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STUDIES IN THE LIFE-HISTORIES OF AUSTRALIAN ODONATA.

i. The Life-History of *Petalura gigantea* Leach.

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(Plate xxiv.)

The student of Nature who lives in a country like Australia, where new forms are still to be found everywhere, will, it is to be hoped, refuse to be carried away by the mere desire of describing and naming them, and treating them as mere specimens to be put away labelled in a cabinet. A chapter in the book to which he aspires to contribute should not be all, as it were, index. The most important part of the work to be done is not the mere "manufacturing" of new species, nor the "proposing" of new genera. Important as these may be for the furtherance of the systematic study of groups, yet of far greater value, both to the systematist and the nature-lover, is the study of the individual life of new forms. The era of mere species-making is passing away, and the demand is more and more for light to be thrown on the strange habits of unknown Nature.

I feel that I owe an apology to many who passed over my first attempt at a "life-history" without comment, for that somewhat crude, and, in one respect at least, inaccurate account of the life-history of *Lestes leda* Selys, contributed by me to these Proceedings in 1906. Before entering on further work of the same sort, I am bound to correct the error, first pointed out to me by Mr. W. Gurney, which I made concerning the oviposition of that species. Mr. Gurney has seen the male and female descend into the water and place their ova in the tissues of water-weeds; and I have, since that time, repeatedly seen the oviposition carried on in a similar manner, but with only the tip of the female abdomen

submerged. One can often gather a stem or leaf of water-weed punctured all over by this common insect, and a little careful observation will show the colourless transparent eggs in the tissue.

Since I wrote the paper referred to, I have been able to obtain many useful works of reference on Odonata which I lacked before, and from which it is clear that the general habits of the genus *Lestes*, with one or two exceptions, are the same the world over. With the detailed knowledge contained in the works of de Selys and others, it would have been impossible to have committed the error I did. I have therefore studied carefully all the information I have been able to obtain concerning the known life-histories of species from other countries, before venturing to publish any more of my own observations on Australian species.

Many species are exceedingly difficult to keep and breed out in aquaria. They apparently do not take kindly to artificial conditions. One has to be always on guard against their cannibalistic propensities, and only a few nymphs of any of the larger kinds can be kept with safety even in a large aquarium. Worst of all is the apparent inability of the full-fed nymph,—in the case of the *Libellulidæ* and *Gomphinæ*—to climb out of the water and undergo transformation. Only with the greatest difficulty can they get up slanting twigs; and it is necessary, for success, to give them a shelving bottom up which they can crawl to dry land. Once out of the water, they seem able to negotiate vertica stems of grass or twigs with fair success, although they generally prefer a clump of several stems together, or, in many cases, remain on the ground to undergo the change.

Breeding the nymph is after all only a small part of the study of life-histories. More can be done by spending long days in the spring and summer, watching the insects in their natural haunts. Besides the method of oviposition, there is need to observe carefully the methods adopted by the males to capture the females and hold them securely during the process of copulation. In this act the accessory appendages of the male, and the head and thorax of the female play a prominent part, and the exceed-

ing difficulty of capture and copulation on the part of some dragonflies is evidence of special precautions developed by Nature to prevent hybridisation. In those families where one form and one colour-pattern predominate, many species can scarcely be distinguished except by means of the parts used in coition, and these may be so diverse in closely allied species as to prevent the accidental copulation of the male of one species with the female of another, captured by mistake. I have myself seen a male of *Austrogomphus collaris* Selys, seize a female and vainly attempt copulation. After a considerable time the attempt was abandoned, whereupon a second male seized the same female and effected connection almost immediately. Here there was probably some local deformity in the first male, which prevented him either from holding the female securely or from completing the act of coition.

The method of oviposition apparently determines the shape of the egg, and often the habits of the larva. In all species where the egg is deposited in tissue by means of the sharp ovipositor of the female, it is of an elongated oval shape, evidently a suitable form for inserting into the narrow opening prepared for it. Where the egg is dropped into the water straightway, it is usually broadly elliptical or almost round, and the vulva of the female possesses no true boring apparatus. Again, the larvæ of nearly all the former species—those having elongated ova—are clean-living insects, inhabiting floating masses of waterweed; while those of the latter crawl on the trashy bottoms or burrow in the sand or mud, and are often very hairy and covered with mud.

The life-histories of all those species peculiar to Australia—with the exception of *Lestes leda*—are quite unknown. Included amongst these are many ancient and isolated forms, true collective types, with no very near allies in other parts of the world; such for example as *Cordulephya*, *Synthemis*, *Petalura*, *Diphlebia*. The larvæ of these four are amongst the greatest desiderata of present-day systematists in Odonatology, and much light may be expected to be thrown on the present methods of classification by their discovery. Fortunately, species of all four genera occur, though not commonly, within 100 miles of Sydney. I have, therefore, while not neglecting less interesting forms, paid as much attention as possible to these, and have achieved a fair measure of success with them. In the first part of this paper, then, I offer the results of my observations upon that remarkable denizen of the Blue Mountain region, *Petalura gigantea*.

The apparent rarity of this huge dragonfly made me almost despair of ever discovering anything about it. During my first four years in Sydney I never saw a single specimen on the wing, though I received on an average about one a year from friends who visited different localities in the Blue Mountains. Mr T. Steel, who has been kind enough to send me from time to time dragonflies from various localities, assured me that he had seen this insect fairly commonly one year in an open space near the Katoomba railway station. This remark put me on the right track. I determined to spend much of my spare time last season in the vicinity of Katoomba For this purpose I selected the small creek running over the Leura Falls, and nearly every Saturday during November and early December, 1908, I made the journey up to Leura and spent all day on the creek. Careful dredging of the weeds and sandy bottom of the clear running stream yielded few larvæ of any kind, the creek being little more than a rocky cataract in most places. Working up, however, away from the Falls, the source of the stream is reached in little over a mile, and consists of a large teatree swamp, at the head of which there is nothing but vile mud and decaying vegetable matter, of an average depth of one foot or more. On November 21st, 1908, just as I had decided to give up for the day, I found my first pair of *Petalura* exuviæ clinging to grass stems above a small mud hole of filthy mud and water that had clearly been made by a post, since removed. During the weeks that followed, I found many exuviæ, several just transforming, in the teatree stems and clumps of sedge in this muddy swamp. The matted stems of decayed vegetation made it quite impossible to use the net here to find living larvæ; nor was it possible to turn over large quantities of

the evil-smelling mass with the hands, so that I had to be content with the exuviæ, some specimens of which are quite perfect and quite as satisfactory as the living larva itself would have been.

Later on, in December, I took upwards of two dozen of the perfect insect in and about this swamp; in fact, they might be described as being fairly common in a restricted area of only a few acres. Outside of that, only a stray male was occasionally to be seen. I was able to determine many interesting points in their habits, though there are still one or two points requiring further elucidation. The following are the results of my study of this species in its native haunts :—

Method of Pairing.—Bearing in mind the unique form of the male appendages, I was most anxious to secure a pair in cop., to see how the male managed to hold the female firmly. During two visits I failed even to observe a pair together. On the next occasion I flushed a pair that had settled on a low bush. They dashed off at a terrific speed, crossed the creek, and settled on a branch of a large Eucalyptus. After approaching carefully, I was able to get underneath them and watch them, but they were too far above me for me to be certain of anything. A week later I came again to the same spot expressly to look out for pairs. Once a pair passed me flying swiftly, with the male apparently holding the female *by the underside of the head*; but this pair separated after executing several gyrations in the air, so that I could not be certain that the male had got a proper hold. Later on I captured another pair settled in some teatree, but unfortunately they separated immediately in the net. Finally, good fortune came my way, in the shape of a pair flying rapidly with the wind straight towards me. I held up my net and they flew straight in, and remained clinging to it. Not until I actually took hold of him did the male release his hold, so that I saw clearly the position he was in. The wide inferior appendage, pointed on each side, was pressed down tightly on the occiput of the female, on which a *very slight* eminence appeared to give a remarkable good hold. By this means the head of the female was pressed well back. The two large leaf-like appendages

enclosed the shoulders of the female, over which they fitted exactly. When the male exerted his full strength, these were pressed so far down as to bring the back of segment 10 of his abdomen into contact with the thorax of the female, and, at the same time, the head of the latter came back so far that the superior appendage became firmly wedged between the shoulder and the back of the eye. This pair was killed and set in position, but, during the process of drying, the original rigid position could not be retained. The sketch in Plate xxiv. (fig.1) shews them as they are at present in my collection, and may be taken to represent exactly the position of the appendages of the male *on first seizing the female.* It can be easily seen how further downward pressure would bring the dorsum of segment 10 of the male on to the thorax of the female, and the back of the eye of the female on to the superior appendage of the male. The whole position gives a strong grip, and justifies the existence of the petaloid appendage as a useful organ.

The most remarkable feature of it is, I think, the position of the inferior appendage. The occiput of the female has no large prominences or depressions, but its slightly raised surface seems to fit exactly the broad appendage of the male; while the curvature of the latter is such that the application of downward pressure from the abdomen forces the head of the female back, and, at the same time, keeps the appendage firmly in position where a slightly straighter appendage would most certainly slip.

When firmly held together, the pair rises into the air, and after a few preliminary evolutions makes straight for some high tree, on the branches of which they settle during the act of copulation. I have sometimes seen a second male, or even two, attack them when paired, but they did not succeed in effecting a separation. The seminal vesicle appears to be charged by the male *after pairing* and during the gyratory flight. He doubles himself completely up, and evidently only effects the operation with some difficulty, as he has to keep a firm hold of the female and also raise her with the end of his abdomen.

Oviposition.—After copulation, the pair separate, and the female hides herself in the teatree scrub at the head of the marsh.

I tried several times to watch the process of oviposition, but the females were so wary that they flew off rapidly as soon as I got close to them. All I can be certain of is that they are *not* accompanied by the male, and that they do not fly hither and thither over the marsh dropping their eggs into it. Every female I flushed appeared to be settled on or near the ground at the edge of a mass of decaying vegetable mud. The probability is that the eggs are actually inserted in decaying tissues. The female possesses a peculiar curved ovipositor, apparently quite suited to this purpose, and the shape of the egg also suggests it.

Ovum (Plate xxiv., fig.2), 1·7 mm. long, elongate-oval, semi-transparent, yellowish; pointed at one end, rounded at the other.

Larva-Nymph.—The larva lives in the foul muddy ooze of the teatree swamps, where there is no real standing water. It may in truth be said to be only semi-aquatic. During the summer these swamps become quite dry. Hence we must conclude either that the larva is perfectly able to exist on dry land, or buried in the dried mud; or that the egg does not hatch until the autumn. In either case, I think there is very little likelihood of its development extending over more than one season. An examination of the ooze will show that it contains hundreds of insect larvæ suitable as food for the voracious *Petalura*, and its growth is probably exceedingly rapid in so favourable a position.

The exuviæ are found clinging to the tufts of sedge or on to trunks of teatree, often being 2 or 3 feet above ground. They are very difficult to dislodge, the strong curved tarsal claws giving such a firm hold that usually the whole leg will come out of its socket before the tarsus can be freed. The only way to get perfect specimens is to take them as soon after emergence as possible, choosing those that have climbed into clumps of sedge. Cut the sedge with the scissors above and below the larva; it will then be found that each stem will slide out of its own accord. Some of these larvæ crawl three or four yards out of the mud before climbing a suitable twig. They are all caked with mud. In one part of the swamp they were all orange-yellow, in another grey, and in the peaty portion dull black.

The exuviæ, on being cleaned, show practically no pattern, The following is the description (Plate xxiv., fig.3):—

♂. Total length 49-50 mm. Head rather flat above, 10 mm. wide; *eyes* fairly large, not prominent; *back of head* well rounded, a small tuft of hairs just behind each eye; *ocelli* small, in a triangle, reniform; *antennæ* 5 mm. long, seven-jointed, curved (Plate xxiv., fig.5), the joints shaped as follows: 1, enlarged, hemispherical; 2, narrower, oval; 3, very narrow, cylindrical, longer than 2; 4, short, oval; 5, nearly twice as long as 4, oval, wider; 6, longer than 5, oval; 7, narrow, cylindrical, not so long as 5; *frontal ridge* small and narrow; *labrum* broad. Labium (Plate xxiv., fig.4) when folded naturally, 9 mm. long, greatest breadth 6·5 mm., joint of mask reaching to just behind procoxæ; *mentum* strong and thick, rectangular, rather flat, concave in middle as seen from below; a tuft of hairs on each side just below joint of lateral lobe; front edge of mentum projecting in a triangle in the middle, a small set of hairs on each side; *lateral lobes* 3 mm. long, 1·7 mm. wide in middle, outer border very slightly curved, rather square at top, inner border more curved, no angle or indentations at apex; *movable hook* 1·4 mm., very strong and thick, pointed, basal joint placed about three-fourths of the way along outer edge of lobe; edges of lobes well ridged, neither mental nor lateral setæ present. Thorax: *prothorax* well formed, nearly as wide as head, not ridged. *Meso-* and *metathorax* rather short, 10 mm. wide, fairly well rounded on each side. *Wing-cases* 13 mm., lying parallel along back of abdomen (in some exuviæ they are turned in all directions), hindwing projecting about 2 mm. beyond forewing and reaching to end of segment 4; width of forewing case 2·5 mm., of hindwing case 3 mm. *Legs* very stout and strong; *coxæ* rather large, 2 mm.; trochanters narrow, 1·5 mm.; measurements of femur, tibia and tarsus respectively as follows: foreleg, 8-9-3 mm.; middle leg, 9-9-3·5 mm.; hind leg, 13-11-5 mm. A tuft of hairs in front of profemora near bases, also a few hairs on protibiæ. *Tarsi* (Plate xxiv., figs. 8-9, protarsus) ending in two strongly pointed spines or hooks, much curved, above which are two smaller spines, also curved;

each tarsus is apparently 3-segmented; the divisions not clearly shown, but apparently slanting forward, and the two basal segments short and carrying a set of longish hairs on the inner side; end of tibia also with spines on each side, especially on the forelegs. Abdomen: length 32-33 mm., greatest breadth 10 mm. at segment 6; subcylindrical, widest at 6, then tapering to 10, which is only 4 mm. wide; dorsal surface well rounded, ventral surface rather flat, segments 1-8 carrying below two deep parallel indentations, separating each segment into a large and somewhat convex central area and a pair of narrower side-portions; *genitalia* showing plainly beneath 2 and basal half of 3. Segments 5-9 with soft hairs along apical sutures. Appendages (Plate xxiv., fig.6; *s*, superior; *i*, inferior appendage) of remarkable form; the superior appendages appearing as small rounded projections on each side, and the wide inferior appendage lying between and *above* them; anus lying between and somewhat below superior appendages, distinctly ridged underneath. The two small tubercles just visible on each side of the inferior appendage represent the two sharp points in the imago.

♀. Measurements usually the same as in the male (I have one dwarf female only 45 mm. long). *Abdomen* slightly wider and more cylindrical from 1-8. Segment 9 with ovipositor showing beneath as a broad and rather blunt curved projection reaching just on to 10. Segment 11 (= appendages in imago) somewhat tetrahedral in shape, with anus rather high up (Plate xxiv., fig.7, *a*, anus; *b*, ovipositor).

In a newly emerged male taken by me, the superior appendages were soft and damp, hanging straight downwards; the inferior was of a pale yellow colour and rather harder, and still having its side points above the superior. Evidently the insect places the latter in position by a muscular effort as soon as they are strong enough. I have also noticed that an immature male captured and placed in a paper triangle, will often force its inferior appendage up into position above the superior ones, which he depresses. Even in their natural position the points of the inferior appendage practically rest against the superiors.

Seasonal Range of Imago.—My first two exuviæ were found on November 21st, 1908; and new ones continued to be found up to December 12th. On December 5th, two males were found just emerging. On December 17th, no new exuviæ were obtained, and many of the imagines were considerably torn and aged. I have never seen this species during visits to Katoomba in early February. Hence its seasonal range is certainly a very short one, extending from the third week in November to about the end of January at the very latest. It is doubtful if many imagines would be found even in January.

Hab.—Blue Mountains and their southern and coastal spurs, N.S.W.

The *Petalurinæ* are, at the present time, only a remnant of a race long past its prime. Included in the subfamily are four genera: *Petalura* (Australia), *Uropetala* (New Zealand), *Phenes* (Chili), and *Tachopteryx* (N. America). A single female exuviæ of the latter has been described by Williamson (Entomological News, 1901, 12, 1-3, Pl. i.). A diagram of the labium and an antenna is inserted here for purposes of comparison. It will be seen that, broadly speaking, the labia of *Tachopteryx* and *Petalura* are very similar. The chief differences are as follow. In *Petalura* the mentum is not so wide as long; in *Tachopteryx* it is wider than long. The middle of the front edge of the mentum in *Petalura* projects forward in a triangle; in *Tachopteryx* it is slightly indented medially. The lateral lobes and movable hooks are very similar in both, though in *Tachopteryx* the former are apparently somewhat longer and narrower, and with the apices more suggestive of the *Æschnid* type than in *Petalura*.

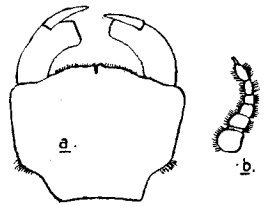


Fig. 1.—*Tachopteryx thoreyi* Selys (after Williamson). *a* labium, *b* antenna.

The antennæ agree in being seven-jointed. In the *Gomphinæ* they are usually four-jointed; in the *Æschninæ* a short, thick, basal joint is surmounted by five or six slender joints forming a slender filament. The antennæ of *Tachopteryx* are hairy, those

of *Petalura* smooth; while the joints of the latter are considerably longer and narrower than those of the former. It should be noticed that, in each, the fourth or middle joint is the shortest.

Like *Petalura, Tachopteryx* deposits its eggs in wet boggy places where there is scarcely any water. The habits of the two nymphs are probably exceedingly similar.

The only other *Petalurine* nymph known is that of *Uropetala carovei* White, discovered in New Zealand, and figured by Hudson ("Neuroptera of New Zealand"). The figure is a "popular" one, badly drawn, and nothing can be gathered either from it or the description.

If any lesson is to be drawn from the study of the early stages of *Petalura*, it seems to me to be that it is in reality a nearer approach to the *Æschnine* type than the *Gomphine*. If we could go back far enough to find the common ancestor of the two, would not its nymph show considerable similarity to that of *Petalura?* We might even trace the divergence of the two groups from one simple circumstance, viz., the natural selection of running water or stagnant marsh for the passing of the early stages. Given the former, it is clear that the ovipositor of the female would be brought more and more into use as a true "borer" by means of which the eggs might be safely lodged in stems in the quiet corners of a rushing stream; the body would become more slender, the antennæ more filiform; and the whole insect more active, thus producing the clean-living *Æschnid* type. On the other hand, if the female continued to deposit her eggs in the mud, what more natural than that she should gradually relinquish the use of the "borer" and just drop them into the mud, like the *Gomphinæ!* And the egg itself, being no longer inserted into a narrow cleft, but merely dropped, would tend to assume the more spherical form now found in all those families where the boring apparatus of the female has gone out of use. Later on, at a time perhaps when the huge swamps of the Mesozoic age were drying up and giving place to definite stream-beds, these early ancestors of the *Gomphinæ* would again be compelled to take to the rivers, where they would naturally

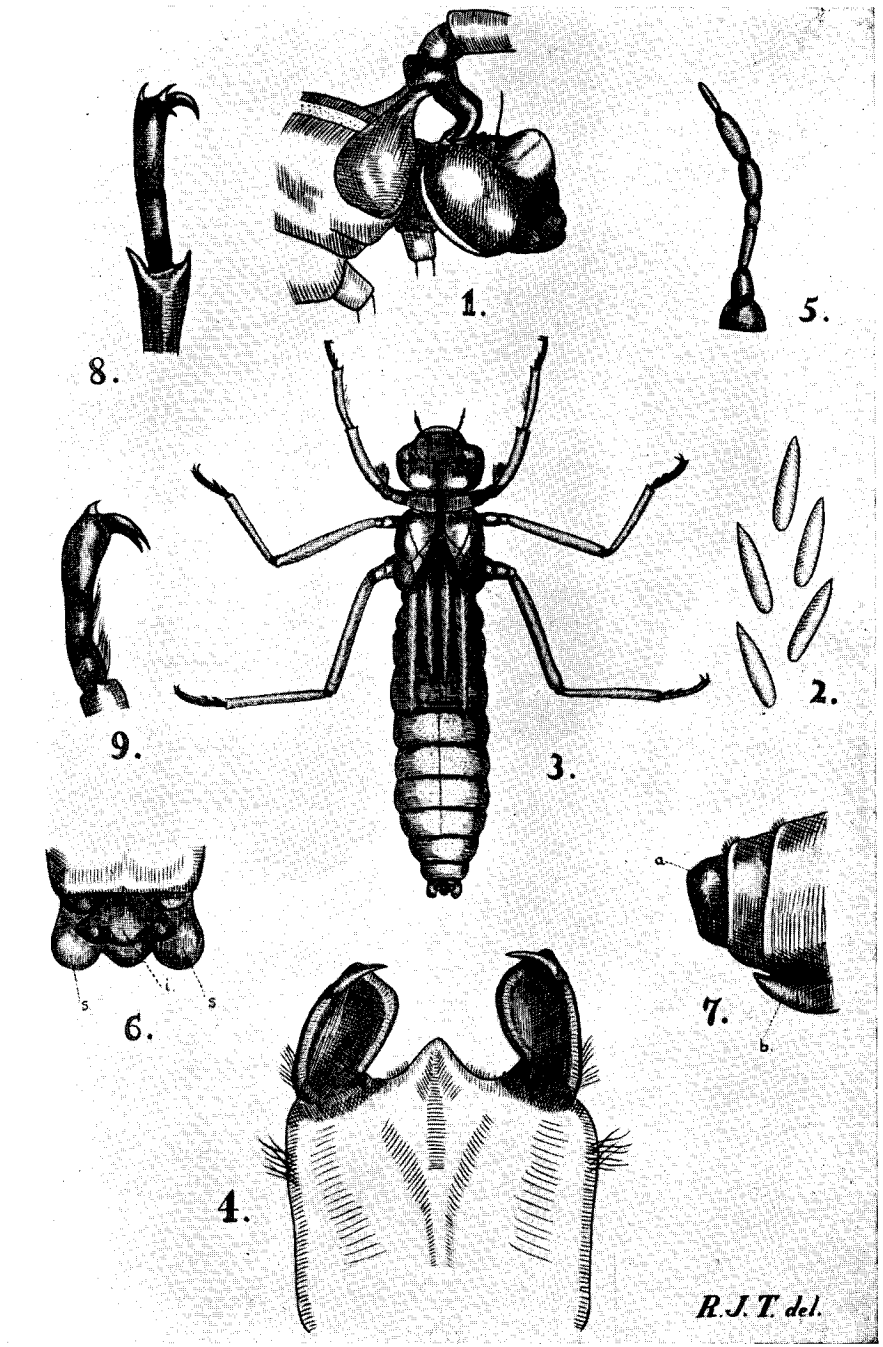
seek the protection of the river-bottoms by burrowing or burying themselves under trash and rubbish. Hence might arise a gradual reduction of the joints of the antennæ, the slender seventh joint first becoming obsolete, then the sixth and fifth, and finally the already small and weak fourth joint, which we now find in a rudimentary state in the present *Gomphinæ*. Or the continual burrowing might have so weakened these organs as to cause the total disappearance, at the same time, of the three top-joints together; the antenna naturally giving way at the weak small joint, and conserving its remainder by the strengthening and broadening of the large third joint which we find in so many *Gomphinæ*. Looked at from this point of view, the *Petalurine* nymphs are objects of great interest and of much speculation about the past. While we can never be certain, yet these ancient types point out the way by which natural selection has worked its changes in past ages, and lend support to theories which must command our attention and interest.

In conclusion, *Petalura* is probably the oldest type of nymph yet discovered. *Tachopteryx* apparently represents a very slight departure from the older form, the change being best seen in the shortening and thickening of the antennæ, which represents a tendency towards the *Gomphinæ*; and a slightly more developed labium, which might also be regarded in that light, or possibly as a tendency towards the *Æschninæ*.

EXPLANATION OF PLATE XXIV.

Petalura gigantea.

Fig.1.—Sketch showing method of attachment between male and female preparatory to coition.
Fig.2.—Ova (enlarged).
Fig.3.—Exuviæ of male nymph (enlarged).
Fig.4.—Labium of ,, ,,
Fig.5.—Antenna of ,, ,,
Fig.6.—End of abdomen of male nymph; *s*, superior appendage; *i*, inferior: (enlarged).
Fig.7.—End of abdomen of female nymph; *a*, anus; *b*, ovipositor: (enlarged; seen sideways).
Figs.8-9.—Protarsus of female nymph (enlarged).



PETALURA GIGANTEA Leach.