[From "The Transactions of the Second Entomological Congress, 1912."]

PROGRESS IN OUR KNOWLEDGE OF THE ODONATA FROM 1895 TO 1912.

By Philip P. Calvert, Ph.D.,
University of Pennsylvania, Philadelphia, Pa., U.S.A. America.

[From "The Transactions of the Second Entomological Congress, 1912."]

PROGRESS IN OUR KNOWLEDGE OF THE ODONATA FROM 1895 TO 1912.

By PHILIP P. CALVERT, PH.D.,

University of Pennsylvania, Philadelphia, Pa., U.S. America.

AT the third International Congress of Zoology, held at Leyden, September 1895, a memoir entitled *Le Progrès dans la Connaissance des Odonates* was presented by M. le Baron EDMOND DE SELYS-LONGCHAMPS, the most eminent authority on this group of insects. For reasons which he gives, DE SELYS was obliged to limit himself to a succinct sketch of the evolution of the taxonomy of the Odonata.

The seventeen years which have elapsed since the Congress of Leyden have seen the publication of many researches dealing with the insects known as Dragonflies, Libellules, or Libellen, in three principal European languages. A Congress of Entomology seems an especially fitting occasion on which to summarise the results of these investigations. The following lines will therefore attempt a review of what seems to be the most important work done between 1895 and 1912, not only in taxonomy, but also in the other divisions of the entomology of the Odonata. A brief outline of the systematic literature from the time of LINNÆUS to the close of the nineteenth century was published by Mr. KIRBY in 1901.

Our views of the relationships of living beings to each other, of their evolution into their present forms, and of the values of the characteristics by which we judge these relationships, are changed from time to time as our knowledge of structure and ontogeny increases. During the period which we here discuss, several important contributions to the morphology and embryology of the Odonata have appeared.

Morphology of the Abdomen and its terminal parts.

Almost at the beginning of the period stands the work of Richard Heymons, *Grundzüge der Entwickelung und des Körperbaues von Odonaten und Ephemeriden* (1896), in which he not only made known many new facts of the embryonic development of these insects, but also demonstrated the existence of twelve segments in the abdomen of young Odonate *larvæ*, a number which up to that time had been observed only in the *embryos* of insects, and which he considers to be fundamental for the class. His results on the appendages and processes with which the body terminates were expressed in the form of a table which is reproduced here, with some slight modifications.

Fate of Larval Abdominal Parts after Transformation (*Odonata*).

+ = present. − = absent or feebly developed.

Young larvæ, all groups.	Imagines.			
	Zygoptera ♀.	*Zygoptera* ♂.	*Anisoptera* ♀.	*Anisoptera* ♂.
Tergite and sternite of 10th segment	+	+	+	+
Processus caudales (outgrowths of the 10th segment)	+ ("Appendages" of taxonomists)	+ ("Superior appendages" of taxonomists)	+ ("Appendages" of taxonomists)	+ ("Superior appendages" of taxonomists)
Appendix dorsalis (= tergite of the 11th segment)	−	−	+ (11th tergite)	+ ("Inferior appendages" of taxonomists)
Appendices laterales (cerci, 11th segment)	− (2-parted sternite)	+ ("Inferior appendages" of taxonomists)	− (2-parted sternite)	− (2-parted sternite)
Laminæ anales (= 12th segment)	−	−	−	−

Heymons emphasised again the absence of any homology between the "inferior appendages" of male Zygoptera and male Anisoptera, already pointed out by Rambur in 1842 (page 14). He also laid stress on his conclusion that the adult Odonata, other than the male Zygoptera, do not possess cerci, as do the Orthoptera, for example.

This view being questioned by Handlirsch (1903) led Heymons to a fuller examination of the whole subject, in which (1904) he re-affirmed his previous belief, although he substituted the name "cercoids" for "processus caudales." While his statement of observed fact was accepted by Handlirsch (1904), a difference of interpretation remained as to whether the "cercoids" or "superior appendages" of the adults represent newly-acquired parts not homologous with Orthopterous cerci (Heymons), or whether they are but reformations of true cerci (Handlirsch). For myself I favour the former idea.

Mating Positions and Structures.

The consideration of the morphology of the terminal abdominal appendages of the adult Odonata naturally leads to that of their function, and while it has long been known that these parts of the males grasp the females in the act of mating, it was not until our own period that the differences in the employment of these parts in the two suborders of the Odonata were pointed out. Previous statements were to the effect that the male's appendages grasped the "neck," that is, the prothorax, of the female, but in 1899, and again in 1906, Williamson called attention to the fact that in the Anisoptera it is the **head**,[1] in the Zygoptera the **prothorax** of the female that is seized. It will be seen, therefore, that the difference in the part of the female grasped coincides with a difference in the morphology of the "**inferior appendage**" of the male which grasps.

Tillyard (1909) has found that in the Australian *Petalura gigantea* both **head and mesothorax** of the female are enclosed between the male's appendages. The fact is interesting for a number of reasons. The Petalurinæ are Anisoptera, and have been considered by some writers (Calvert 1893, Ris 1896, van der Weele 1906) as, of all their suborder, nearest to the Zygoptera. This copulatory position of *P. gigantea* gives some suggestion as to the divergence in this position between Zygoptera and Anisoptera. *Petalura*, however, is a true Anisopter in that

[1] There is, however, a recent discordant statement—that of Tillyard (1910), who asserts that the male *Synthemis eustalacta* clasps the female's prothorax.

*

the single inferior appendage (appendix dorsalis of HEYMONS), of the male is applied to the dorsal surface of the female's head.

Previous to February 1899 (the date of WILLIAMSON'S *A Note on Copulation among Odonata*), systematic descriptive writers had called attention to differences in the shape and structure of the prothorax in the female Zygoptera, and referred to them as correlated with differences in the form of the male appendages, and KOLBE (1881) in particular had summed up these correlations. The list of such mutual sexual adaptations in this suborder has been increased during our period by various writers, while in consequence of WILLIAMSON'S discovery similar adaptations or lacerations on the head of Anisopterous females have been demonstrated or rendered probable, as, for example, by RIS (1910), E. M. WALKER (1912), and CALVERT (1912).

COPULATORY APPARATUS OF THE MALES.

A well-known peculiarity of the Odonata, and one which distinguishes them from all other animals except the Araneina and the Cephalopod Mollusks, is the wide separation in the male of the orifice of the ejaculatory duct from the penis and its accessory copulatory structures, the orifice lying on the ventral surface of the ninth abdominal segment, as in insects generally, the penis, etc., on the ventral surface of the second and third abdominal segments. Before copulation can occur, therefore, the sac, or vesicle, of the penis must be charged with sperm by such a bending of the male's abdomen that the ventral surfaces of its second and ninth segments may be brought in contact.

The penis and its adjacent accessory copulatory structures (described under such names as anterior lamina, vesicle of the penis, genital lobes, etc.) have been utilised for taxonomic purposes by many writers, but the investigation of the morphology of these parts lies wholly within the time under our consideration. On purely anatomical grounds Miss GODDARD (1896) suggested that hamules and penis in certain Libelluline genera are modified abdominal appendages of the second and third segments. THOMPSON, in an almost purely comparative anatomical paper (1908), did not touch on this deeper question, but sought to establish the homologies of the parts found in

different representatives of the Odonata with each other. BACKHOFF (1910) has studied the development of the copulatory apparatus in males of the genus *Agrion* (*Cœnagrion* Kirby) by means of surface preparations and microtome sections, finding no trace of these structures previous to the ante-penultimate larval stage (instar); they arise from unpaired cell-masses and show no indication at any time of origin from fusion of paired rudiments, and hence cannot be homologised with the other paired segmental appendages. His summary of the differences in the apparatus of the Zygoptera and of the Anisoptera respectively may be expressed as follows:

Zygoptera (regarded as the more primitive): Penis unjointed; its lumen communicating at its basal end with the body cavity, but not with the seminal vesicle (vesicle of the penis), and without a distal aperture to the exterior; muscles, nerves, and tracheæ lacking from the copulatory apparatus.

Anisoptera: Penis jointed; its lumen not communicating with the body cavity, but continuous with that of the seminal vesicle, and having an opening to the exterior near its apex; muscles, nerves, and tracheæ present in the copulatory apparatus.

Nothing is yet known as to the details of the transference of the spermatozoa from the ejaculatory duct until they reach the female, and we are still entirely in the dark as to how the localisation of the copulatory apparatus of the male, near the anterior end of the abdomen, remote from his genital orifice, came into existence, although BACKHOFF has suggested the resemblance in position of this apparatus to that of the genital opening of the progoneate Arthropods. He infers, from the palæontological data of HANDLIRSCH (1906–8), that this localisation occurred previous to Jurassic time.

THE OVIPOSITOR: ITS DEVELOPMENT AND ITS REDUCTION.

We may turn naturally to the ovipositor of the female. The late H. W. VAN DER WEELE gave us an extended account of the *Morphologie und Entwicklung der Gonapophysen der Odonaten* in 1906. He confirmed the general results of PEYTOUREAU (1895) and HEYMONS (1896) that the gonapophyses are not the remains or vestiges of embryonic abdominal limbs, but epidermal out-

growths which first arise after the last traces of the abdominal limbs have disappeared, and in a more median position than the latter occupied. The first traces of gonapophyses, contrary to earlier statements, were found in very young larvæ or nymphs of *Agrion pulchellum* of but 2 mm. abdominal length. These traces are referred to the lateral gonapophyses of the ninth segment, and characterise both sexes. In larvæ of 3 mm. abdominal length and more, the sexes can be distinguished owing to the appearance of the first rudiments of the median gonapophyses of the same segment in the female but not in the male, soon followed by the rudiments of the anterior gonapophyses of the eighth segment in the former sex. He found rudiments of the gonapophyses in quite small Æshnid larvæ, but not in those of Gomphidæ, Cordulegastridæ, Corduliдæ, and Libellulidæ. While all three pairs of gonapophyses are present in the imagos of the Zygoptera, of the Æshnidæ and of the Petaluridæ and form an ovipositor, reduction in size in the lateral gonapophyses is apparent in the latter two groups and becomes almost absent in the Cordulegastridæ. In the remaining Anisoptera the lateral and the median gonapophyses are almost, or altogether, absent, and the anterior pair show all degrees of reduction and fusion. This reduction of the gonapophyses coincides with VAN DER WEELE's idea of the higher differentiation of the Anisoptera. The genital pore arises originally in both sexes behind the middle of the ninth sternite, and persists in this position in the male. In the female it is shifted forward so that it has been described as at the hind end of the eighth segment.

A reduction of the female gonapophyses within a more limited group (*Synthemis*—Cordulinæ) has also been demonstrated by TILLYARD (1910), who has emphasised (1909) the correlation between elongated eggs and the presence of an ovipositor on the one hand, and the wider, less elongated eggs of those Odonata in which the female lacks such an organ, on the other.

WING VENATION.

Although the general characteristics of the wings were employed by LINNÆUS and his successors in defining the various

groups of insects, the peculiarities of venation did not receive attention until a later date. VAN DER HOEVEN (1828) was probably the first to point out the differences in the veining of the wings of different Odonata, and from his time onward there has been an ever-increasing study of this field.

It will not be, I hope, an injustice to any of the numerous investigators to credit the greatest advance in our knowledge of the wing-veins of insects to Professors COMSTOCK and NEEDHAM, whose *Wings of Insects* appeared in 1898 and 1899. Speaking as I do on English soil, I trust that I may be pardoned for a slight digression from my subject if I assume to express, on behalf of American entomologists, our deep appreciation of the honour which the Entomological Society of London conferred upon Professor COMSTOCK last November in making him one of its honorary members.

It is not necessary to linger here on the embryological method which led the two authors to the establishment of the homologies of the wing-veins throughout the class Insecta and of a common nomenclature for the highly different orders. The application of this method to the Odonata led to the realisation of the full significance of the assumption by one wing-trachea during larval life of a position posterior to that which it originally occupied, and the crossing of the radial sector, determined by this trachea, was announced as "a character quite distinctive of this order." The morphology of the arculus, the triangle, and the anal loop was also elucidated.

The subject was still further illumined by Professor NEEDHAM in his *Genealogic Study of Dragon-fly Wing Venation* (1903). This memoir advanced our knowledge of the homologies of the veins within the order, traced changes in venation from genus to genus, supplied developmental data for the determination of the values of venational characters in classification, suggested mechanical causes for the peculiarities of wings and veins, and developed ideas as to what constitute generalised and specialised conditions in these organs. No work on the Odonata within the period of our survey has had a greater influence on other investigators, due partly to the great variety of detail which the venation presents, but chiefly to the underlying method and the novelty of ideas in which the *Genealogic Study* abounds.

**

The Larva.

The great increase in our knowledge of the larvæ[1] of the Odonata is a striking characteristic of our period. As shown above, many of the authors already cited, following the embryological method, have found in the larvæ the starting-points for their special investigations and have in consequence added information on these early stages.

Gilson and Sadones (1896), and Sadones alone in a longer paper (1896), described the anatomical and histological features of the alimentary canal of the larva of a *Libellula* in greater detail than had been given previously. They supported the view that the gizzard with its teeth has a triturating and subdividing action on the bolus, although not on the food particles themselves. They described for the first time two epithelial plates or disks in the pre-rectal ampulla and a blood-cavity in the gill-plates of the rectum, and called attention to the situation of the terminal loops of the tracheoles in the subcuticular layer of cells of these gill-plates. They suggested that the absorption of oxygen from the water which is drawn into the rectum through the anus is accomplished by the vital activities of this subcuticular layer, which in turn continually delivers the oxygen as a gaseous secretion to the tracheoles; and that the oxygen is caused to pass along the tracheæ of the rectal gills and of the body by the alternate increase and decrease of the tracheal lumina. The increase was thought to be due to elongation of the tracheæ by a smoothing out of their cuticular linings, the decrease by the reverse process. The elongation and shortening of the tracheæ were referred in turn to the oscillations of cœlomic and intrarectal pressures which must accompany the respiratory movements so familiar to those who have watched living Anisopterous larvæ. On the other side of the respiratory account, the elimination of carbon dioxide was suggested to be the rôle of the blood-cavities in the gill-plates, and of the epi-

[1] In my "Introduction to the Study of Odonata" (*Trans. Amer. Ent. Soc.*, xx., p. 195 and elsewhere), I have used, in common with other writers, the term *nymph* to designate "that stage of Odonate existence between the egg and the transformation into the imago," but I do not see now why the more general term *larva* should not be employed instead.

thelial disks of the pre-rectal ampulla. It may be pointed out that this theory of larval respiration rests on anatomical and histological data, not on physiological experiments.

Sadones also called attention to the lack of correspondence in position between the rows of gill-plates of the rectum and the so-called rectal glands, as the latter alternate with the former, and to the bearing of this fact on the homologies of the rectal glands in insects generally.

Calvert (1911) has discovered well-developed, paired, ventral, tracheal gills on a number of the abdominal segments of the larva of the Costa Rican *Cora*, one of the Calopteryginæ, structures hitherto known only on a couple of Old World (Indian) genera of the same subfamily. The presence of such organs naturally suggests a very primitive condition and a point of contact with the larvæ of Ephemeridæ and Sialidæ.

Needham (1897) traced the changes which occur in the epithelium of the stomach or mid-gut of larvæ during fasting and after feeding, finding in the latter case that the most turgid cells, containing presumably digestive ferments, are bodily discharged into the lumen to mix with the food and are replaced by other previously smaller cells. His results were confirmed and extended by Voinov in the following year (1898), who showed that, previous to the actual detachment of whole cells into the lumen, clear or coloured liquids may be secreted from them. By mixing colouring matters with the food, Voinov ascertained that the same cells which secrete these liquids also absorb material from the lumen at the same time. He traced methylene blue absorbed in this way into the body cavity and thence into many other organs, *e.g.* the developing ovaries. Other colouring matters, such as cochineal, introduced into the alimentary canal, were not absorbed, showing a selective absorptivity on the part of the intestinal epithelium. He also obtained evidence of absorption in the opposite direction, for, on injecting congo red in physiological salt solution into the body-cavity, granulations of this dye-stuff were found not only in the pericardial cells, but also in the peritrophic sac of the mid-gut lumen. Eosin, similarly injected into the body-cavity, appeared in the Malpighian tubes and in the mid-gut lumen. Only in the mid-gut was there evidence of the absorption of fats and other

soluble substances from the food, this power being possessed throughout this part of the alimentary canal and not confined to a special zone, as Cuénot had previously determined for fat absorption in Orthoptera, while fore- and hind-guts do not absorb. The peritrophic sac is apparently the inner surfaces of the epithelial cells, which become detached when these cells are in active secretion. Experimental evidence was also given for the eliminating action of pericardial cells, heart-walls, and Malpighian tubes.

That very characteristic organ of Odonate larvæ, the labium or mask, has been the subject of a special study, embryological and comparative anatomical, by Miss Butler (1904), from which the conclusion is drawn that the lateral lobe represents merely the labial palpus while the middle lobe is formed of laciniæ and galeæ more or less consolidated in the different groups. This is essentially the theory of Rambur (1842) and of Hagen (1854), in opposition to that of Gerstacker (1873), Heymons (1896), and Börner (1909).

Length of Larval Life.

It was not until 1909 that any definite statements existed as to the actual length of larval life and the number of moults passed through by the Odonata. In that year, Balfour-Browne gave the results of rearing *Agrion pulchellum* and *Ischnura elegans* from the egg to the imago, the first and only species for which such a complete developmental record has yet been published. He found, however, that the number of moults, consequently the number of larval stages, or instars, and the total length of larval life are not constant even in the same species. After distinguishing the form which leaves the egg and which has not free limbs as the **pronymph**, and counting as the "first nymphal" stage that which follows the pronymphal moult, Balfour-Browne found that in *Agrion pulchellum* the transformation to the imago may follow the tenth, eleventh, twelfth, or thirteenth larval (nymphal) stage. The shortest time which elapsed from hatching of the egg to the emergence of the imago in this species was 230 days; another individual occupied 634 days. The body-length in the last larval stage varied from 14

to 22 mm. He was unable to correlate the size, the number of moults, the length of larval life, and the temperatures to which the insects had been exposed, except to point out that there is a tendency "for the larger nymphs in any stage to be those which ultimately complete in the smallest number of stages." *Ischnura elegans* passed through twelve larval stages; other species of Agrionines were thought to have from eleven to fourteen. Much information is given on the rate of growth of body-length, of the antennæ, the labium, and the wing-rudiments.

Backhoff (1910), in the paper already quoted, estimated the number of larval stages in *Pyrrhosoma nymphula* (*minium*) at nine, from comparisons of the sizes of different larvæ. East (1900) observed the last seven moults in the larva of *Æshna cyanea* and inferred a total of nine, ten, or eleven. E. M. Walker (1912) observed the last eight moults in Canadian *Æshnæ* and believes they are preceded by three or four others, making a probable total of twelve or thirteen larval stages, occupying probably three years.

Certain Larval Limitations and Peculiarities.

R. C. Osburn (1906) conducted a series of experiments to determine the ability of eggs and larvæ of various species of Odonata to live in saline solutions of different densities, but none were able to withstand a density over 1·01. He demonstrated that there exists "a very definite barrier to their assumption of marine life, and that this barrier remains unchanged during the life of the individual."

Perkins (see Sharp, 1895) (1899), in the Hawaiian Islands, and Knab and Calvert (1910, 1911), in Mexico and Costa Rica, have found that certain Agrionine larvæ (*Agrion* and *Mecistogaster* respectively) live in the small accumulations of water between leaf-bases of terrestrial and epiphytic plants, or, in the Hawaiian case, even between dry leaves. Similar habits on the part of undetermined Agrionid and Libellulid larvæ in Malaya have also been reported by Leicester (1903). The food of such larvæ consists of the early stages of mosquitoes, of other Diptera, etc., living in the same situations.

The discovery of Petalurid larvæ (*Tachopteryx* by William-

SON, 1901; *Petalura* by TILLYARD 1909), and of that of *Petalia* (TILLYARD, 1910), have been noteworthy events. Those of the former group live in boggy swamps, and in the case of the Australian *Petalura* in foul, muddy ooze which cakes solidly on the larva at the time of transformation. A mud-dwelling habit is also that of the larva of the Australian *Synthemis eustalacta*, which, encased in dry mud, has been known to resist drought for ten weeks, and to fast for three months (TILLYARD, 1910).

TAXONOMY.

A comparative study of Odonate larvæ and their corresponding imagos led RIS (1896) to what may be termed the first phylogenetic classification of Odonata based on the ontogeny of an organ followed throughout the entire order. This organ was the gizzard. RIS showed that the larvæ of the Calopteryginæ and some Agrioninæ have the most complexly armed gizzard, the teeth being arranged in sixteen longitudinal folds, reduced to eight in *Lestes*, to four in *Gomphus* and *Æschna*, and further reduced to four bilaterally symmetrical *teeth* (not folds) in *Cordulegaster* and the Libellulidæ. He also showed that a reduction in the folds and in the teeth takes place in the development of the individual in each of these groups, scarcely more than traces of the teeth remaining in the imagos of the Anisoptera. Combining these results with data drawn from other organs, some of which had already been employed by previous writers, RIS presented his ideas of the relationships of the subfamilies of the Odonata in the form of a genealogical tree, confessedly a modification of that of CALVERT (1893), from which it differs chiefly in placing the Cordulegastrinæ as ancestral forms of the Libellulidæ.

Both CALVERT's and RIS's views agreed in regarding the Zygoptera as more primitive and in looking on the Calopteryginæ as ancestral to all other Odonata. NEEDHAM, and his students Miss BUTLER and THOMPSON, whose work has been quoted above, have made many suggestions as to the generalised or specialised conditions to be found in various structures of both the Zygoptera and Anisoptera, but have refrained from formulating any detailed statement of the relationships of these

two suborders to each other, probably for the reason, as NEEDHAM himself has expressed it (1903, page 758), of not making "any suggestion that might hinder future studies."

VAN DER WEELE (1906), accepting BRONGNIART's Protodonata as the ancestral forms of the Odonata, recognised the living *Palæophlebia* Selys,[1] of Japan, as the continuation of the Protodonata, and from the Palæophlebiidæ, as a starting-point, derived the Zygoptera on the one hand, the Anisoptera on the other.

HANDLIRSCH (1906-1908) created the term **Anisozygoptera** to include the living *Epiophlebia*, a number of Mesozoic and fewer Tertiary forms, placed it as equivalent to the Zygoptera and Anisoptera, and, like VAN DER WEELE, regarded it as ancestral to these latter two. A fourth suborder, **Archi-Zygoptera,** was also proposed for a single genus, the Mesozoic *Protomyrmeleon* Geinitz.

The Anisozygoptera present a combination of characters some of which are characteristic of the Zygoptera, such as the quadrilateral, others of the Anisoptera, as the greater breadth of the hind-wings in comparison with the anterior pair.

The great Belgian master, EDMOND DE SELYS-LONGCHAMPS, died December 11th, 1900. His wonderfully rich collection of Odonata has been placed in the Museum of Natural History at Brussels by the far-sighted wisdom and generosity of his sons, Baron WALTHER and the late Baron RAPHAEL DE SELYS-LONGCHAMPS. In pursuance of the wishes of their father, they authorised the publication of a *Catalogue Systématique et Descriptif des Collections Zoologiques du Baron Edmond de Selys-Longchamps*. This is much more than a catalogue, many of its fascicules being elaborately and beautifully illustrated monographs of the groups of which they treat.

We are concerned at present only with those fascicules dealing with the Odonata. These comprise, as far as published, one

[1] CALVERT, in a review (*Ent. News*, xiv., p. 208, June, 1903) of NEEDHAM's *Genealogic Study*, pointed out that SELYS's name *Palæophlebia* was preoccupied by *Palæophlebia* Brauer, and suggested *Epiophlebia* to replace SELYS's name. Three years later, HANDLIRSCH, in *Die Fossilen Insekten*, proposed the term *Neopalæophlebia* for *Palæophlebia* Selys, but both names must fall as synonyms of *Epiophlebia*.

on the Cordulines (1906) and three on the Æschnines (1908-9), by M. RÉNÉ MARTIN, and five on the Libellulines (1909 onward) by Dr. F. RIS.

The fascicules on the Cordulines and the Æschnines are essentially expansions of DE SELYS's own publications on these groups, with the addition of such genera and species as were unknown at those earlier dates. That on the Cordulines has given rise to two attempts to establish a more natural classification of this subfamily by WILLIAMSON (1908) and by NEEDHAM (1908) respectively, based on venation, and to still further modifications, in which both larval and adult characteristics are taken into account by TILLYARD, in an excellent *Monograph of the genus Synthemis* (1910), and in later articles (1911).

The fascicules on the Libellulines represent an enormous amount of work on the part of their author, Dr. RIS, not only because of the very great number of forms which this subfamily contains, but also because of the inherent difficulties of the group itself. DE SELYS had never outlined a classification of the Libellulinæ, the only subfamily which even his long life did not enable him to reach. Although BRAUER (1868), KIRBY (1889), and KARSCH (1890) had revised the genera from time to time, no one had attempted to describe all the species and refer them to their genera in one monographic treatment. This is the task which Dr. RIS has on his hands and for which he receives the hearty thanks of Odonatologists everywhere.

It is of interest here to point out that the starting-point for the arrangement of the genera within the Cordulinæ by NEEDHAM (1908), and within the Libellulinæ by RIS in the work just noticed, is the similarity of form and venation in fore- and hind-wings, a point of view not taken in DE SELYS's work.

Other articles in which some of the larger features of the classification of the Odonata have been considered are those of CALVERT (1902) on Zygoptera, NEEDHAM and HART (1901) on the Æschnidæ (*sensu Selysii*), NEEDHAM'S reports (1901, 1903) on the *Aquatic Insects of the Adirondacks*, TILLYARD in his *Synthemis* monograph (1910) already quoted, and MARTIN'S Æschnines (1911) in the *Genera Insectorum* of WYTSMAN.

The taxonomic study of the larvæ has also made great progress, and the number of species whose early stages have been distinguished is very great as compared with those so known in 1895. For this advance we are principally indebted to NEEDHAM (1901–1903, etc.) for North America, LUCAS (1900) in England, ROUSSEAU (1908, 1909) in Belgium, RIS (1909) for Switzerland and Germany, and TILLYARD in Australia. These specific identifications were chiefly made by actual rearings of larvæ to the imago. By microscopic examination of the rudimentary larval wings, NEEDHAM (1904, etc.) has been able to recognise the venational peculiarities of the future adults, and to determine the species by this method, which has been employed by other students also.

FOSSIL ODONATA.

MEUNIER has photographically figured (1896–1898 a number) of specimens from European museums, and COCKERELL (1907, 1908) has made known some interesting forms from Florissant, Colorado; but for the chief advance in this field, we are indebted to the voluminous handbook of HANDLIRSCH, *Die Fossilen Insekten* (1906–1908), of wide-reaching view, from which we have already quoted in dealing with the classification of the Odonata. HANDLIRSCH enumerates nine species of Paleozoic Protodonata from the Upper Carboniferous and the Permian of Europe (no Odonata being known from this series of rocks, nor are the Protodonata known from any later epoch), and of the Odonata proper, sixty-seven Mesozoic and ninety-two Tertiary species.

The Protodonata are considered to be ancestral to the Odonata and derivable from the still more ancient Palæodictyoptera, from which latter they differ by the narrower inter-alar tergites, the fusion of the basal parts of some of the longitudinal veins of the wings, the transformation of many longitudinal veins into so-called interposed sectors which apparently arise from cross-veins, and the presence of numerous, more regularly arranged, straight cross-veins.

On the other hand, the Protodonata differ from the Odonata by the lack of nodus, of pterostigma, and of the crossing of the radial sector over the first two branches of the media.[1]

[1] This last difference is denied by SELLARDS (1906).

A further advance in our understanding of the fossil Odonata, due to HANDLIRSCH, is in placing the Mesozoic forms in genera distinct and separate from those to which they had been referred previously. Their previous positions, as summed up in KIRBY's Catalogue of 1890, gave the false impression that many of our living genera reached backward to the Jurassic.

FAUNAL STUDIES.

Time and space forbid us to do more than mention the larger and more comprehensive papers or series of papers which have appeared in this division of the subject. The general distribution of Odonata throughout the world was summarised by CARPENTER in 1897. LUCAS (1900) has given us a volume on British Dragonflies, TÜMPEL has included the central European species in his *Geradflügler Mitteleuropas* (1898–1900), and FRÖHLICH (1903) has produced a work of similar scope for Germany, and KOHAUT (1896) for Hungary. RÖSSLER (1900), DZIEDZIELEWICZ (1902), PUSCHNIG (1905–1908), and STROBL and KLAPALEK (1906) have treated in considerable detail of the Odonate fauna of various parts of the Austrian Empire. For Italy are the memoirs of GARBINI (1897) and BENTIVOGLIO (1897–1908). NAVAS (1905–1910) has furnished much information for the Iberian peninsula, while the dragonflies of Russia, Siberia, and other parts of Palæarctic Asia are receiving attention from BARTENEF (1908–1912), whose papers, being in the Russian language, are unfortunately sealed to most of us. PETERSEN (1905–10) is the principal worker on the Scandinavian representatives of the Order.

For the Oriental region we have the series by KRÜGER on *Die Odonaten von Sumatra* (1898–1902), and papers by FOERSTER (1896–1905), KARSCH (1900), LAIDLAW (1902–1907), WILLIAMSON (1904, 1907), MORTON (1907), and NEEDHAM (1909) on other subdivisions.

The Ethiopian region has attracted much attention, and there are many memoirs by DE SELYS (1896–8), CALVERT (1896–8), KARSCH (1896, 1899), KIRBY (1896, 1900, 1909), FÖRSTER (1897–1909), SJÖSTEDT (1899), MARTIN (1900–08) and GRÜNBERG (1902–1903).

MUTTKOWSKI has given us a Catalogue (1910) of the Odonata of North America. KELLICOTT, HARVEY, NEEDHAM, WILLIAMSON, CURRIE, HINE, and MUTTKOWSKI have been the principal writers on the dragonflies of the United States, E. M. WALKER on those of Canada; the last-named having just published an admirable monograph on the Nearctic Æshnas (1912).

For Mexico and Central America is the Neuroptera volume of the *Biologia Centrali-Americana* by CALVERT (1901–08), the same author having also written extensively (1895–1912) on Neotropical Odonata, but especially on those of the province of Matto Grosso, Brazil. Important papers on South American forms are those of RIS (1904, 1908) and of FÖRSTER (1903–1910).

The last-named has also published much on the Australasian fauna, especially New Guinea, while in Australia itself TILLYARD (1906–1912) has given us a wealth of interesting observations on habits as well as taxonomic and distributional data. Among the last must be mentioned the discovery in New South Wales of a species of *Phyllopetalia*, a genus of large dragonflies hitherto known from Chile only; of the existence of so many species of the Corduliinæ as to amount to two-ninths of the total number credited to this subfamily (*sensu Selysii*) throughout the world, and representing fourteen genera out of a total of thirty-six. He has also brought forward evidence (1910) that the distribution of Australian Odonata on the whole is distinctly adverse to the acceptance of D. S. JORDAN's law, viz.: "Given any species in any region, the nearest related species is not to be found in the same region, nor in a remote region, but in a neighbouring district separated from the first by a barrier of some sort, or at least by a belt of country, the breadth of which gives the effect of a barrier." In the *Fauna Hawaiiensis*, PERKINS (1899, 1910) has described the Odonata of these interesting islands.

In such a survey as this, it is proper to notice the deaths of DAVID S. KELLICOTT, on April 13th, 1898, and of FRANCIS LE ROY HARVEY, on March 6th, 1900, who added much to our knowledge of the Odonata of Ohio and of Maine, respectively.

We have already alluded to the decease of Baron EDMOND DE SELYS-LONGCHAMPS. Two other entomologists of high repute must be numbered among the Odonatologists who passed away during the period under review—ROBERT M'LACHLAN, who died

May 23rd, 1904, and FRIEDRICH MORITZ BRAUER on December 29th, 1904. The principal entomological work of both lay outside the Odonata, although BRAUER did more synthetic work in this order than M'LACHLAN, especially on the Libellulinæ; but both have left their impress on the taxonomic and faunistic literature. ALPHEUS S. PACKARD, who died February 14th, 1905, was still less deeply concerned with the Odonata, but he was a distinguished entomologist, and he is to be remembered for his morphological work on the thoracic sclerites and the ovipositor of the dragonflies. Still more recently have we had to record the deaths of H. W. VAN DER WEELE on August 29th, 1910, and of SAMUEL H. SCUDDER on May 17th, 1911. VAN DER WEELE'S work has already been noticed; Dr. SCUDDER wrote on the Odonata of the White Mountains of New Hampshire and of the Isle of Pines, before he began those palæoentomological studies which have so largely contributed to his reputation, and which included careful original accounts of American Tertiary Odonata.

In conclusion, what has chiefly contributed to the progress of Odonatology during the period under review is the application of the developmental method as a means of tracing the origin, and so comprehending the significance, of the various parts of the Odonate's body. If the application of this method to these insects seems to students of other animal classes to have been slow, the excuse must be the great number of insect forms, the consequent great mass of detail to be mentally digested, and the relatively smaller number of investigators.

(In order not to unduly extend this paper, no bibliography is appended. The dates placed after each author's name will enable any one desiring to consult the original memoirs to find them by referring to the *Concilium Bibliographicum*, the *Zoological Record*, or the *International Catalogue of Scientific Literature, Zoology*, for the appropriate years.)