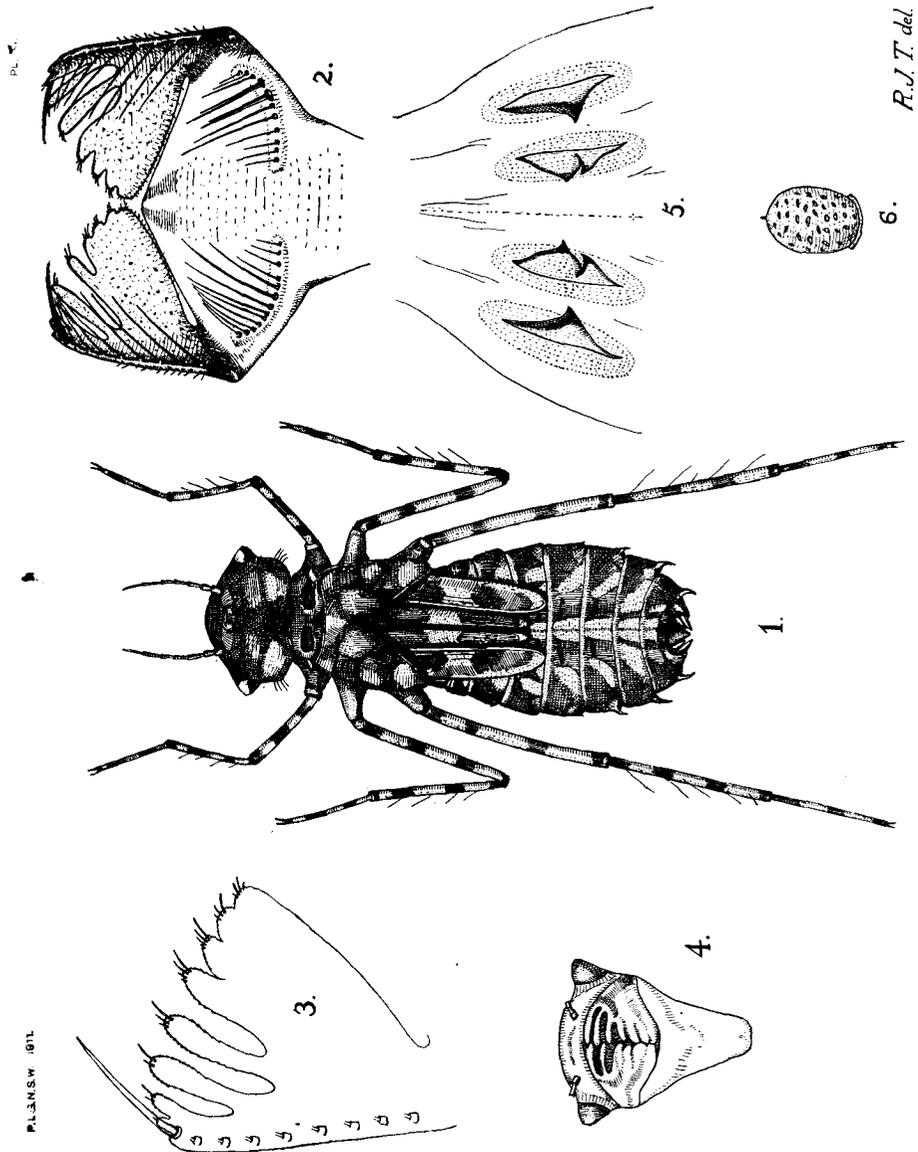
Fig. 12.— " " " " of *C. montana*, ♀ ( $\times 10$ ).

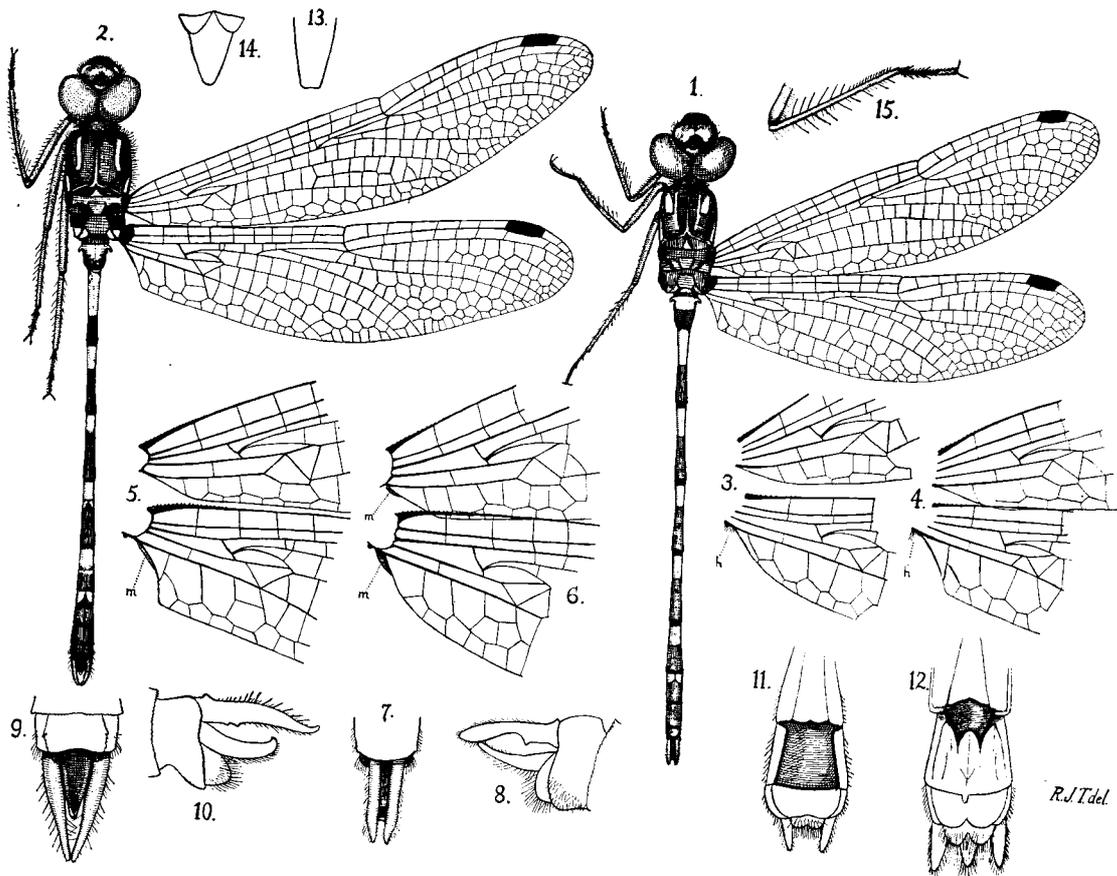
Fig. 13.—Outline of inferior appendage of *C. pygmaea*, ♂, sketched from below ( $\times 10$ ).

Fig. 14.—Outline of inferior appendage of *C. montana*, ♀, sketched from below ( $\times 10$ ).

Fig. 15.—Tibia and tarsus of foreleg of *C. pygmaea* ♂ ( $\times 5$ ).

(The tibial lamella is on the underside, and cannot be seen).





Genus *Cordulephya*.