XII ON AN ANISOZYGOPTEROUS LARVA FROM THE HIMALAYAS (ORDER ODONATA.)

By R. J TILLYARD, *M.A., Sc.D. (Cantab.), D.Sc. (Sydney), F.L.S., F.E.S., Entomologist and Chief of the Biological Department, Cawthron Intitute, Nelson, New Zealand.*

(Plate XIII).

The Order Odonata is usually subdivided into two Suborders, the Zygoptera and the Anisoptera, of which the principal characters are by now so well known that it is not necesary to recapitulate them here. Besides these two universally recognised types, there existed in Liassic times an extensive group of Dragonflies, which, to a considerable extent, appears to have combined the characters of the two Suborders in approximately equal measure. Handlirsch, who has studied these insects carefully, has separated them out into a new Suborder, to which he gave the name Anisozygoptera.[1]

There exists at the present day, so far as is known, a single genus and species of Dragonfly, *Epiophlebia superstes* (Selys), from Japan, which appears to combine the characters of the Zygoptera and Anisoptera in such a manner that it may legitimately be classified in the Anisozygoptera, if Handlirsch's decision regarding the Liassic types be accepted. This remarkable dragonfly possesses a Gomphine type of coloration, a Gomphine form of head, thorax and abdomen, and an archaic Zygopterous type of wing-venation. In my book on the "Biology of the Odonata",[2] I included Handlirsch's Anisozygoptera within the Suborder Zygoptera, and have placed *Epiophlebia* in the family Lestidae, making it form by itself a subfamily Epiophlebiinae.

Up to the present time, the larva of *Epiophlebia* has remained undiscovered, though it is certainly the greatest prize awaiting discovery in this Order. It was safe to assume, considering the large number of larval characters in which the Zygoptera differ from the Anisoptera, that the discovery of this larva would definitely settle whether *Epiophlebia* was a true Zygopteron, as I had provisionally assumed, or whether it combined Zygopterous with Anisopterous characters in such proportion that it would support the recognition of Hardlirsch's new Suborder Anisozygoptera.

For a number of years Mr. F. F. Laidlaw, of Uffculme, Devon, has been working on the Odonate fauna of India. He has a wide knowledge of the whole Oriental fauna, and is our recog-

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[1] *Die Fossilen Insekten*, p. 463 (Leipzig, 1908).
[2] Pp. 276, 307 (Cambridge Univ. Press, 1917).

nised expert on the Dragonflies of this region. Recently a small collection of Dragonflies from the Himalayas was sent to him for determination. These were collected in June, 1918. In the consignment was a single larva, at first sight very much like a Gomphine larva, which was taken from a rapidly running stream, between Ghum and Sonada, (S. Kemp coll.) at the very high elevation of 7000 feet. The larva, to judge from the length of its wing-sheaths, which reach slightly beyond the end of the second abdominal segment, is in the penultimate instar. The wing-sheaths, of which a pair were dissected off, show the imaginal venational pattern fairly plainly, though the tracheation, of course, had collapsed through long immersion in alcohol. The result of Mr. Laidlaw's study of this interesting larva was to lead him to believe that it belonged to the genus *Epiophlebia*. This result was so startling that he had the larva and its wing-sheaths photographed at the British Museum, where he also consulted Mr. Herbert Campion as to its probable identity. As will be seen from the photographs, which are reproduced in plate XIII, it was scarcely possible to come to a definite conclusion on the matter, though Mr. Laidlaw felt very strongly that his original determination would prove correct.

On June 1st, 1920, I arrived in London from Sydney to attend the Imperial Conference of Economic Entomologists. Shortly after, I met Mr Laidlaw and Mr. Campion at the British Museum, where the photographs of the larva were submitted to me for my opinion. I must confess that from the photographs alone, I could see little evidence in support of Mr. Laidlaw's opinion. The general appearance of the larva is distinctly that of a Gomphine or Petaline, while the photographs of the wing-venation did not seem to me sufficiently definite to go upon one way or another. As the antennae were five jointed, the labial mask Gomphine-like and the tarsi of normal form and not formed for burrowing, I was inclined to see in this new form the missing larval type of one of the Chlorogomphinae, and suggested the genus *Orogomphus*.

The outcome of the discussions at the British Museum was that Mr. Laidlaw urged me to come down to Devonshire and study the specimen itself, and the slides which he had prepared from it. In July I had to go to Bristol for a few days, and this gave me the necessary opportunity of visiting Mr. Laidlaw for a week-end. I spent the greater part of the time studying this problematical larva, with the result that I came away fully convinced that it belonged to a new species of the genus *Epiophlebia*. I urged Mr. Laidlaw most strongly to write a paper upon it at once; but he most generously and insistently urged me, on the other hand, to undertake the work myself, and finally I consented to do so. He also lent me his notes and description of the larva, for use in the preparation of this paper.

I desire here to thank Mr. Laidlaw for his generous help and to state that full credit for the original determination of this larva as belonging to the genus *Epiophlebia* is due to him alone. I consider

that the evidence obtained from a study of the larva itself, and from the slides of the two wing-sheaths and the gizzard, prepared from it, is sufficient to prove this. Most unfortunately, Mr. Laidlaw did not succeed in obtaining a good preparation of the rectal region, the larva, when I came to study it, had had the contents of the distal half of the abdomen removed, so that we cannot now say whether it possessed any rectal gills, or, if it did, what type of gills they were.

In describing this larva, I propose to depart from a practice which I have hitherto followed most stringently, viz. never to give a name to a larval type. The reasons for this departure may be shortly stated here. Firstly, the larva is of such absorbing interest, that it seems necessary to give it a name, to facilitate future discussions upon it. Secondly, it seems reasonably certain that, if I refrain from naming it, after having described it, some, body else will certainly step in and do so seeing that the precedent for the naming of larval types has already been set up in America. And thirdly, as this is only the second species of the Suborder known to exist in the world to-day, the other being in Japan, the likelihood that *two species* of the same genus *Epiophlebia* would occur in one locality on the Himalayas, at such a high elevation, seems so remote that it may be reasonably ignored. That being so, it is clear that the figure given of the imaginal venation on the wing-sheath of the larva is, to all intents and purposes, an imaginal character, and sufficiently clear and detailed to make the recognition of the imago, when it is at last captured, a certainty. For these reasons, I have decided to name the larva, and now have much pleasure in dedicating the new species to my old friend Mr. Laidlaw in recognition of the fact that he was the first to determine its true affinities.

Epiophlebia laidlawi, n. sp.

(Plate XIII and text-figures 1–4.)

Description of the penultimate larval instar.

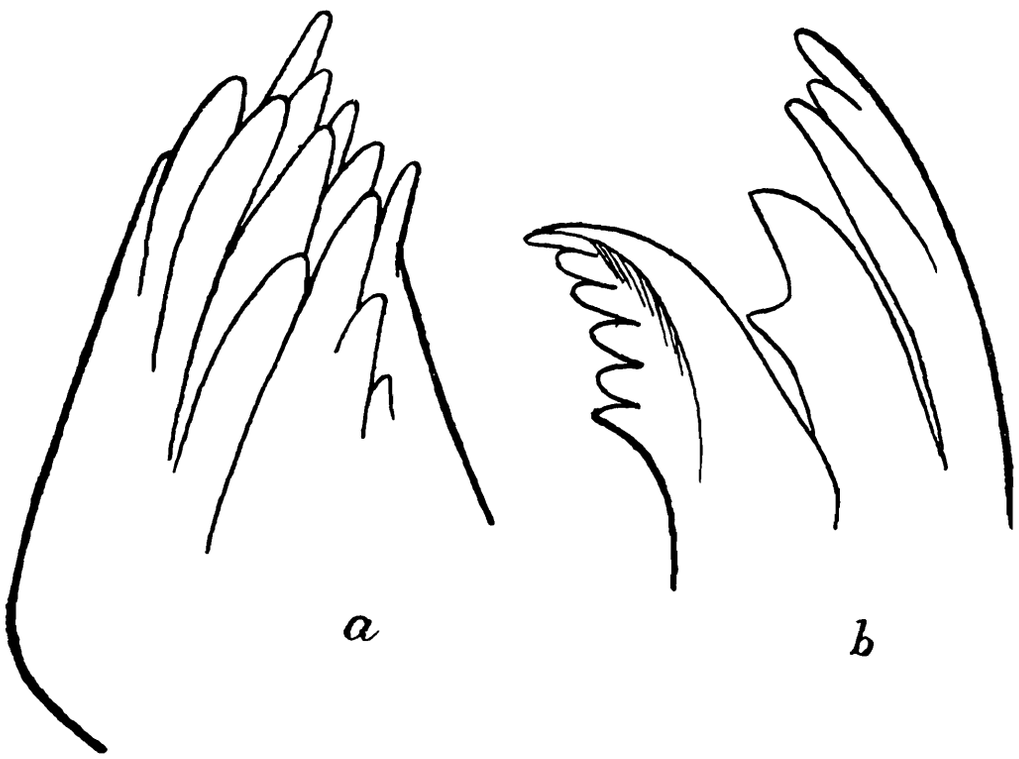
Total length 20.2 mm., *length of abdomen* 11·5 mm., *breadth of head across eyes* 5·3 mm.; *greatest breadth of abdomen at seventh segment* 5·4 mm.

Build stout, in general appearance superficially Gomphine-like but more closely resembling the larval type of the Petaliini. Hairs are entirely absent (except those of the maxillae, and a few small ones on the underside of the tarsi). Surface of the body and wing-sheaths strongly rugose, being covered with small, but very distinct, wart-like prominences. *General colour*, a medium brown.

Head.—Eyes large, dark brown, well-rounded, placed at the antero-lateral angles of the head. Postocular lobes well developed, somewhat projecting, convex externally, but cut off rather straight internally where they converge inwards to the rather narrow occipital region. *Ocelli* present, small but well marked, and placed far apart to form a triangle. *Antennae* (text-fig. 2*a*) stoutly

built, five-jointed, arising from the outer ends of an epicranial ridge bordering the crescentic line which marks the division of the epicranium from the clypeus; first and second joints (scape and pedicel) stouter than the rest, the pedicel about twice as long as the scape, its surface pitted all over; of the distalia, the third joint is as long as the fourth and fifth together, and slighty longer than the pedicel; the fourth joint is slightly narrower than the third, while the fifth is much narrower fusiform, and ending in a minute conical sense-organ. A deep groove separates the *clypeus* from the *labrum*, which is wide, and arched slightly from side to side.

The *mandibles* are shown in text-fig. 1. Each mandible is short with a broad base, and carries two series of teeth, one apical and

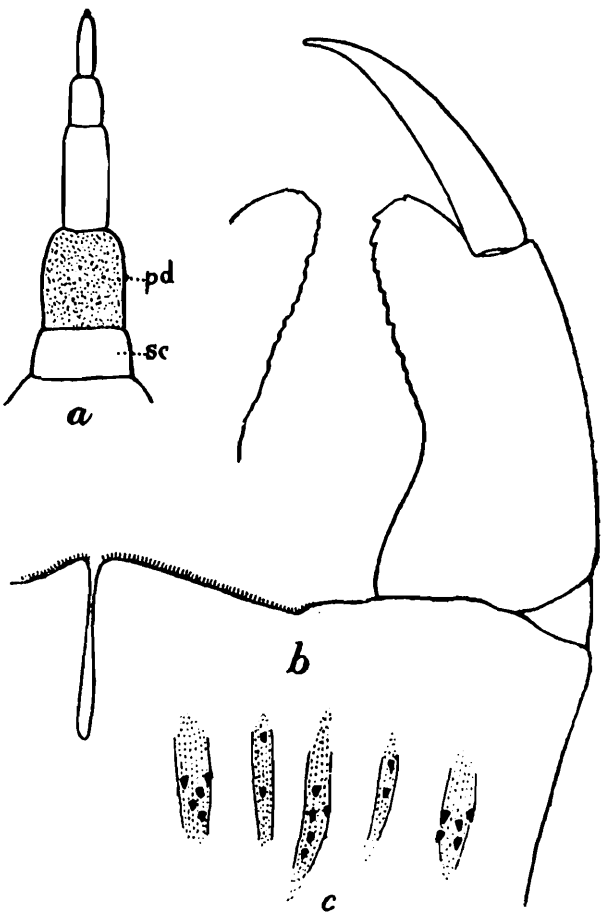


TEXT-FIG. 1.

Mandibles of the larva of *Epiophlebia laidlawi* n. sp. *a*, right mandible, viewed from the inner side; *b*, left mandible, similarly viewed but with the two lobes somewhat split apart.

one internal. They were studied by laying the larva on its back and pressing each mandible in turn outwards with the point of a dissecting needle. In doing this, the left mandible split apart down its middle, thus exposing more clearly the separate teeth forming the two series. The two mandibles differ greatly as may be seen from the figure. The right mandible (text-fig. 1*a*) has five prominent teeth in the apical series, all more or less conical, but the two end ones somewhat narrower than the others; the internal series consists of four larger teeth, conical, with somewhat rounded apices, together with a much smaller flattened tooth appressed to the surface of the outermost larger tooth, two smaller teeth placed internally from the fourth large tooth, and a large

tooth placed lower down and somewhat appressed into the space between the bases of the third and fourth teeth of the internal series. In the left mandible (text-fig. 1*b*), the apical series carries three narrow conical teeth on the outside, followed internally by a single large unequally bifid tooth, separated from the rest by a deep notch, the internal series consists of six smaller conical teeth with well rounded apices, all set in a row along the internal edge of the internal lobe of the mandible, from which the apical lobe was torn away somewhat during examination.



TEXT-FIG. 2.

a. Antenna of larva of *Epiophlebia laidlawi* n. sp. ; *pd*, pedicel, *sc*, scape. *b*. Part of the labial mask of the same larva, showing a small portion of the mentum, the median lobe with its median cleft, the right lateral lobe and movable hook, and part of the left lateral lobe (displaced), for comparison of its denticulation with that of the right side. *c*. Portion of the gizzard of the same larva, showing five consecutive dental folds, three major and two minor.

The *maxillae* have a well developed inner lobe, with five strong teeth; the palps carry some stiff hairs, and their tips are considerably hardened.

The *labial mask* (text-fig. 2*b*) is of the generalised type found in the Gomphinae and Petaliini. The submentum is short; the mentum somewhat longer than broad, the distal portion squarish, but narrowing towards the base; a median groove runs up from the base for more than two-thirds the length of the mentum. The median lobe is small, only slightly projecting, furnished with a

row of short hairs, and split in the middle by a moderately deep, very narrow, cleft. The lateral lobes are large, slightly concave internally, the distal border rounded, with a slight notch near the apex; the inner border is slightly and irregularly denticulate along the distal half of its length; the denticulations of the right and left lobes do not correspond, as may be seen from text-fig. 2*b*. The movable hook is large, strongly built, nearly as long as the outer margin of the lateral lobe below its insertion, and with a slightly nodding apex. No setae present either on the mentum or on the lateral lobes.

A comparison between this labium and the types found in the Gomphinae and Petaliini shows that it differs from them mainly in the relative proportionate length of the parts of the lateral lobes and movable hook. In the two groups mentioned the movable hook is always either longer than or at least equal to, the length of the margin below its insertion: the shorter movable hook here decribed suggests a comparison with the Megapodagrioninae and Synlestinae. The proportionate amount of projection of the apical portion of the lateral lobe, internally to the movable hook, is again much less than in the Gomphinae and Petaliini, while the notching of the apex, and the appearance of the most prominent denticulations just below it, suggest the beginnings of the division of this part of the lobe into distinct teeth, as in Zygoptera.

Thorax stoutly built, the *prothorax* without spines but with its antero-lateral angles produced somewhat cephalad, as two lobes with rounded apices. The prothorax and median portion of the synthorax are very strongly rugose or tuberculated.

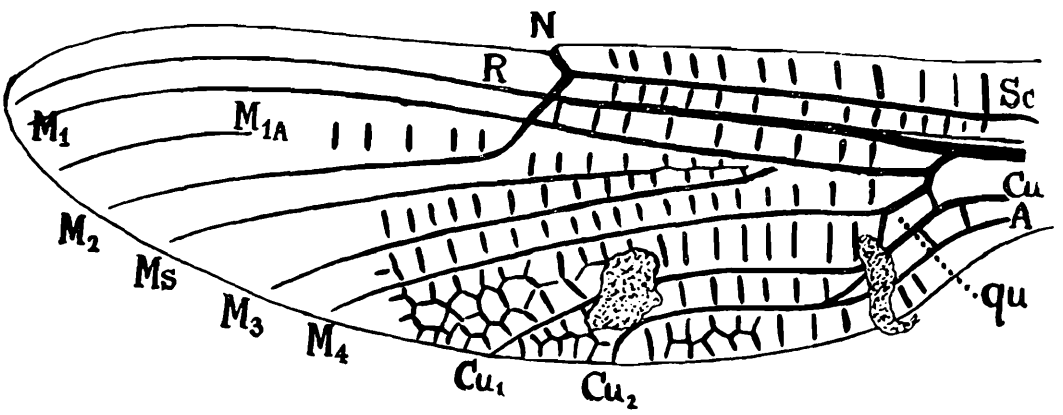
Wing-sheaths laid parallel along the middle line, those of the hindwing projecting backwards to about the middle of the second abdominal segment. This probably indicates that the larva was in the penultimate instar. The sheaths are hairless, but with some patches of dirt adhering to them; the sheath of the hindwing is a little broader and very slightly shorter than that of the forewing. (The right pair of wing-sheaths was dissected off by Mr. Laidlaw, as shown in plate XIII, fig. 1, and mounted on two separate slides, from which the photomicrographs in plate XIII, figs. 2, 3, were taken).

The *wing-venation* is of the very greatest interest. But a study of the photomicrographs shown in plate XIII, figs. 2, 3, although it reveals many points of interest, does not yield enough evidence to allow of a definite placing of the larva in its correct systematic position. After examining these, and also the slides from which they were prepared, I obtained Mr. Laidlaw's permission to cut off the *left* hindwing and examine it separately on a slide. The canada balsam mounts prepared from the right fore and hind wings were not satisfactory; hence I examined this further wing in 70% alcohol only By using a strong light, transmitted vertically upwards through the wing, it was possible to bring out much more definitely the pale bands foreshadowing the actual imaginal venation, especially on the basal part of the wing, which,

owing to its greater thickness, did not yield any very clear result in the photomicrographs. In drawing the left hindwing, I used an Abbe camera-lucida, and prepared a "negative" by the simple process of blacking in all the pigment bands which appeared pale on the wing itself. This "negative", which, of course, would represent very closely a "positive" of the imaginal wing, (in which the veins are black on a hyaline background), is reproduced in text-fig. 3.

The cross-venation of the distal part of the wing was not definitely enough outlined to allow of the drawing being completed distally; but a fairly good idea of the position of the cross-veins in this part of the wing may be obtained from a study of the photograph of the *right forewing* in plate XIII, fig. 2.

In the left hindwing, the number of actually visible antenodals of the first series is twelve, of the second series fourteen; none of these appear to correspond exactly except the first and fourth



TEXT-FIG. 3.

"Negative" of imaginal venation in left hind-wing of larva of *Epiophlebia laidlawi* n. sp. *A*, anal vein; *Cu*, cubitus with its branches Cu_1, and Cu_2; *M*, media with its branches M_1, M_2, M_3, and M_4, ; M_{1A}, postnodal sector; *N*, nodus; *qu*, quadrilateral; *R*, radius; *Sc*, subcosta.

of the first series, which are in line with the first and sixth respectively of the second series. These, moreover, are much more strongly marked than any of the others. Consequently it seems a legitimate assumption that they represent the two so-called "hypertrophied" antenodals, which are found in all the Anisoptera, but outside of that Suborder only in the genus *Epiophlebia*. From the photograph of the right forewing (plate XIII, fig. 2) it can be seen that there are eight or more postnodals, though the exact number cannot be determined.

The nodus is <—shaped and very clearly marked, with M_2 arising directly from the subnodus below it. I have not marked the position of the oblique vein in text-fig. 3, as I could not make out the cross-veins clearly in this region of the wing, but in the photograph of the right hindwing (plate XIII, fig. 3), the oblique vein can be clearly seen, lying about three cells distad from the origin of M_2, below it.

In the right forewing the pterostigma can be seen to be about three times as long as broad and covering several cells.

There are no interpolated veins, except only M_{1A}, which can be clearly seen, both in text-fig. 3, and in the photograph of the right forewing.

Ms is a nearly straight vein lying below, and almost parallel with, M_2. Its anterior portion, forming the so-called "bridge vein", is clearly marked, though the pigment-band becomes very thin basally, so that it is impossible to determine whether it arises from M_{1+2} above, or from M_3 below. It is quite clear, however, that its point of origin lies not far distad from that of M_3, far basad from the subnodus. The origin of M_3 appears to be placed closer to the arculus than to the level of the nodus, viz. about four or five cells distad from the arculus. M_3 and M_4 are nearly parallel for most of their lengths, and are separated by a single row of cells, except for a short space distally.

The arculus is strongly marked, with the sectors arising separately near its middle. The quadrilateral can be quite clearly seen in the left hindwing; it is broad, strongly built, with the lower distal angle about 45°, and the upper or costal side only about two-thirds as long as the lower or anal side. The basilar space is broad and free. The discoidal field is broad, but carries only a single row of cells for the first half of its length; distad from this, M_4 and Cu_1 diverge widely, so that the number of cell-rows rapidly increases. In the right forewing, the quadrilateral can be seen to be considerably narrower than in the left hindwing.

Between the cubitus and anal vein, basally, there is a clearly marked cross-vein lying basad from the quadrilateral; this is certainly the *anal crossing*, *Ac*. Further distad, under the quadrilateral itself, there is another cross-vein. The anal vein itself appears to run without any break below the quadrilateral, and Cu_2 leaves the distal angle of the latter obliquely, and joins the anal vein at a fairly acute angle. Thus the continuation of the vein which we usually call Cu_2 appears, in the wings of this larva, rather as if it were really *A*, with Cu_2 descending like an oblique vein upon it.

Cu_1 and Cu_2 are separated by a single row of cells for most of their lengths. Distally, however, Cu_2 arches strongly over before reaching the wing-margin, so that the number of cell-rows above it is much increased. Cu_1 ends up very slightly beyond the level of the nodus, Cu_2 somewhat before the same level, the ends of the two veins being separated by six very small but quite clearly marked cells.

The very distinct narrowing of the base of the larval wing shows quite clearly that the imaginal wing is of a somewhat petiolate type. The most basal cross-vein visible in the anal space is situated distad from the level of the arculus; in fact, it lies distinctly beyond the level of the cross vein already noted as occurring in the subquadrangular space, below the quadrilateral itself.

Two patches of dirt which I failed to remove from the wing are shown *in situ* in text-fig. 3. They do not hide any important details.

The *legs* are fairly short, the hind femora reaching nearly to the middle of the sixth abdominal segment. The femora are fairly wide, flattened; they carry two longitudinal ridges anteriorly and a single well marked ridge posteriorly. The tibiae are much narrower than the femora, but similarly ridged. The tarsi are three-jointed, not constructed for burrowing or digging, and having the third or apical joint longest. The claws are well developed, with strongly hooked ends. Ventrally, the last tarsal joint carries a well defined ridge furnished with hairs on either side, and projecting slightly as a small rounded prominence between the claws.

Abdomen broad, subcylindrical from base to seventh segment, then tapering rapidly to anal end. Dorsal surface generally convex, carrying a low median ridge interrupted segmentally, and having on each segment, from 1 to 8 on either side of this median ridge, a set of four shallow hollows separated by narrower, low ridges. On segments 2 to 9 the median ridge is notched anteriorly by a somewhat triangular, narrow slit or hollow. The ridges are more strongly rugose or tuberculated than the hollows. Neither dorsal nor lateral spines are present, but the lateral angles of the segments, dividing the dorsal from the ventral surface, are strongly marked. The ventral surface is somewhat flattened, trilobate in form, the middle division being slightly convex, the two lateral divisions flattened. From 1 to 7, the segments become consecutively slightly longer and wider; 8 is somewhat longer than 7, but not quite so wide; 9 is both shorter and narrower than 8, but is produced backwards on either side so as to embrace 10, which is very narrow, and about half as long as 9 measured mid-dorsally. The rudiments of the male valvules are visible ventrally on segment 8.

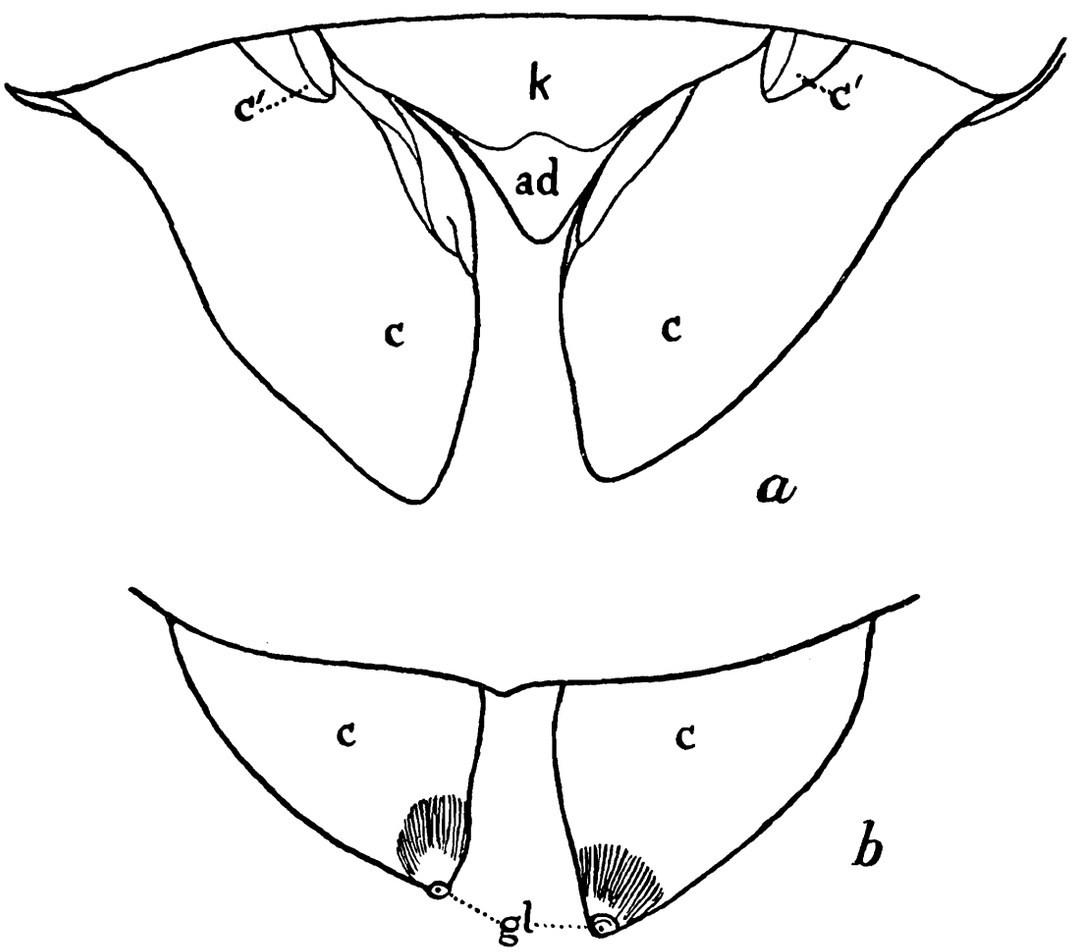
Anal Appendages:—Caudal gills are not present. The appendages may be said to be generally similar to those of the Anisoptera, but possess at least one feature not before noted in any type of anal appendage within the Odonata (text-fig. 4).

The *appendix dorsalis* (text-fig. 4 *ad*) is small, not as long as segment 10, and triangular in shape. Dorsally it carries a raised area which is somewhat bifid in the middle of its distal margin (text-fig. 4, *k*); this would appear to indicate the position of the involucre of the male inferior appendage.

On either side of the appendix dorsalis can be seen the small and somewhat conical *cercoids* (*c'*), which become the superior appendages of the imago.

The *cerci* (text-fig. 4*c*) are broad and somewhat leaf like appendages, more than twice as long as the appendix dorsalis. They are placed far apart at their bases, which are broad, and converge inwards towards their tips, which are well pointed. Their internal sides, bordering the appendix dorsalis, appear to be rather complexly folded; but this may be partly due to the mode of preservation of the specimen.

Viewed ventrally, the cerci show at their apices a very conspicuous whitish swollen area, which is protected by a brush of strong, stiff hairs arising from around its base. The tip of this swelling, which is also the apex of the cercus itself, carries a tumid pore (*gl*) evidently the opening of some gland or internal cavity. One might perhaps hazard the guess that water may be drawn in through these pores, and that by this means the cerci first began to function as gills. These structures are, in any case, unique amongst Odonate larvae, and are therefore of the greatest interest.



TEXT-FIG. 4.

Anal appendages of larva of *Epiophlebia laidlawi* n. sp. ; *a*, dorsal view ; *b*, ventral view. *ad*, appendix dorsalis ; *c*, cerci ; *c'*, cercoids ; *gl*, pore at apex of cercus ; *k*, involucre of male inferior appendage of imago.

If more material of this species, properly fixed, could be obtained, the internal morphology of these organs should most certainly be carefully worked out.

Gizzard :—The gizzard was extracted by Mr. Laidlaw, and the following description is made from a study of his slide.

The armature consists of sixteen *dental folds*, eight of these being major folds and eight minor. All the folds carry only generalised, separate teeth. A feature not before noted, I believe, in any Odonate gizzard, is the further specialisation of the eight major folds into four distinctly broader and shorter, and four

distinctly narrower and longer ones, in text-fig. 2*c*, two of the former and only one of the latter are shown. The minor folds alternate, as usual, with the major, and the two types of major folds also alternate with one another. Each major fold carries from four to six, or even in one case, seven teeth, the usual number being five. Each minor fold carries from two to four teeth only, the usual number being two. The teeth are placed irregularly on the fold, those of the broader major folds tending to become grouped close together, while those of the narrower tend to become arranged into a single longitudinal line. The teeth are subconical, set on fairly broad bases, and having their apices somewhat hooked.

It will be seen that this type of gizzard comes closest to the more generalised type of sixteen-folded gizzard, which is found in the Calopterygidae and the older sub-families of the Agrionidae. The folds are, however, more reduced than in the generalised type and carry a much smaller number of teeth; in this respect the gizzard shows some affinity with that of the Synlestinae, though this latter has undergone reduction to a total number of eight folds. One might also see some affinity with the eight-fold gizzard of the Petalurinae, in which the reduction of the individual folds has proceeded even further, there being seldom more than two teeth on any given fold.

The structure of the rectum could not be studied, as it had been removed. In his notes, Mr. Laidlaw remarks: "I have failed to make any satisfactory preparation of the rectum."

Type.—Specimen No. 1448/H2 in the collection of the Indian Museum at Calcutta.

Habitat.—Rapidly running stream, 7000 feet above sea-level, between Ghum and Sonada, Darjiling district, Himalya Mountains.

Discussion of the systematic position of the larva.

In dealing with this problem, we may begin by listing those characters which appear to be Anisopterous into one column, and then arranging in another column those characters which appear to be Zygopterous. We then get the following result:—

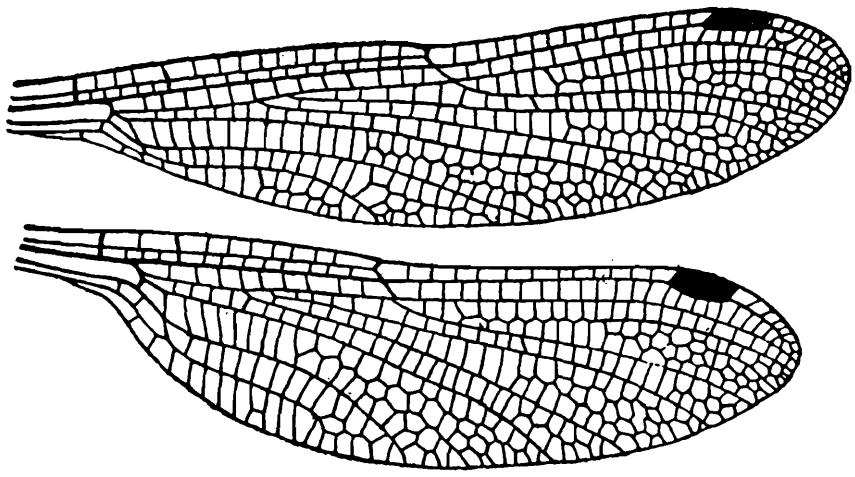
Anisopterous Characters.	*Zygopterous Characters.*
General build and facies of the larva.	Wing-venation.
Labial mask.	Gizzard.
Anal appendages.	

In addition to these, we may say that the characters offered by the antennae and legs do not incline us perceptibly towards the one Suborder more than the other.

Bearing in mind the fact that the Petalurinae alone of all known Anisopterous types possesses a gizzard of eight folds, while all the rest of the Anisoptera have only four, I have always been prepared to admit the likelihood of eight folds occuring in the gizzard of the so far undiscovered larva of the Chlorogomphinae,

though I think it much more unlikely that there should be sixteen. Apart from this, the general build of this larva, the form of its labial mask, and the structure of the anal appendages, might very well be those belonging to this sub-family. It is, therefore, to the wing-venation that we must finally turn for a decision. That is absolutely conclusive. After a careful study of the two slides of the right wings prepared by Mr. Laidlaw, and a more detailed study of the left hindwing dissected off by myself, I have no hesitation in saying that this larva belongs to the family Epiophlebiidae and that there is no character visible in the venation which would require its allocation to any other genus than to *Epiophlebia* itself.

In text-fig. 5, I show the venation of the imago of *Epiophlebia superstes* (Selys) from Japan, in order to institute a close compar-



TEXT-FIG. 5.

Venation of *Epiophlebia superstes* (Selys) from Japan, (Hw. 31 mm.) After Needham.

ison with that of the larva here dealt with. It will be seen at once that, if we allow for the fact that the wing is not yet expanded, the comparison is overwhelmingly in favour of the conclusion that the larva belongs to the genus *Epiophlebia*.

The characters in which *Epiophlebia* differs from all other known non-Anisopterous genera are the following :—Presence of the two thickened or "hypertrophied" antenodals; difference in the shape of the fore and hindwing quadrilaterals, the latter being much wider than the former, and both being acutely angled distally, form of the discoidal field, which is strikingly broader than the spaces above and below it, but at the same time possesses, for most of its length, only a single row of cells.

Each of these three important characters appears to be present in the larval wings exactly as in *Epiophlebia*.

This evidence should be sufficient to place the larva within the family Epiophlebiidae. But we may reinforce it by enumerating the other venational characters, which, though not peculiar to *Epiophlebia*, are to be found in that genus, and which, taken together with the three characters mentioned above, practically define the genus as far as its wing-venation is concerned. These

are:—the slightly petiolate wing-base; the <-shaped nodus placed about half-way along the wings; the form of the pterostigma, strongly built, elongated, about thrice as long as broad; the presence of the oblique vein; the absence of any straight or well formed supplementary sectors except M_{1A}; the positions of the points of origin of *Ms* and M_3, the origin of M_2 directly from the subnodus, the great divergence of Cu_2 from Cu_1 distally, with the strong arching of the former, especially in the hindwing. All these characters are to be seen in the wings of the larva here under discussion.

We may now reinforce the argument from the wing-venation by considering the general build and facies of the larva. This is undoubtedly Anisopterous. What non-Anisopterous types are there known which could conceivably possess a stout larva of this type? Most certainly only those genera of stout, heavy build. The only two non-Anisopterous types known which could possibly satisfy these conditions are *Philoganga* and *Epiophlebia*. *Philoganga* is such a huge, clumsily built insect for a Zygopterid that it might well possess such a larva as this, also, the locality in which the larva was found might well be a habitat for this Oriental genus. Many details of the venation, however, preclude our acceptance of this solution. *Philoganga*, for instance, to mention only a few obvious characters, has no hypertrophied antenodals; its nodus is much closer to the base of the wing than to the pterostigma; it has no oblique vein between M_2 and *Ms*, its quadrilateral is almost rectangular, and extraordinarily short, nor does it differ much in fore and hind-wings; its discoidal field is much narrower than the space below it; and Cu_2, instead of diverging from Cu_1 distally, converges towards it. Thus we may with safety rule *Philoganga* out.

There remains, then, *Epiophlebia* as the only possible known genus in which the general build of the imaginal body would lead us to expect a stoutly built larval type of the form we have here. The general build of *Epiophlebia*, apart from the wings, is distinctly Gomphine, the same may be said of the larva before us.

To settle the question whether we ought to place this larva in the genus *Epiophlebia* itself, or relegate it to a new genus in the family Epiophlebiidae, we have to rely only upon the wing-venation, since the larva of the only known species of *Epiophlebia* has not yet been discovered. Against the overwhelming array of characters which we have marshalled, in which the wings of this larva agree with those of *Epiophlebia superstes*, we can only mention the following doubtful points: the peculiar condition of the anal vein which appears to run continuously through to Cu_2, receiving the basal portion of that vein from above like an oblique vein, and the presence, in the hind-wing, of a double row of cells for five cells' length, between Cu_2 and the posterior margin of the wing; whereas, in text-fig. 5, the hind-wing of *E. superstes* is shown with only one divided cell in this area.

Regarding these points, it can easily be seen that, in the process of expansion of the wing at metamorphosis, the slight angula-

tion of *A* at its junction with Cu_2 might be brought about as a purely imaginal character. Also, the pigment bands of the larval wing are so wide that, even if some slight angulation is really present there, it might easily be overlooked. As regards the double row of cells below Cu_2 in the hind-wing, it may be noted that a closely similar set occurs in the *forewing* of Needham's specimen (text-fig. 5); so that we may regard this character as being probably a variable one in the different wings of separate individuals of *E. superstes*. Even if we grant the presence of these differences, they are not of greater moment than such as we should expect to find in two species of the same genus, from such widely different localities as Japan and the Himalayas.

From the above evidence, it may, I think, be legitimately concluded that the larva belongs to the genus *Epiophlebia*.

The Suborder Anisozygoptera.

We have still to answer the question as to whether the erection of the Suborder Anisozygoptera by Handlirsch was justifiable; and, in particular, whether the discovery of this larva adds to or detracts from Handlirsch's opinion.

It seems clear that we must now answer this question in Handlirsch's favour. For a more complete blending of Anisopterous with Zygopterous characters, within one single larval type, could scarcely have been hoped for, even by the most ardent supporter of Handlirsch's view. The larval evidence is so strong that, taking it in conjunction with the imaginal characters already known, I have no hesitation now in accepting Handlirsch's Suborder Anisozygoptera, and, consequently, a family *Epiophlebiidae* must also be recognised. Also, as it is clear for many reasons that the fossil type *Heterophlebia*, from the English Lower Lias, is a close ally of *Epiophlebia*, and the same is true of the genus *Triassolestes*, from the Upper Trias of Ipswich, Queensland, it follows that this Suborder is the oldest of the three at present existing, so far as our evidence goes. The fact that we have, in *Heterophlebia*, a type in process of changing from an Anisozygopteron to a true Anisopteron, by formation of a true triangle and supertriangle in the hind-wing, seems to indicate clearly enough that the Anisoptera are descended from the Anisozygoptera; and, indeed, true Anisoptera do not appear in the fossil record before the Upper Lias. There does not seem to be as definite evidence that the Zygoptera are descended from the Anisozygoptera, for there are certainly *some* venational characters, notably the absence of an oblique vein, in which the Calopterygidae still remain more generalised than *Epiophlebia* and its allies. Our decision in this case would probably rest upon what forms amongst the earliest known fossil Odonata we were prepared to accept as Anisozygopterous, on the evidence of their wing-venation, and what forms we considered Zygopterous. Probably the earliest true Odonate type combined the more generalised characters of the Calopterygidae on the one hand with those of the Epiophlebiidae on the other. Such a type

might very well have arisen, in its turn, from that remarkable group of Protodonata of which *Typus permianus*, discovered by Dr. Sellards in the Lower Permian of Kansas[1] was a representative.

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[1] *Amer. Journ. Sci.* (4) XX, pp. 249-258 1906.