

THE LARVAL CHARACTERS OF THE *PROTONEURIDAE* (Odon.),  
with special reference to the genus *Selysioneura* FÖRSTER, and with notes  
on other Indo-Australian genera

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1. INTRODUCTION

It is generally understood that the Protoneuridae, particularly as regards wing-venation, are the most specialized group among the coenagrionid Zygoptera, the tendency having been towards reduction as well as amplification. Owing to the very unsatisfactory state of our knowledge of the true affinities of the members of this family, even of the imagines, no attempt will be made here to speculate on the phylogeny of the Protoneuridae as a whole or to draw conclusions as to the course of evolution of the various groups within the family. In the last chapter of this paper, the problem which are the most primitive or generalized types and which are to be considered specialized and advanced members will therefore only be touched with respect to Old World forms. Admittedly, the Protoneuridae consist of a very heterogeneous assemblage of forms, which show considerable diversity of character, and the first serious attempt to create order has yet to be made. The fact that two African genera, *Chlorocnemis* SELYS and *Isomecocnemis* COWLEY, both originally included in this family, have recently been removed therefrom and placed in the Platycnemididae <sup>1)</sup>, reflects the confusing state of

<sup>1)</sup> E. SCHMIDT (1951). Ueber neue und weniger bekannte afrikanische Platycnemididen. *Mitt. Münch. Ent. Ges.* 41: 217-240, figs.

affairs and the existing uncertainty as regards their mutual relationship. As I have hinted at in a previous paper <sup>1)</sup>, it is also obvious that at least the Australo-Papuan *Isosticta* group of genera can hardly continue to be representative of the family as originally characterized.

The immature stages of these tiny zygopterids are still very imperfectly known. Of the twenty-six described genera, the larvae of only four (*Disparoneura*, *Neoneura*, *Caconeura* and *Elattonneura*) have so far been described. Though a detailed account of the respiratory organs (caudal gills) of the larvae of the Australian genera *Neosticta* and *Isosticta* has been published by TILLYARD, unfortunately nothing else is known of their morphology. Protoneurid larvae are only to be found in running water, mostly in dense jungle, and hence are difficult to discover.

With the exception of *Prodasineura autumnalis* (FRAS.), which I had reared from larvae already more than twenty years ago, the nymphs of *Notoneura* and *Selysionneura* are fairly recent discoveries, and these bring the number of more or less completely known genera up to eight, i.e. about one-third of the total. Thus pending the discovery of many more larval types and a more intimate knowledge of the generic characters of extra-regional members of the family, the discussion in the present paper must necessarily be confined to giving a hint at some facts in relation to the affinity of some eastern Protoneuridae. Probably several groups ultimately should be given the rank of subfamilies.

## 2. DESCRIPTIONS OF FOUR NEW SPECIES OF *Selysionneura* FÖRST., WITH A KEY TO THE KNOWN SPECIES

*Selysionneura thalia*, sp.n. (fig. 1, 5, 9 and 12).

Material. — 18 ♂, 5 ♀ (ad.), Central N. H a l m a h e r a I., Tuguaer-Tasoa, 100-150 m, 20-24.ix. (3 ♂, 1 ♀), Mumar River, 200-300 m; 25.ix. (4 ♂, 3 ♀), Mts Sembilan & Siu, 600-700 m, 27.ix.-6.x.1951 (11 ♂, 1 ♀), Sundanese collectors AMSARI & MANIS. Holotype ♂ & allotype ♀: Mumar River, 200-300 m, 25.ix.1951, in the Leiden Museum; paratypes in Mus. Zool. Bog.

Male (ad.). — Labium pale yellow, the lateral lobe with the end-hook blackish. Mandibles and labrum black, very shiny, the labrum finely bordered with pale yellow anteriorly, this line not visible when viewed from above. Anteclypeus dark brown marked with a squarish green twin-spot on middle above and a subtriangular green spot of much smaller size, situated more anterad, on either side of it. Postclypeus bronzy-black

<sup>1)</sup> M. A. LIEFTINCK (1951). Odonata of the 1948 Archbold Cape York expedition, with a list of the dragonflies from the peninsula. *Amer. Mus. Novit* 1488: 46 pp., figs.

with a pair of small, oval, green lateral spots, placed wide apart near its base. Dorsal surface of head black, rather shiny and with distinct dark metallic-green lustre, marked with light green as shown in fig. 1: a pair of triangular spots in front of frons, broadly sessile basally and bordering the entire anterior margin; these spots are inclined towards each other but indented by black in the median line, each of them pointing towards the median ocellus but not reaching as far as that. Laterally, a broad and clearly defined light green stripe runs from half-way down the rear of the head upwards along the inner margin of the compound eye as far as the base of antenna; at that level this band suddenly contracts to a stripe about half the width as before, extending a little way up to as far as the level of the median ocellus, where it ends abruptly. There are also a green point at the base of each antenna, a cordate green median spot behind the lateral ocelli bordering the occipital margin, and a slightly smaller, triangular or comma-shaped spot of the same colour bordering the lobes on either end of the occipital ridge, which itself is also green on middle. Antennae with the first joint black tipped with yellow, the second joint light green tipped with brown, the flagellum brown. Rear of the head black, the lower part of the occiput marked on each side with a very large triangular patch of green.

Prothorax, dorsum metallic greenish-black, marked longitudinally with a broad green median band extending from end to end; lower part of the sides and anterior coxae light grape green to mytho green (RIDGWAY); posterior lobe very short, depressed and not produced behind.

Synthorax, dorsum (including the ante-alar triangles) metallic greenish-black with slight reddish, purple or bronzy reflections. Mytho green are: the mid-dorsal carina and the lateral ridges of the ante-alar triangles; a small spot or hook-like streak immediately in front of the ante-alar triangles; a narrow longitudinal band, widest about half-way its length, joining the median carina; and a small rectangular or rather oval juxtahumeral (mesepisternal) spot situated exactly mid-way the length of the humeral suture. Sides, including the coxae, mytho green, except the antero-dorsal half of the mesinfraepisternite, a shoulder-spot filling in the antero-ventral edge of the mesepimeron, a sharply defined and isolated rectangular bar upon the middle of the mesepimeron, and a narrow stripe (irregularly expanded and spot-like at its upper end) along the second lateral suture. Ventral surface of thorax deep greenish glaucous, adorned with four well-defined blackish dots placed in the long axis of the body: a twin-spot on metasternum, one on each side on anterior portion of metepimeron, and a lanceolate spot on middle of poststernum.

Legs (except the coxae) bright cream-buff or colonial buff, the femora slightly intermingled with green. All femora with a thick, deep black exterior stripe and with a black apical dot on the "knees"; apices of tarsal segments slightly brownish; all spines black. Tarsal claws of simple structure, light brown.

Wings hyaline, venation brown up to level of nodus, further outwards black or almost so. Neural characters as for genus. *Arc* distinctly distal to

$Ax_2$ ,  $M_3$  and  $Rs$  well separated at their origin,  $M_3$  arising mid-way between subnodus and  $Px_1$ ,  $Rs$  somewhat beyond that level. Subnodus situated at level of first anal cross-vein following quadrilateral. Origin of  $M_2$  usually at  $Px_6$  on fore wing, at  $Px_5$  on hind wing.  $M_{1a}$  arising 4—5 cells further distad on both fore and hind wing.  $M_4$  zig-zagged from before origin of  $M_2$  till the end of its course under the pterostigma. 13—14 postnodals of second series on fore, 12—13 on hinder wing. Pterostigma very oblique, slightly swollen, only little longer than high, proximal and distal sides approximately parallel; colour dark brown or black, usually surrounded by a fine ochreous line (except along costal side). No five-sided cells in the space between  $C$  and  $R$  distal to  $pt$ .

Abdomen of the usual very slender form, ratio of length of separate segments as shown in fig. 1. Ground-colour of segm. 1—2 and base of 3 deep greenish glaucous to mytho green, that on succeeding segments 3—6 a delicate cream-buff to chamois with the ill-defined baso-dorsal rings mikado- to snuff brown, the basal part of the dorsal mark on 3 rather more bister-coloured; dorsal marks on 1—2 sharply delimited, deep black in matured specimens; terminal segments darker brown than preceding segments, almost or fully black on 8—10. Segm. 9 with complete and clearly defined light blue submedian ring.

Superior anal appendages (fig. 5 and 9) cinnamon-coloured with some obscuration on the inside and at the apices; inferiors very short and rounded, black in colour.

There exists some variation in the extent and shape of the green marks on the head and thorax. The spots on postclypeus may be enlarged and more approximated to each other; also, the tiny lateral postocular spots may be either vestigial and isolated, or somewhat enlarged and narrowly confluent posteriorly with the light streak bordering the middle of the occipital margin. In a few specimens the juxta-humeral green spot on mesepisternum is so small as to be scarcely discernible. The pterostigma occasionally is uniform brown or black, and the superior appendages are at times also much darkened.

Female (ad.). — Resembling the  $\delta$  in most respects, but differing as follows. Labrum ochreous, the black colour restricted to its basal three-fifth and in the form of a broad marking pointing triangularly forwards. Mandible-bases, genae and the antero-lateral divisions of the frons throughout mytho green, as is also the anteclypeus. Postclypeus with the two green points on each side of the middle vestigial in all specimens examined; pale markings in front of frons also different in size and shape, reduced to crescent-shaped (or even linear) transverse spots on each side of the middle. Pro- and synthorax marked similarly to the  $\delta$ . Legs coloured less vividly yellow, with the black exterior stripe of the femora narrower and obliterated, at times broken up in a series of small dots.

Wings as in  $\delta$ , the pterostigma brown, almost twice longer than high.

Abdomen much shorter and more heavily built than in the  $\delta$ , shaped similarly to that of *S. venilia*, sp. n., as shown in fig. 4. Markings similar in principle to the  $\delta$  but never so deep in tint and much less sharply

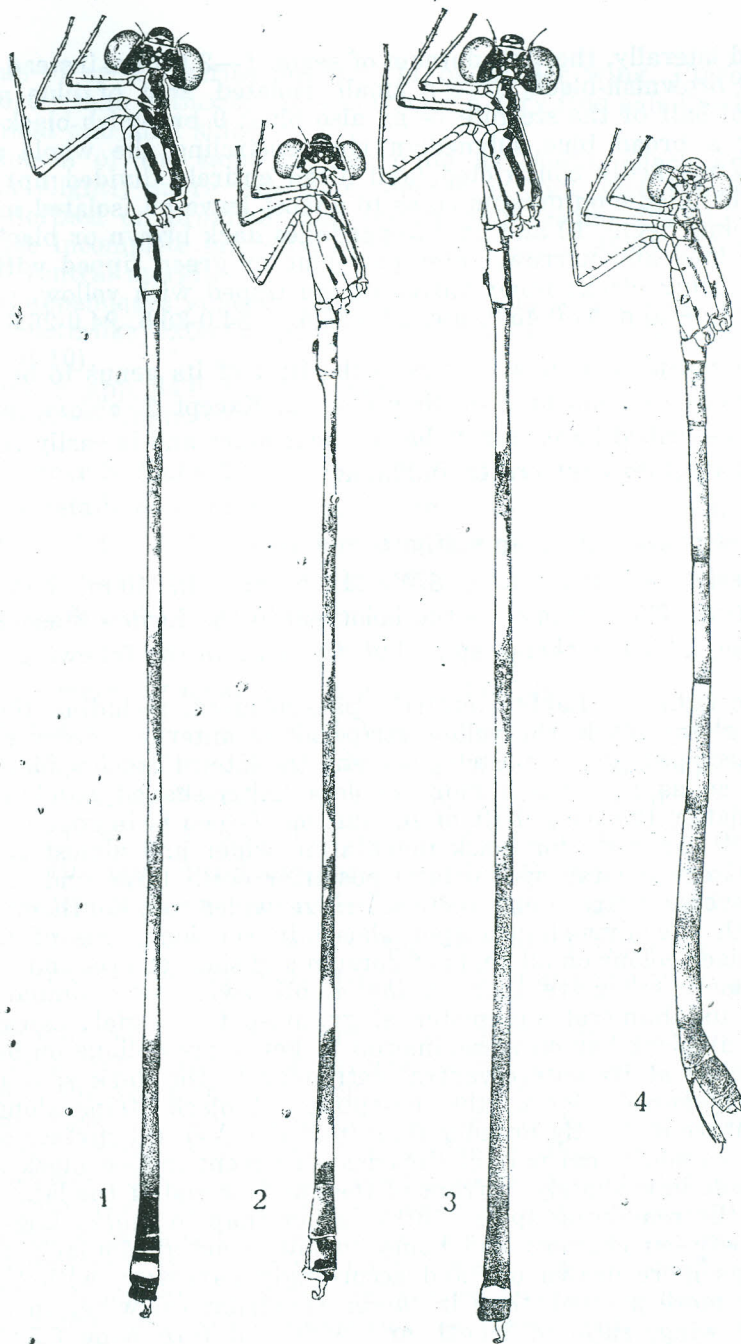


Fig. 1. *Selysioneura thalia*, sp.n. ♂, Halmahera (paratype). Fig. 2. *S. cornelia*, sp.n. ♂, Klamono, W. New Guinea (paratype). Fig. 3. *S. aglaia*, sp.n. ♂, Morotai (holotype). Fig. 4. *S. venilia*, sp.n. ♀, Klamono, W. New Guinea (holotype). All drawn on the same scale ( $\times 3.3$ , approx.).

delimited laterally, those on dorsum of segm. 1—2 brown instead of black. Segm. 8 brownish-black, save a small, isolated, spot of blue alongside, the apical half of the sternite being also blue; 9 brownish-black or black carrying a broad blue submedian ring encircling the whole segment; this ring markedly constricted (and often entirely divided up) on each side of the middle on dorsum so as to almost leave an isolated mid-dorsal spot of blue. Segm. 10 and anal appendages dark brown or black. Valves (fig. 12) long and narrow, outer pair blue or green tipped with brown, the styli being black; inner valves brown tipped with yellow.

♂ abd. + app. 41.0-45.0, hw. 24.5-26.5; ♀ 34.0-36.5, 24.0-26.5 mm.

This conspicuous new species is the first of its genus to be reported from outside the continent of New Guinea. Except *S. aglaia* sp.n., from Morotai, described hereafter, it has no near allies and is easily recognized by the characters enumerated in the key.

*Selysioneura aglaia*, sp.n (fig. 6 and 10).

Material. — 1 ♂ (ad.), S.W. Morotai I., 10 m, v.1949, A. J. KOSTERMANS. The specimen is the holotype, in the Leiden Museum.

Closely allied to *thalia*, sp.n., but differing in the following respects:

Male (ad.). — Labium entirely pale-coloured, including the palpus. Labrum glossy black, the yellow stripe along anterior border extremely fine. Anteclypeus green, postclypeus with the lateral green spots confluent mesially so as to form a more or less halter-shaped band occupying approximately the basal half of its surface. Green twin-spot in front of frons with the posterior black indentation wider and almost circular in outline. Green median spot behind posterior ocelli large and triangular, the transverse stripe along occipital ridge wider and confluent on both sides with a comma-shaped spot placed in the long axis of the head. Bronzy-black colour on all parts of dorsum and sides of pro- and synthorax slightly more extensive than in *thalia*, otherwise very similar to that species; juxtahumeral mesepisternal green spot vestigial; elongate sub-rectangular black bar on mesepimeron longer, more oblique on both ends, and attached at its antero-ventral extremity to the dark spot filling in the antero-ventral edge of the mesepimeron; black stripe along second lateral suture distinctly broader than in *thalia*. Ventral surface of thorax carrying an additional pair of divaricate crescent-shaped black dots, one on each side immediately in front of the anterior end of the latero-ventral carinae; the remaining spots a little larger than in *thalia*. Legs slightly darker, between chamois and honey yellow, marked similarly to *thalia*.

Wings more drawn out and accordingly narrower, with the apices distinctly more pointed, than in *thalia*. Quadrilateral wider in both fore and hind wing, ratio of length and width on fore wing 5.5:1 (*thalia* 8.6:1), on hind wing 7.8:1 (*thalia* 8.1:1). Neuration otherwise very similar in the two species.  $M_2$  arises at  $Px_6$  on fore, at  $Px_5$  on hind wing,  $M_{1a}$  4 cells further distad (5 in one of the fore wings). 12—13

postnodals of second series on fore, 11 on hinder wing. Pterostigma a trifle shorter than in *thalia*, black in colour, a very fine pale line bordering its proximal and anal sides.

Abdomen of the same slender build as *thalia*. Black and brown markings slightly more extensive, deeper in tint and somewhat less sharply defined on proximal and intermediate segments. Blue ring on 9th tergite incomplete laterally, squarely cut off a short distance away from the ventral margin.

Anal appendages, superior pair dark ochreous with the incurved apices and the tooth-like exterior projection black, the inferiors dark brown (fig. 6 and 10).

♂ abd. + app. 44.0, hw. 25.5 mm.

Female. — Unknown.

Very near *S. thalia* LIEFT., from Halmahera, but differing from that species in details of coloration and in the structure of the superior anal appendages of the ♂. In addition to the distinguishing features as given in the key to the species, other slight differences between *aglaia* and *thalia* are noted in the above description.

***Salysioneura cornelia*, sp.n. (fig. 2, 7, 11, 13).**

Material. — 2 ♂, 4 ♀ (ad.), N.W. point of New Guinea, Sorong, 50 m, 24, 26 & 30.x.1948, M. A. LIEFTINCK; 1 ♂, 2 ♀ (1 ♀ juv.), same area, 40 km inland, Klamono Oilfields, 40-50 m, 24.viii.1948, M. A. LIEFTINCK. 1 ♂, 2 ♀ (ad.), W. Misool I., Fakal, ca 50 m, 18.ix. & 2.x.1948, M. A. LIEFTINCK. Holotype ♂ and allotype ♀: W. New Guinea, Sorong, 30.x.1948, in the Leiden Museum; paratypes in Mus. Zool. Bog. Living colours: "Ground-colour of body glaucous, the abdominal rings light blue" (♀ Misool); "thorax pale glaucous, abdomen brown and yellow" (♀ Klamono).

Male (ad., Sorong). — Labium cream buff, palpus blackish apically. Mandibles glossy black, genae greenish-blue. Labrum throughout deep black, only the anterior border when viewed from beneath rather more brownish mesially, apical fringe of bristle-like hairs ferruginous. Anteclypeus brown with a pair of bluish median points; postclypeus brownish-black. Head above dull bronzy black, as far back as the level of the lateral ocelli, the postocular lobes only with an ill-defined cloudy brown patch occupying the anterior portion of each; a transverse median dot immediately posterior to the lateral ocelli cinnamon-buff, and a pair of crescent-shaped green spots, one on each side of the middle, in front of frons. Compound eyes bordered on the inside with a clearly defined blue-green stripe which is only narrowly interrupted half-way up the dorsum, continuing rearwards along the eye-margin to as far as the occipital border where it merges into the brown colour of the occipital lobes. Rear of the head pale greenish, only the centre of the occipital

region black. Antennae, first joint black with green apical ring, second joint green tipped with brown, the remaining joints dark brown.

Prothorax mainly sepia-coloured, with a broad, mid-dorsal, longitudinal glass-green band from end to end, the lower portion of the sides rather more olivine.

Synthorax, ground-colour deep lichen green, the mid-dorsal stripe chrysolite green, marked with bronzy brownish-black or black, as shown in fig. 2. The mesepisternal green stripe against the dorsal carina includes the interepisterna and is at first narrow, then widens rather abruptly before mid-way its length, and upwards tapers gradually to a point just before reaching the ante-alar triangles, which themselves are black; outer one-third of each episternite with three green spots against the humeral suture, the middle spot largest and broadly confluent laterally across the suture with the light colour of the sides. Pleurae with a black dot confined to the middle of the mesepimeron, a second black spot filling in the antero-ventral edge of the mesepimeron, and a much smaller wedge-shaped metepisternal streak along upper portion of the second suture. Anterior half of mesinfraepisternum also black. Ventral surface of thorax pale glaucous green, unmarked except a tiny median black spot, shaped like an arrow-head and pointing basad, on distal half of post-sternum.

Legs with the coxae palest olivine, the trochanters, tibiae and tarsi light cream-buff, and the femora cream-buff intermingled with light green; all femora with complete and thick black exterior stripe on their outer surfaces and the knees also blackish-brown or black. Spines dark brown, tarsal claws ochreous.

Shape and neuration of wings very similar to *stenomantis* (fig. 8), but pterostigma higher and less oblique, quadrilateral markedly longer and vein  $M_1$  also longer. Membrane hyaline, venation yellow-brown up to level of nodus, from there on brown to almost black at the apices. Neuration without peculiarities: *Arc* far distal to  $Ax_2$ .  $M_3$  and  $R_s$  well separated at their origin, arising on each side of the middle of the distance between subnodus and  $Px_1$ . Subnodus at level of first anal cross-vein following quadrilateral. Origin of  $M_2$  at  $Px_6$  on fore wing, at  $Px_5$  on hind wing.  $M_{1a}$  arising 3 cells further distad on fore wing, 4 on hind wing.  $M_1$  zig-zagged from well before the basal half of its length as far as the end of its course, under the proximal side of *pt.* 10—11. postnodals of second series on fore, 10 on hinder wing. Pterostigma moderately oblique, little or not swollen, slightly longer than high, proximal and distal sides approximately parallel; colour black surrounded by an extremely fine orangish line (except along costal side).

• Abdomen very slender. Ground-colour of segm. 1—2 and base of 3 lichen green, on distal portion of succeeding segments 3—7 ochraceous-tawny above, fading to ochraceous-buff laterally and underneath; brown markings, especially the apical rings, rather sharply defined, black on dorsum of segm. 1, dark brown on 2, cinnamon-brown on the succeeding segments, turning almost wholly dull black on 8—10. Dorsal mark of 2 strongly constricted just beyond the middle so as to form a 8-shaped





Fig. 5—7. Male anal appendages of *Selysioneura thalia*, sp.n., Halmahera (5), *S. aglaia*, sp.n., Morotaj (6), and of *S. cornelia*, sp.n., Sorong, W. New Guinea (7).  
Not drawn on the same scale.

spot, the anterior portion of which does not entirely reach the basal margin; markings on following segments as shown in fig. 2. Segm. 8—9 more obscured, the middle of the back of 8 as well as the lower part of its sides indistinctly russet; 9 almost black, except the middle one-third which carries an ill-defined brown lateral patch (possibly blue in life); 10 black, the lower part of the sides becoming green. Sternites of 8 and 9 clear yellow, the gonapophyses surrounded by blue.

Anal appendages, superior pair yellow, turning reddish black in distal half; inferiors very short, not visible in dorsal view, colours obscured.

In one paratype from Sorong the dark colour on the dorsum of the prothorax is confined to a pair of dark streaks, one on each side of the pale median band, and the two juxtahumeral (mesepisternal) light-coloured dots are coalescent mesially so as to partly surround a black crescent along upper end of the humeral suture. Wing-veins from base to nodus pale reddish-brown; 12—13 postnodals on fore wing. No traces of yellow or blue spots on upper surface of segm. 9—10 of abdomen. In the ♂ from Klamono the posterior limit of the black marking that occupies most of the dorsal surface of the head is sharply delimited, carrying five rather conspicuous indentations, but in the others (including the ♂ from Misool) the dark colour is more extensive, leaving only a median point behind the posterior ocelli, and a pair of triangular spots on either end of the light-coloured occipital ridge. 11—13 postnodals on fore wing. Other differences are slight and scarcely worth attention.

Female (ad.). — Differs from the ♂ chiefly in the greater extent of light colouring on all parts of the body, the dark pattern very similar in principle to the opposite sex. Labrum bright ochraceous-orange or yellow ocher, with a single deep black spot on the middle at base, attached to a fine black basal line. Anteclypeus blue, postclypeus black carrying two oval tawny spots; a continuous light-coloured band in front of frons surrounding the antennae and confluent on either side with the pale stripe bordering the inner margin of the compound eyes. Occipital lobes less obscured than in the ♂, the posterior limit of the black dorsal surface irregularly indented behind the lateral ocelli.

Prothorax mainly pale, yellowish with small and diffuse tawny dots on each side of the middle, pleurae cream-coloured. Synthorax as in ♂, but ground-colour paler, yellowish glaucous to pale turtle green; dorsal flecks more brown, ill-limited and fading to tawny laterally; three juxtahumeral dots more extensive, the upper pair nearly always coalescent mesially, but the lowermost two spots also confluent in most specimens. In one ♀ from Klamono all three spots broadly confluent in dorso-ventral direction so as to cut off the dark mesepisternal band (which itself is also obliterated above) from the black dots along either end of the humeral suture; in this example the dark metepisternal spot is also reduced to a mere ferruginous streak.

Legs cream-buff, the coxae and tibiae somewhat paler still; femora without exterior black stripe but marked instead with a series of minute diffuse brownish dots and points, the knees of the anterior femora usually also with some small brown specks; spines isabella coloured or brown.

Wings as in the ♂; pterostigma dark brown, but in one mature example from Misool yellowish-brown.

Abdomen much shorter and more stoutly built than in the ♂, segments 1—7 gradually increasing in width and, after a slight constriction towards the end of 7, again a little expanded, the terminal segments much swollen, shaped rather as shown in fig. 4 for *venilia*, but 9 and 10 shorter and with the valves also less prolonged backwards than in that species. Ground-colour generally paler than in the ♂, yellowish glaucous on the first two segments, but deepening to cream-buff or charcoal on the succeeding segments; 1 with squarish deep black mark occupying the entire dorsal surface; 2 longer than in ♂ and with the dorsal spot strongly constricted after the middle, its anterior division oval and attached to the basal margin by a fine median projection, the posterior division shorter, broadly sessile and of a darker brown colour than the rest of the spot. On segm. 3—6 the brown dorsal marks are progressively more expanded, so as to occupy also most of the sides, at the same time acquiring successively a darker brown tint, changing from snuff brown to sepia on the posterior segments; on 3—6 these markings are clearly defined and completely interrupted well after the middle so as to leave bright yellow subapical rings of about twice the length of the dark brown apical annules (cf. fig. 2). Segm. 7 with indistinct sub-apical pale ring and with the sides dark brown; 8 dark brown above, glaucous-grey laterally; 9 also dark brown on the back, but the sides bear a conspicuous light blue-green spot of very large size that occupies from two-thirds to three-fourths of the surface, extending half-way up the dorsum so as to nearly meet its fellow from the opposite side. Genital valves (fig. 13) light blue or yellowish with an obscure stripe along ventral margin. Ovipositor dark reddish-brown. Segm. 10 dark brown above, bluish aside. Anal appendages yellow tipped with black.

♂ abd. + app. 38.5-39.5, hw. 21.5-23.5; ♀ 32.5-34.5, 22.5-25.0 mm.

By its very slender forms and variegated colour-pattern, this delicate little species shows undeniable affinity with the two previously described species, *thalia* (from Halmahera) and *aglaia* (from Morotai), with which it forms a natural group of western distribution. The males of these three species may be distinguished from the other known members of the genus by the presence of a row of minute wart-like tubercles on the middle of the spatulate apex of the superior appendage, and all agree in having the dark body-markings more sharply pronounced than the remaining species.

Very local and probably confined to the Vogelkop and some adjacent islands of West New Guinea.

*Selysioneura venilia*, sp.n. (fig. 4 and 14).

Material. — 2 ♀ (ad.), N. W. New Guinea, Sorong, 40 km inland, Klamono Oilfields, 40-50 m, 23-24.viii.1948, M. A. LIEFTINCK. One of

the specimens is the holotype, in the Leiden Museum; paratype in Mus. Zool. Bog. Living colours: "Head and thorax vivid pale green; abdomen vinaceous-tawny".

Female (ad.). — Labium pale yellow; labrum light ochraceous-buff with an indistinct brown spot on the middle at base. Mandibles, gertae and clypeus yellowish glaucous, indistinctly marked with brown; a cloudy spot upon middle of mandibles, the lateral portions of anteclypeus, and a diffuse stripe roundabout postclypeus. Dorsal surface of head greenish-glaucous, mottled with dark brown somewhat similarly to the ♀ of *S. stenomantis* LIEFT.<sup>1)</sup> but still less extensively: dark spot in front of anterior ocellus cup-shaped, no lateral prolongation on either side of the insertion-point of antenna, brown arcs surrounding pale postocular areas narrower (fig. 4). Rear of the head pale glass-green except a small area around the foramen. Antennae with the first two joints light green, the second obscured apically, the flagellum brown.

Pro- and synthorax, including the coxae of legs, light turtle green, indistinctly marked with brown, as shown in fig. 4. The brown bands on each side of the middle on prothorax only slightly broader than the pale median stripe. Mesepisternal stripe against the dorsal carina ferruginous, deepening to brown on either end just above the interepisterna and beneath the ante-alar triangles, which themselves are reddish-brown. Brown marks on the thoracic pleurae shaped as shown in fig. 4, not sharply delimited. Ventral surface of thorax unicolorous cream-buff.

Legs cream-buff, apices of anterior pair of femora and of the tarsal joints very slightly obscured; spines dark brown.

Wings almost identical in shape to those of *stenomantis* (fig. 8), but the apices distinctly more pointed. Venation also much as in that species, with the same short quadrilateral; vein  $M_4$  longer, entering the wing-margin 2—3 cells before level of pterostigma. Origin of  $M_2$  at  $Px_6$  on fore wing, at  $Px_5$  on hind wing.  $M_{1a}$  arising 4 cells further distad on fore wing, 4—5 on hind wing. 12 postnodals of second series on fore, 10—11 on hind wing. Pterostigma a little longer than high, slightly shorter and with the anal border somewhat more convex than in *stenomantis*, proximal and distal sides sub-parallel; colour yellowish or dark brown.

Abdomen shaped as shown in fig. 4. Colour of segm. 1 pale greenish, this colour somewhat deepening in tint on the dorsum; sternite cream-buff, carrying a sharply defined deep black median carina. Segm. 2—7 rather uniform vinaceous-tawny without any indication of dark markings, a small basal and a more extensive sub-apical area at the sides of these segments a little lighter in colour; intersegmental membranes narrowly brown and segment 2 moreover with three dark points, one mid-dorsal one at extreme base, and one on either side just posterior to the antero-ventral edge of the tergite; mid-dorsal longitudinal carinae of all sternites finely black. Segm. 8—10 darker than the preceding segments; 8 vinaceous-russet, growing darker apically, 9 Vandyke brown with a diffuse

1) *Nova Guinea* 15, Zool. 5, 1932, 550 (66 sep.), fig. 46.

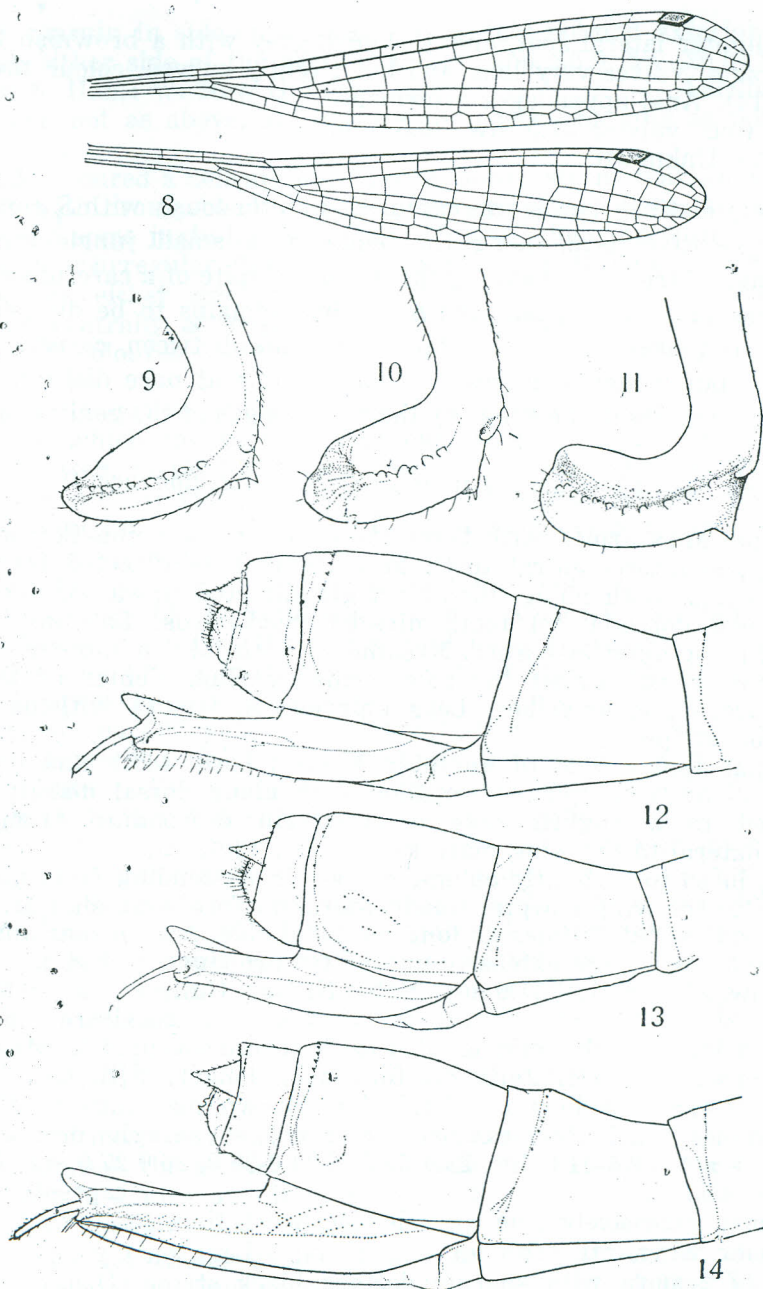


Fig. 8.—Right pair of wings of *Selysioneura stenomantis* LIEFT., N. New Guinea. Fig. 9—11. Interior view of apex of right ♂ superior appendage of *Selysioneura thalia*, sp.n., Halmahera (9), *S. aglaia*, sp.n., Morotai (10), and of *S. cornelia*, sp.n., Sorong, W. New Guinea (11). Fig. 12—14. Right lateral view of apex of ♀ abdomen of *S. thalia*, sp.n., Halmahera (12), *S. cornelia*, sp.n., Sorong, W. New Guinea (13), and of *S. venilia*, sp.n., W. New Guinea (14).

somewhat lighter lateral spot, and 10 bluish-grey with a brownish band on mid-dorsum. Valves very long and but, slightly curved, colour tawny-olive (fig. 14). Anal appendages brownish.

♀ abd. (incl. valves) 31.5, hw. 22.5 mm.

Male. — Unknown.

This very distinct species was captured simultaneously with *S. cornelia* on two consecutive days, along the banks of a small jungle stream, among foliage of trees overhanging the water. In spite of a careful search, no other specimens were seen; the male thus remains to be discovered. By its green thorax, *S. venilia* forms the link between *cornelia* and *stenomantis*, but it comes nearest the latter. It is at once distinguished from all other species in the genus by the great length of the genital valves.

Key to the known males of *Selysionera* 1)

1. Sup. anal apps armed with three strong tooth- or spine-like projections: one intero-ventral tooth at extreme base directed inwards, one median tooth along dorsal margin directed upwards, and one sub-apical dorso-lateral tooth directed backwards. Labrum black, except along anterior border. Mesothorax with joint mid-dorsal light-coloured stripe against the pale median carina. Venter of thorax unicolorous creamy-yellow. Legs unicolorous, femora without dark exterior stripe . . . . . 2
- 1<sup>1</sup>. Sup. anal apps devoid of an intero-ventral basal tooth and usually also lacking a conspicuous median tooth along dorsal margin. *Cu*<sub>1</sub> reduced to a slightly oblique cross-vein descending from the quadrilateral to the wing margin . . . . . 3
2. *Cu*<sub>1</sub> reduced to a slightly oblique cross-vein descending from quadrilateral to the wing margin. Quadrilateral on fore wing shorter, with costal side about 6 times as long as distal side. Brown markings on thorax darker, more extensive and better pronounced. ♂ abd. + app. 43.0, hw. 29.0; ♀ 41.0, 31.0 mm. Hab.: N. New Guinea . . . . . *cervicornu* FÖRST.
- 2<sup>2</sup>. *Cu*<sub>1</sub> reaching to the middle of the first cross-vein following the quadrilateral. Quadrilateral on fore wing longer, with costal side amply 7 times as long as distal side. Brown markings on thorax usually less dark, less extensive and not so sharply pronounced. ♂ abd. + app. 36.5-41.0, hw. 23.0-26.0; ♀ 34.0-36.0, 26.0-27.0 mm. Hab.: N. New Guinea . . . . . *capreola* LIEFT.
3. Abdomen excessively long and slender, more than twice as long as posterior wing, 5th segment 11 mm long. Legs pale yellow; outer sides of femora with sharply defined black stripe. Distal half of sup. anal apps strongly downcurved almost under a right angle;

1) See also LIEFTINCK 1932, *Nova Guinea* 15, Zool. 5:541-551 (57-67 sep.), figs., and 1949, *ibid.*, (N.S.) 1: 76-82, figs.

- upper margin in side-view with two acutely pointed exterior teeth, one on either side of the bend. ♂ abd. + app. 55.0, hw. 26.0; ♀ 37.0, 27.0 mm. Hab.: W. New Guinea . . . . . **bacillus** RIS.
- 3<sup>1</sup>. Abdomen not as above, always less than twice as long as posterior wing . . . . . 4
4. Thorax coloured a delicate light green. Mesepisterna marked conspicuously with bronzy-black or black, carrying either a straight median band and some juxta-humeral spots of that colour, or with a pair of straight or irregular (but always uninterrupted) longitudinal black stripes on either side at some distance from the median carina. Thorax ventrally at least with blackish marginal streaks or spots. Legs pale-coloured, but outer side of femora with sharply defined black stripe . . . . . 5
- 4<sup>1</sup>. Thorax olive-yellow, cinnamon-buff, or tawny-olive (except *venilia*, sp.n., in which the thorax is green). Mesepisterna predominantly pale-coloured, marked with a number of isolated and usually somewhat diffuse brownish or black dots. Abdomen rod-like, almost of even width throughout, hence intermediate segments not very slender and apical segments not expanded . . . . . 8
5. Dorsum of mesothorax with a straight (or ventrally somewhat constricted), deep black, mid-dorsal band against the median carina, which itself is finely yellow; this joint band approximately equal in width to each of the green band-like outer halves of the mesepisterna which, however, carry two black spots against the humeral suture. Interepisterna, and ante-alar triangles filled in with black. Mesepimeron unmarked. A tiny black streak along upper end of second lateral suture. Underside of thorax with a pair of brownish-black dots just behind metasternum on ventral part of metepimeron, Labrum ochreous with an impressed black spot on middle at base. Legs unicolorous light ochreous. Pterostigma almost two times longer than high (fig. 8). Abdomen rod-like, segm. 3—10 almost parallel-sided, intermediate segments slightly flattened dorso-ventrally; colour uniform tawny with narrow and indistinct light rings or spots. Segm. 9 not conspicuously spotted or ringed with blue. Sup. anal apps without median tooth along dorsal margin, the apical edge of the latter obtuse-angulate. Species of small size: ♂ abd. + app. 30.5-32.0, hw. 18.0-19.5; ♀ 28.0-30.0, 19.0-21.0 mm. Hab.: N. New Guinea . . . . . **stenomantis** LIEFT.
- 5<sup>1</sup>. Dorsum of mesothorax at least with a narrow light green mid-dorsal stripe against the median carina, which itself is also pale-coloured; ante-alar triangles and interepisterna filled in with black. A conspicuous elongate dark streak on middle of mesepimeron and a complete black line over the second lateral suture. Labrum black, except a fine line along anterior border. Legs pale-coloured, but outer sides of all femora with sharply defined black stripe. Pterostigma shorter. Abdomen not rod-like, the intermediate segments extremely slender, not flattened dorso-ventrally, apical segments distinctly expanded; colour of 3—7 brighter, usually cream-buff to ochraceous-

- tawny, with conspicuous reddish- or dark brown markings and black apical rings . . . . . 6
6. *Episterna* of mesothorax with a series of three conspicuous, more or less confluent, green spots along humeral suture. A pair of tiny transverse green streaks in front of frons. Postocular lobes at least partly light-coloured above. Green mesepisternal spot half-way down the humeral suture confluent posteriorly across the suture with the pale colour of mesepimeron. Venter of thorax with a single longitudinal black streak on distal half of poststernum. Abd.-segm. 3—6 predominantly dark brown or black, pale sub-apical rings fairly well-defined, not much longer ventrally than dorsally. Sides of segm. 9 with some blue colouring. Sup. anal apps with apices strongly curved downwards and inwards, tips abruptly truncated with rounded angles (fig. 11). Species of smaller size: ♂ abd. + app. 38.5-39.5, hw. 21.5-23.5; ♀ 32.5-34.5, 22.5-25.0 mm. Hab.: W. New Guinea & Misool . . . . . *cornelia*, sp.n.
- 6<sup>1</sup>. *Episterna* of mesothorax with only one green spot situated about mid-way along humeral suture, the dorsal and ventral spots much reduced in size and usually absent altogether. A pair of triangular green spots, pointing upwards, in front of frons, these spots whether or not united basally against the fronto-clypeal suture. Postocular lobes bronzy-black above. Green mesepisternal spot half-way down the humeral suture much smaller, variable in size but always isolated from the green colour of mesepimeron. Venter of thorax marked with at least four blackish points or streaks. Abd.-segm. 3—6 predominantly and conspicuously cream-buff or chamois, the reddish-to dark brown markings more withdrawn and also retracted to the dorsal surface, the dark apical rings incomplete ventrally. Segm. 9 with conspicuous blue median ring. Sup. anal apps with apices less strongly curved downwards and inwards, tips not truncated but more or less finger-shaped and bluntly pointed (fig. 9 and 10). Species of larger size . . . . . 7
7. Green spots on postclypeus usually small and always separated by black on middle. Juxta-humeral mesepisternal green spot very distinct. Elongate black patch on middle of mesepimeron isolated. Ventral surface of thorax with four black dots: a median spot on metasternum, one oblique spot on each side at base of ventral part of metepimeron, and a median longitudinal streak on poststernum. Sup. anal apps as in fig. 5, with a series of 9—10 wart-like denticles on the inner surface of the apical portion and with the apex gradually narrowed towards the tip, which is almost pointed (fig. 9). ♂ abd. + app. 38.5-39.5; hw. 21.5-23.5; ♀ 32.5-34.5, 22.5-25.0 mm. Hab.: Halma-hera . . . . . *thalia*, sp.n.
- 7<sup>1</sup>. Green spots on postclypeus confluent mesially so as to form a transverse mark. Juxta-humeral mesepisternal green spot vestigial. Elongate black patch on middle of mesepimeron attached antero-ventrally to the dark spot filling in antero-ventral edge of mesepimeron. Ventral surface of thorax with six black dots: a median spot



- on metasternum, one on each side at the base of the latero-ventral carina, one much larger spot on each side at base of ventral part of metepimeron, and a median longitudinal spot on poststernum. Sup. anal apps slightly differently shaped (fig. 6), with the wart-like denticles on the inner surface of the apical portion less numerous and with the apex more bluntly rounded (fig. 10). ♂ abd. + app. 44.0; hw. 25.5 mm; ♀ unknown. Hab.: Morotai . . . . . **aglaia**, sp.n.
8. Large species: abdomen at least 37 (♂) and 33.5 (♀) mm, hind wing at least 24 (♂) and 25 (♀) mm. Labrum deep black. Thorax ventrally without distinct black spots or streaks. Segm. 3—7 of abdomen with fairly distinct yellowish sub-terminal annules of about the same length as the brown terminal rings . . . . . 9
- 8<sup>1</sup>. Smaller species: abdomen at most 35 (♂) and 33 (♀) mm, hind wing at most 21.5 (♂) and 23 (♀) mm. Labrum pale-coloured with a ⊥-shaped black basal spot, or with indistinct brown spot on the middle at base (♂ *venilia* unknown). Legs uniform pale-coloured, femora unmarked. Segm. 3—7 of abdomen without definite pattern, uniform orange-cinnamon or vinaceous-tawny, lacking yellowish sub-apical annules and with the apices not or only slightly obscured . . . . . 10
9. A fairly distinct brown or blackish stripe (sometimes incomplete basally) along exterior surface of all femora; knees also darkened. Sup. anal apps forcipate, evenly curved inwards with the dorsal submedian prominence low and obtuse-angulate and the apices more bluntly rounded than in *ranatra* (loc. cit. 1932:548, fig. 43). More stoutly built insect. Size variable: ♂ abd. + app. 37.0-45.0, hw. 24.0-28.5; ♀ 34.0-38.5, 26.0-30.0 mm. Hab.: N. New Guinea . . . . .
- . . . . . **phasma** LIEFT.
- 9<sup>1</sup>. Femora isabella-coloured, tibiae cream-buff, all unmarked with black. Sup. anal apps thinner and more twisted, basal part in dorsal view more angulate, the middle portion straighter, the dorsal prominence better pronounced and more angulate, the apical expanded part comparatively larger and more abruptly incurved, the extero-lateral tooth removed more caudad (loc. cit. 1949: 74, fig. 82—83). More slenderly built species. ♂ abd. + app. 37.5-40.5, hw. 24.0-26.5; ♀ 33.5-36.5, 25.0-27.0 mm. Hab.: N. New Guinea . . . . . **ranatra** LIEFT.
10. Ground-colour of pro- and synthorax tawny-olive and olive-buff (♂), of greyish-brown to grey-green (♀). Thorax ventrally with deep black (♂) or rusty-brown (♀) longitudinal spot or streak, variable in size and extent, on middle of meta- and poststernum. Pterostigma distinctly longer than high. Abdomen of ♀ uniform dark reddish-brown, the basal segments with some pale colouring and 9th tergite also somewhat paler laterally. Genital valves short, surpassing apex of 10th segment for slightly less than this segment's length, ventral margin strongly convex in profile view. ♂ abd. + app. 33.5-35.0, hw. 20.5-21.5; ♀ 32.0-33.0, 22.0-23.0 mm. Hab.: N. New Guinea . . . . . **umbratilis** LIEFT.
- 10<sup>1</sup>. Ground-colour of pro- and synthorax light turtle-green (♂ unknown). Thorax ventrally without any indication of dark markings. Pterostigma scarcely longer than high. Abdomen of ♀ more vividly coloured:

sides of 1st segment light green, 2—7 vinaceous-tawny with indistinct, slightly obscured apical rings and faintest indication of paler sub-apical areas, apical segments brownish. Genital valves considerably longer than in *umbratilis*, surpassing apex of 10th segment for almost twice this segment's length, ventral margin very slightly convex in profile view. ♀ abd. (incl. valves) 31.5, hw. 22.5 mm. Hab.: W. New Guinea . . . . . *venilia*, sp.n.

### 3. OBSERVATIONS ON THE HABITS AND LIFE-HISTORY OF

#### *Selysioneura cornelia* SP.N., WITH A DESCRIPTION OF ITS LARVA

##### Habits and flight

On August 24, 1948, while collecting along a forest-brook near Klamono, I took for the first time a few specimens of a unknown *Selysioneura*. These slender, narrow-winged insects attracted my attention because they were repeatedly noticed flying about among the foliage of trees overhanging the water high overhead. Their variegated colour-design of light green, pale ochreous and bronze-brown harmonized very closely with the surroundings, and when resting among the leaves the insects were all but invisible.

Surely it had always puzzled me to find specimens of *Selysioneura capreola* LIEFT., — collected many years previously by the late Mr W. STÜBER in the Humboldt Bay country — marked with the words "Nur auf Bäume!" affixed to their locality labels. It was not until the above observations were made that STÜBER's notes proved to be quite significant and well worth further attention, since no instances were known of Protoneuridae being in some way associated with or dependent on trees. When visiting New Guinea myself, I soon discovered that *Selysioneura*'s, except on emergence, are retiring insects with truly arboricolous habits. When not especially searched for they are but seldom seen; yet they may quite frequently be beaten up from the foliage of trees overshadowing the water of small rivers and brooks, or when passing slowly under bushes growing on the banks near by. In such surroundings they may even form small colonies. Quite unlike other protonEurids they have a skipping and undulating flight, tipulid-fashion, darting to and fro from one branch to another with rapidly whirling wings, the extravagant body held stiffly and straight out. When on the wing they cover only short distances and usually come to rest on leaf stalks or tiny branches, hanging themselves up with wings folded together on the back and with the abdomen drooping.

##### Environment

The next observations were carried out in the bed of a tiny brook flowing through dense virgin forest, which covers the rugged hill country

of Remu, western extremity of New Guinea. These rain forests extend far into the interior of the Vogelkop peninsula, occupying an immense and uninterrupted area of hills and mountain ranges. The low hills fringing the entire westcoast north of the capital settlement of Sorong, rise fairly steeply behind a narrow swampy strip of mangrove and sago forests at some distance from the coast. During our stay (August till November, 1948), many small streams and tiny water courses on the bottom of innumerable deep ravines found their way through the forest and debouched into the muddy creeks and marshes at the foot of the hills. None of the brooks on the dissected plateau were of great length and all were fed only by rain water. In their lower course they were supplied with water trickling down from the surrounding hills in sufficient quantity to keep flowing, but on working slowly upstream towards their probable sources, I found the current in several instances slowing down after a while and breaking up into a series of pools and cascades connected by mere trickles. Further ahead the stream bed contained only small puddles filled with rain water, until finally the rocky bed dried up completely, leaving only patches of fine gravel and sand. At some places fallen trees and small landslips had permitted the sunlight to penetrate through the dense canopy overhead and to illuminate in patches the rocks and vegetation in the narrow bed of the stream.

It was here that a small number of zygopterous dragonflies occurred, at least three of them being new to science. Owing to the constant high humidity and temperature, collecting was difficult; also the lack of sunshine and the abundance of ceratopogonids and mosquitoes were decided handicaps. The object of my visits being the assembling of all kinds of animals, little attention could therefore be paid to the biology of Odonata or other insects, and unfortunately my observations on *Selysioneura* are only too fragmentary.

On October 24 and 26, 1948, the weather was fair but cloudy, dragonflies being on the wing only during brief intervals of sunshine, between 10 and 12 a.m. Besides *Selysioneura cornelia*, two species of *Argiolestes* were noticed, the males settling on boulders and dead branches with half outspread wings. Dark recesses under the bank yielded a small species of *Drepanosticta*, and two different species of *Notoneura* attracted the attention in sunlit openings, while suspended in the air over cascades or beside rocks overhanging deep pools. A slender *Teinobasis* was also met with in some numbers, several couples being observed while ovipositing in submerged root-mats. Lastly, the re-discovery of the exceedingly rare *Palaiargia rubropunctata* (SELYS) is worth recording. With the rising of

the sun the brilliant blue males of the latter descended from their resting places high up in trees, fluttering down by stages, one by one, until each had occupied a suitable place on the gravel bars or on some pebble near

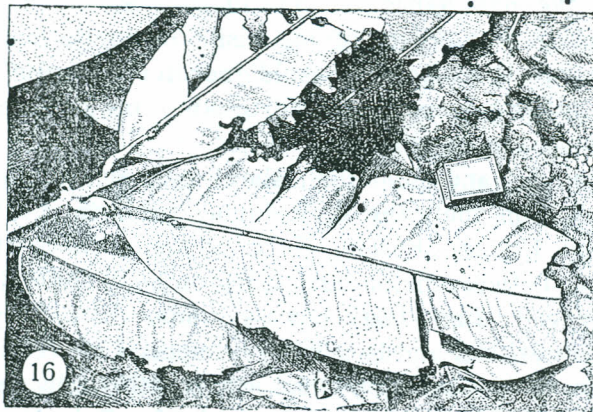


Fig. 15. Forest-brook on bottom of deep ravine near Sorong, W. New Guinea, showing leafy projecting twig of small tree overhanging the water. Habitat of ovipositing *Selysioneura cornelia*, sp.n. Fig. 16. Underside of leaves of same tree-branch (to the left of match-box), showing 'galls' and punctured mid-ribs.  
Drawn from photographs.

the water's edge. With the exception of a single *Nannophlebia*, no examples of Anisoptera were noticed.

#### Oviposition

On October 24, a female *Selysioneura* was seen crossing the stream-bed and, flying in a straight line towards a horizontal branch of a tree, some eight feet above the stream, disappeared among the foliage. Following its trail I found that it had just alighted on the lower surface of a broad leaf and almost instantly began ovipositing in the main nerve of it. The end of the abdomen was first tapped vigorously against the midrib of the leaf, but then it was retracted, so as to form a double right-angled bend at the fourth segment. After about twenty seconds she withdrew the needle-like terebra of her ovipositor, walked slowly back, remaining in the same hanging position with her feet holding on to the midrib, and repeated the process two more times. Almost two minutes had elapsed when the insect ceased ovipositing and flew down, then immediately raised up again towards another leaf, about four inches away from the first, swooped up under it and started ovipositing in exactly the same way as before. The leaves were of large size, measuring 27—28 cm by a width of 6.5—7.5 cm. I had noticed that the midribs selected by this female were considerably swollen in places, so as to form elongate gall-like swellings, the biggest of these having a length of 15—20 mm and a diameter of about 2—2.5 mm. Some of the side nerves of the leaf were apparently also punctured as the surrounding tissue was similarly thickened, the last mentioned malformations being only much smaller in size than those on the midribs. In all three cases observed the eggs — probably one egg each time — were inserted into the cortical layer of these swollen parts of the midrib, the female on every occasion drawing the tip of her abdomen up until her body formed a loop with the ovipositor between her legs, when she made the thrust. Apparently, the most suitable attitude of the insect during egg laying was the one shown in fig. 17 and 19, but at times the body was brought into a different position by pressing it against the leaf and pushing the distal half of the abdomen forward between the legs as if to measure off the distance required (fig. 18). After I had finished some sketches of the egg-laying process, the specimen was caught.

Before it started raining, a photograph was made of the stream-bed (fig. 15), showing the bough with its large leaves overhanging the water <sup>1)</sup>. *Since I had no occasion to examine the infested leaves that same day,*

1) In fig. 15 the nearly horizontal branch is clearly shown above the middle of the picture, to the left of the butterfly-net.

some of those on which I had watched *Selysioneura* ovipositing were picked off and photographed (fig. 16), and afterwards preserved in alcohol. It was not until many months later that these leaves could be studied more closely. The galls, then, proved to be rather lignified (partly on account of a "hardening" action of the strong alcohol?). Two out of seven large galls contained eggs, one in each swelling, and one of the two small galls on the side nerves also held a single egg. All eggs were of the same elongate form, corresponding closely in size and shape to mature ones extracted from the insect's body. They were inserted horizontally, parallel to the long axis of the gall and leaf. Thus it is quite evident that *Selysioneura* oviposits in the midrib and nerves of some broad-leaved trees, but it remains uncertain whether the galls are produced also by this dragonfly or had been caused already earlier by the larvae of some other insect. Though no excrements or remains of other insect matter could be found, the last possibility, in my opinion, is the most likely one.

On October 26, which was the last date on which collecting could be done in this locality, oviposition was again in progress, and a male and female of *S. cornelia* could be secured. On approaching the twig on which I had seen the insects before, an egg-laying female had just been caught from under its leaf by a small spider; the dragonfly could in time be rescued from its fangs, only to disappear into the cyanide bottle. Thus it would seem that, in spite of their retiring habits among the foliage and the excellent protection against rain afforded by the broad leaves under which the females take shelter, adult *Selysioneura* nevertheless has its enemies, even when at rest!

So far as observed, the female is never accompanied by the male, who may not even be in attendance. Unfortunately, nothing is yet known of the courtship and copulatory process of this interesting species.

#### Comparison with allied genera

The oviposition of *Selysioneura*, as described and illustrated above, is unique among the Protoneuridae. In most, if not all, other members of the family, the female during oviposition is accompanied 'per collum' by the male and the eggs are deposited in the tissue of aquatic plants or in matted rootlets in or near the water. The curious habit of ovipositing in leaves or twigs far above the water-level is reminiscent of the methods employed by some Lestid and Synlestid genera, but in these cases the female is usually attended by the male and the insects in question have no such pronounced arboricolous habits as *Selysioneura*. In this connection it is of great interest to recall TILLYARD's notes on the habits of some

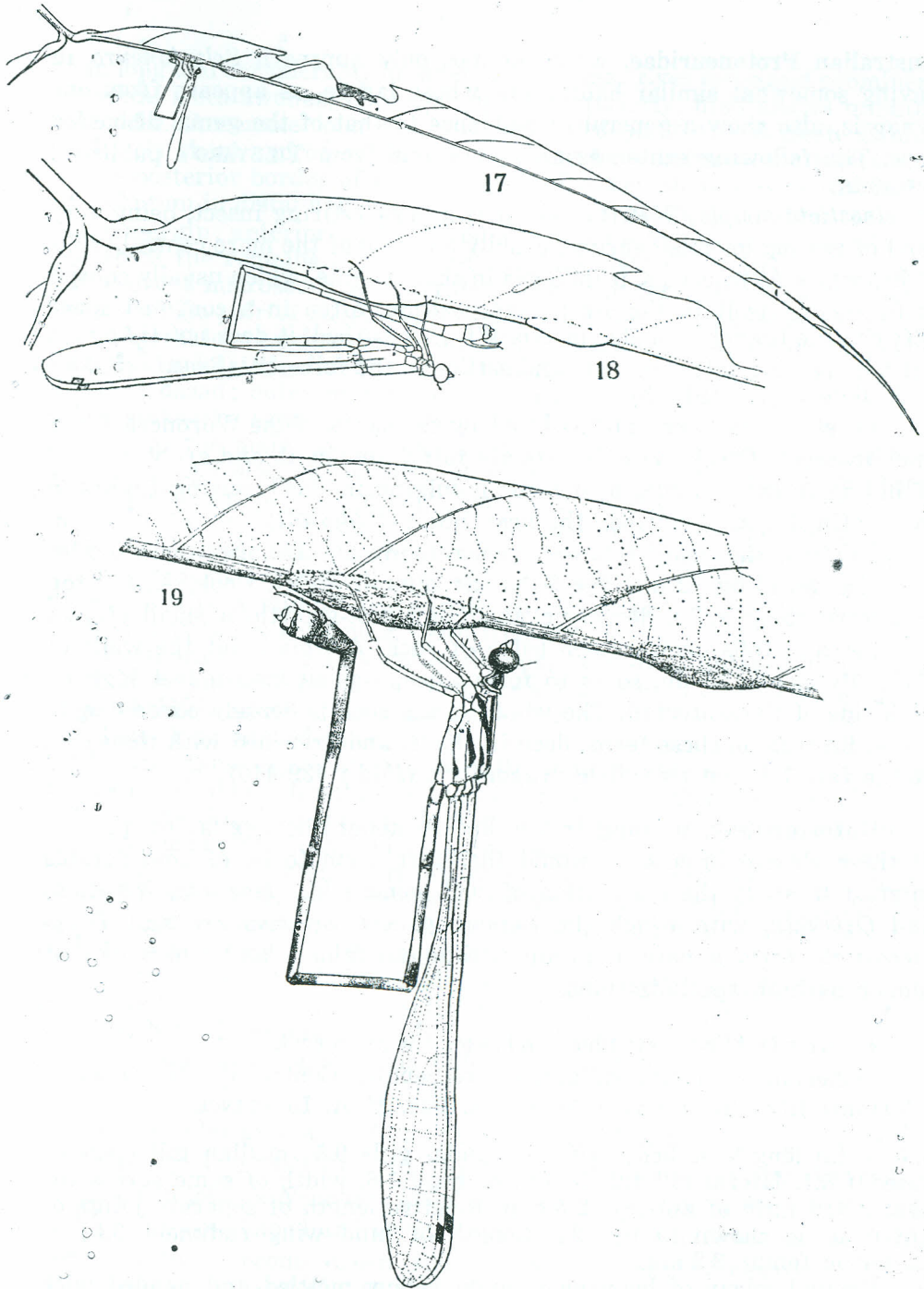


Fig. 17—19. Oviposition of *Selysionaura cornelia*, sp.n., on underside of leaf. Forest-brook near Sorong, W. New Guinea, 24.x.1948. (17,  $\times \frac{1}{2}$ ; 18,  $\times 2$ ; 19,  $\times 3$ ). Original, drawn from sketches and notes in the field.

Australian Protoneuridae, which do not only approach *Selysioneura* in having somewhat similar habits, but whose larvae, as appears from our synopsis, also show a general resemblance to that of the genus discussed here. The following sentences are quotations from TILLYARD'S published accounts:

*Isosticta simplex* MARTIN. — "It is a most retiring insect, being very fond of resting on small shrubs, usually on some of the more central twigs or branches. At intervals, it indulges in short flights, which usually consist in balancing itself in the air in one position, often in a confined space between the branches of its shelter. When disturbed, it does not fly away, but flits further into the bush, and settles in the foliage". (*Proc. Linn. Soc. N. S. Wales*, 37, 1913: 433).

*Neosticta canescens* TILL. — "Along the banks of the Woronora River and Heathcote Creek, these insects are fairly abundant, and are very fond of hiding in overhanging bushes, or indulging in short poising flights in the confined spaces between the branches". (*Ibid.*: 437).

*Oristicta filicicola* TILL. — "This retiring and inconspicuous species was discovered by me not far from the summit of Mt. Cook. At the top of a very steep gully, densely clothed in forest-growth, a small stream emerges and falls over a steep ledge of rock. At this point the walls of the gully are closed in, so as to form a ledge about twelve feet high on each side of the waterfall. The whole of the rock is densely covered with ferns. Resting on these ferns, deep in shade, and drenched with the spray of the fall, I found this little dragonfly". (*Ibid.*: 439-440).

Unfortunately, nothing is yet known about the egg-laying process of these elusive insects. It would therefore seem to be of considerable interest to study the oviposition of such genera like *Isosticta*, *Neosticta* and *Oristicta*, with which the Papuan genera *Selysioneura* and *Tany-mecosticta* form a natural group within the family, and which exhibit numerous high specializations.

#### Description of the full-grown larva

Material. — Three ♂ examples (two penult), Central W. Misool I., Wartama River near Fakal, 50 m, 3.x.1948, M. A. LIEFTINCK.

Total length of body without caudal gills 9.5; median gill (regenerated!) 3.1, lateral gill 4.2; length of head 1.8, width of same across the eyes 2.8; length of antenna 2.5 mm. Relative length of separate joints of antennae as shown in fig. 21. Length of hind wing rudiment 3.5; of posterior femur 3.2 mm.

Ground-colour of body pale sandy yellow mottled and banded with light brown as shown in fig. 20. Head flat and of large size, much wider



than long and considerably broader than thorax. Eyes large and prominent. Occipital lobes swollen, obtuse-angulate posteriorly, hind angles minutely spinulose. Antennae long and slender, third joint the longest. Labium relatively short and of small size, reaching back between the legs almost to the posterior border of the first pair of coxae, shaped as shown in fig. 23. Mentum in distal half with a row of 15—18 short spinulose setae along outer margin; anterior portion produced in a broadly rounded middle lobe on which the remains of a (closed) median cleft are clearly visible (fig. 25); border microscopically serrulate, carrying irregular scale-like setae. Only a single pair of short mental setae, placed on each side of the middle line. Lateral lobe exceptionally long, almost parallel-sided, its inner margin slightly undulate, finely but distinctly denticulate, the serrulations directed basad; outer margin on the inside with two irregular rows of short spike-like setae; end-hook bifid, the outermost branch about half as long as the main apex, which is more strongly curved; movable hook very long and slender, evenly and strongly curved. Lateral setae absent in ult larva, but present in both penult larvae, one on each side, situated about half-way the length of the lobe and somewhat shorter than the movable hook. Mandibles normal, not differentiated into incisor and molar groups, provided with five very strong apical teeth, both right and left mandible with a minute acute tooth on the inner surface, the right one with an additional sub-apical tooth (fig. 22).

Prothorax flat and exceptionally long, disc-like, antero-lateral edges coarsely spinulose. Synthorax moderately long and of slender build. Wing cases parallel, reaching back almost to the end of the sixth segment.

Legs long and slender, surface smooth; femora slightly flattened; tibiae and tarsi sparsely fringed with long hairs on exterior margin. Femora and tibiae all with two brown rings at one-third their length and with an additional incomplete dark ring about the trochanters and knees.

Abdomen smooth, not much longer than in the alcoholic larva shown in fig. 20; last segment dorsally with a row of minute spinules along posterior border. Lateral ridges of segments not produced apically and distal angles rounded. Cercoids conspicuous, slightly curved inwards, somewhat shorter than 10th segment.

Gizzard with 16 dental folds, not clearly arranged alternately into major and minor folds, but dentition differentiated alternately: "major" folds with 0—2 minute anterior teeth and a loose group of 3—5 larger posterior teeth; "minor" folds only with 2—3 large teeth placed in a longitudinal row.

The caudal gills are of the "Constricted Saccus" type, as described in detail by TILLYARD (*loc. cit.* 1917a) for the larvae of the Australian protoneurid genera *Neosticta* and *Nososticta*. They are of large size, more or less sausage-shaped and greatly swollen, but not as tense in the living larva as they become when fixed in alcohol, semitransparent. As in *Neosticta*, the constriction between the joints is strongly marked and only just sufficiently wide to allow of the passage of the main tracheae. The

cuticle of the lateral gills is sparsely covered with thin shaggy hairs upon the proximal part of the basal joint, and clothed with very long dense pencil-hairs on the whole of the distal joint. The basal one-third of the median gill carries about 15 distinct short setae placed in a row on each side of its basal joint, the latter on its ventral surface carrying moreover a weak longitudinal ridge furnished with long pencil-hairs; the distal joint resembles that of the lateral gills closely in shape and hairiness. The median and lateral gills are normally sub-equal in length and also approximately similar in shape, the median gill almost straight, the lateral gills somewhat inclined towards one another; inner face of the lateral gills in cross-section slightly less convex than the outer side, so as to offer space for the median gill (which is weakly longitudinally carinate ventrally) to fit partly in between the lateral ones.

The tracheal system is difficult to follow, but appears to be very similar to that of *Isosticta*. There are only two main tracheae in each gill, which pursue a somewhat tortuous course, giving off very short and unapparent branch tracheae. The median and one right lateral gill are shown in fig. 26. As is clearly seen in the upper figure of the median gill, the tracheae in the basal joint are of much smaller size than usual, the two main stems having been broken up at extreme base into many small branches; this is, in fact, a regenerated gill, the median gill of all other larvae of *Selysioneura* examined by me being similar to the lateral ones. Hence it is clear that, at least so in *Selysioneura* and *Isosticta*, there are always two main tracheae in all three gills<sup>1</sup>). In this connection it should be noted that the close relationship between these two genera is manifest also in several other respects.

The above described larvae were obtained from the slow-flowing stream Wartama, a tributary of the Kasim (central Misool), at a point where the stream was overhung with trees and bushes. All the time during my visits to this river, the water was low and thus afforded an opportunity to collect aquatic insect larvae. Two species of *Selysioneura* occurred here, of which only one is described in the previous pages.

In spite of a prolonged search, exuviae of *S. cornelia* were looked for in vain, but the pale-coloured larvae were finally discovered by turning over a great many half-submerged pebbles under which they found concealment, resting on the bottom with sprawling legs, each individual in its own depression. When emerging the larva probably crawls up the small pebble under which it took shelter, just above water-level, and transforms there. At any rate the newly emerged insect rests only just out

<sup>1</sup>) See TILLYARD (1917a: 74 and 93).

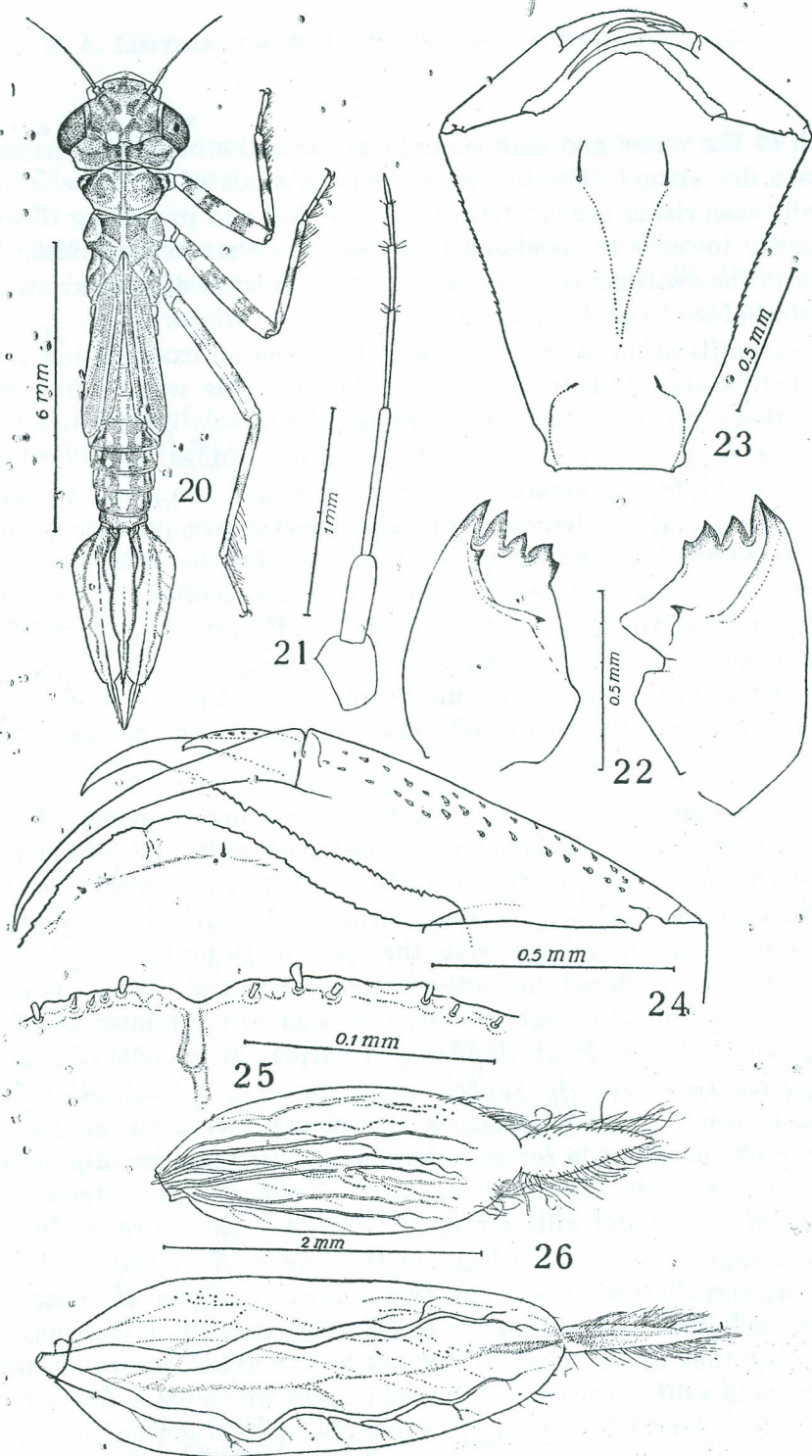


Fig. 20—26. Larval structures of *Selysionaura cornelia*, sp.n., from Wartama River, Misool I. Full-grown larva, spirit specimen. (20), antenna (21), right and left mandibles (22), interior view of labium (23), right lateral lobe of labium (24), apex of median lobe, showing closed cleft (25), left side-view of median gill and interior view of right lateral caudal gill (26).

of reach of the water and flies straight off into the bush as soon as its wings are dry enough. Freshly emerged individuals of *S. cornelia* were repeatedly seen rising heavily from the gravel-bed and propelling themselves clumsily towards the sheltering bushes on the river bank. Many fell a victim to the swiftlets (*Collocalia* sp.), which snatched them away time and again before I could interfere.

The identification of these larvae is based on an examination of the wing-venation and of their general morphology. This was confirmed by an inspection of the larva of another species, *S. capreola* LIEFT., discovered by the late W. STÜBER near Hollandia, N. New Guinea. On January 1, 1936, he found a freshly emerged ♂ with its skin, and two penult larvae, in the bed of an almost dried-up river. These larvae are practically indistinguishable from the penult examples of *S. cornelia*, discussed above, and all agree in the characters of the caudal gills and labium. The shape of the head in these younger nymphs is a little different from that of the full-grown larva: it has a more squarish outline, the rounded occipital edges being almost rectangulate; at the same time the distance between the hind angles and the compound eyes is greater than the diameter of the eye.

This peculiar larva suggests several interesting problems. As will be seen from the figures, its labial mask, the mouth-parts and the antennae, have the characters that mark the family to which it belongs; save for the significant indication of a cleft median lobe and the tendency to lose (?) the mental and lateral setae, the labial mask presents no features that could be considered 'primitive'. The large flat head, enormous disk-like pronotum and slightly flattened legs are reminiscent of the condition found in the Platystictidae and various Megapodagriid larvae, but it seems reasonable to suppose that they are specializations and, perhaps, to some extent adaptations to a changed environment; at any rate there are no grounds for considering any close relationship between *Selysionaura* and the members of these families. The extraordinary structure of the caudal gills strongly recalls the same organs in some Amphipterygidae, various Epallagidae (*Dysphaea*, *Euphaea*), and *Cora*, as well as the Platystictidae. The two-jointed condition of these gills, however, links them unquestionably to *Neosticta* and allies. One may well ask whether they are a primitive feature lost in allied genera or merely adaptations to a different habitat, but as long as we do not know anything about the first larval instars of these insects, speculation on such points seems useless.

4. DESCRIPTIONS OF THE LARVAE OF *Prodasineura* COWLEY AND OF THREE SPECIES OF *Notoneura* TILLYARD*Prodasineura autumnalis* (FRASER) (fig. 27-31, and 36).

Material. — Six examples, both sexes (two ♂ penult), W. Java, Bogor, 250 m, brook in wooded part of the Botanic Garden, 5.x.1930, M. A. LIEFTINCK.

Total length of body without caudal gills 9.0—11.0 (11.0 mm with normally distended segments); median gill 2.8—3.1, lateral gill 3.3—3.5; length of head 1.4—1.5, width of same over the eyes 2.6; length of antenna 1.6—1.7 mm. Relative length of separate joints as shown in fig. 27. Length of hind wing rudiment 2.9—3.0, of posterior femur 2.7 mm.

Ground-colour of body dark greyish-yellow variegated with pinkish-brown and deep black; antennae and legs pale pinkish-yellow, ringed with greyish-black or black, as shown in fig. 27. Head moderately large, rather flattened, about two times wider than long and broader than the thorax, strongly diminished in width posteriorly. Rounded hind angles of occipital lobes carrying a number of short, strong spinulose setae. Antennae of moderate length, third joint the longest but not much exceeding 2nd and 4th joint in length. Labium slightly longer than wide, reaching back to the base of mesocoxae, shaped as shown in fig. 29. Mentum in distal two-fifth with a row of 10—14 short and thick spinulose setae along outer margin; anterior portion but slightly produced in a middle lobe carrying a pair of minute spike-like setae on each side of the middle near margin and a variable number of still smaller setulae; border almost straight, carrying a continuous row of short scale-like setae. Only a single pair of strong mental setae, placed on each side of the middle line. Lateral lobe short and strong, distal two-third almost parallel-sided, its inner border very weakly serrulate; outer margin on the inside with a row of minute setulae; end-hook deeply bifid, the outermost branch short and broad, slightly curved, apically subtruncate and weakly serrulate, apex more strongly curved and hook-like, followed mesially by a blunt denticle; movable hook strong and curved, but of moderate size. Lateral setae four on either side, the longest approximately equal in length to the movable hook. Mandibles as in fig. 36, armed with four unequally sized apical teeth and four irregular teeth on the inner surface, the right mandible moreover with a minute sub-apical tooth.

Prothorax moderate, broader than long and widest posteriorly, hind angles rounded. Synthorax rather robust, wider than prothorax. Wing-cases parallel, reaching back as far as half-way between the fourth and fifth or to the end of the fifth segment.

Legs long, femora with exterior row of very short spinules and sparsely pubescent, tibiae and tarsi more densely pubescent, tibiae and first tarsal joint moreover with short spinulose setae, densest apically along interior margin. Femora with two dark rings at one-third their

length and an additional dark ring near base; tibiae with one sharply defined ante-median black ring and one larger and indistinct ring near the apex.

Abdomen relatively strong and compactly built, tapering to the end, as shown in fig. 27 for the living larva; segm. 7—10 dorsally and laterally with a dense row of minute spinules along posterior border. Lateral ridges of segments not produced apically, but lateral carinae of 8—9 armed with a row of short acute spinules; 10th segment shallowly emarginate mid-dorsally. Cercoids inconspicuous.

Gizzard with 16 dental folds clearly arranged alternately into 8 major and 8 minor folds, the latter only half as long as the former; major folds with 2—4 small anterior teeth and a loose group of 3—4 larger posterior teeth; minor folds with only 2 teeth placed longitudinally.

Caudal gills of the "Vertical Lamella" type, elongate-oval, completely devoid of a node and with well-rounded tips. In transverse section both median and lateral gill are somewhat swollen. Median gill with two distinctly denticulate mid-ribs, right and left, from base up to a point near the apex, the dorsal and ventral border of the gill carrying also a row of short spinulose setae, both approximately of equal length and running to about the same point as the mid-ribs, thus marking the end of the original basal joint of the gill. Lateral gill similar to median gill, but asymmetrical and a little longer; inner surface distinctly concave, its surface smooth and devoid of a median carina, the outer surface only bearing a distinct mid-rib which however bears no denticles; dorsal and ventral border of gill with a row of short spinulose setae similar to those along margin of median gill. Cuticle of both median and lateral gills almost bare, margin densely fringed with pencil hairs, which become increasingly longer and more abundant towards the apex. Pigmentation of gills strong and concentrated mainly in a longitudinal zone at the middle, and a sub-apical band across the gill, coloured in various shades of dark brown, the apical "blade" slightly pink-coloured. Tracheal system moderately distinct; main longitudinal tracheae concealed under the mid-rib, apparently two in each gill; branch tracheae simple, coming off from the main tracheae obliquely.

The larvae of *Prodasineura autumnalis* and allied species, like those of the genus *Notoneura*, are frequently found among the submerged tangle of roots of vegetation fringing the edge of a stream. In the Botanic Garden at Bogor and elsewhere in low country, the pendent aerial roots of lianas often form broom-like bundles of rootlets which hang down freely into the water, and it is among the matted outcrop of these current-swept roots that a rich aquatic fauna develops. Apart from various kinds of shrimps, worms and other small fry, these ecological niches are also the dwelling-place of the nymphs of Zygoptera and mayflies. Apparently these creatures here not only find the necessary protection against enemies, but also an abundant supply of food. Other dragonfly larvae found,

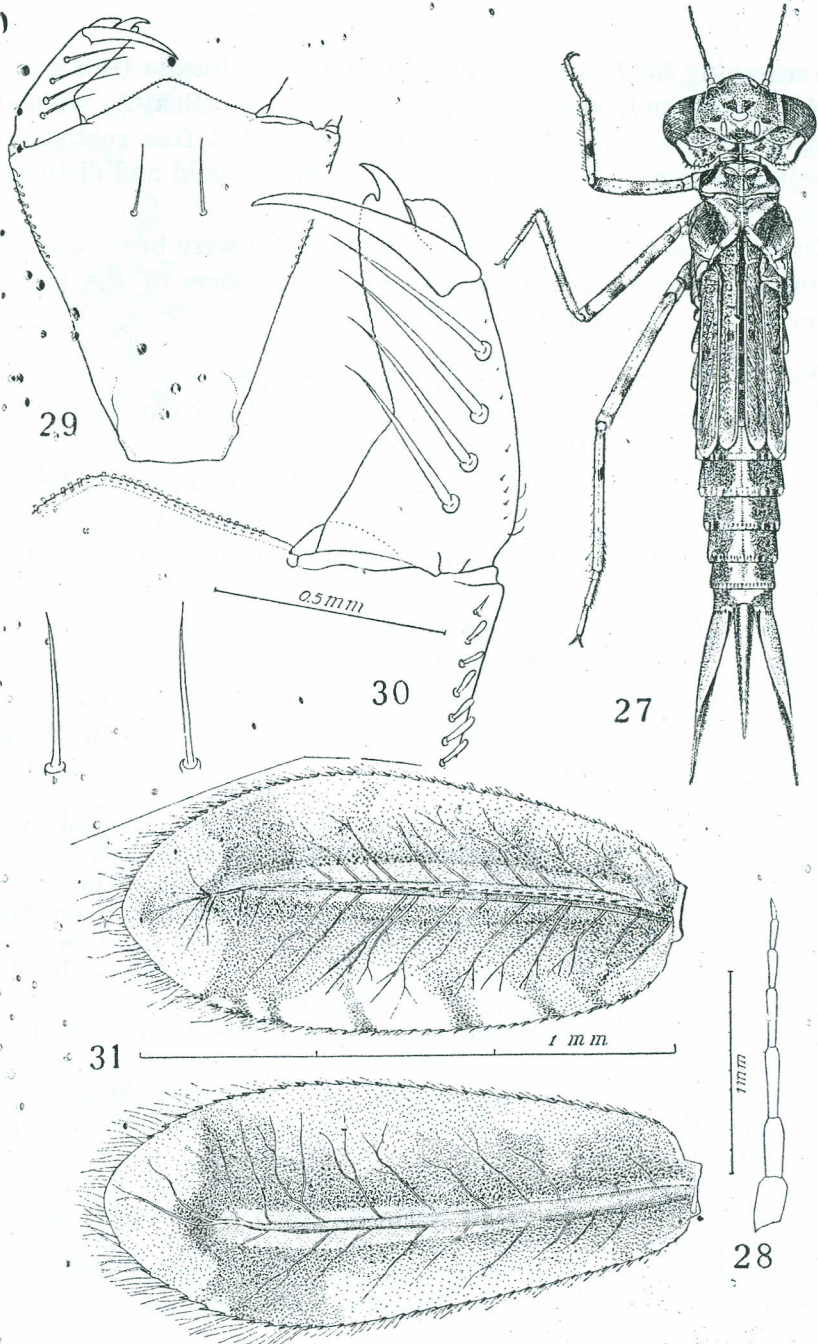


Fig. 27—31. Larval structures of *Prodasineura autumnalis* (FRAS.), from Bogor, W. Java. Full-grown larva, live specimen (27), antenna (28), interior view of labium (29), portion of median and of right lateral lobe of labium (30), right side-view of median gill and exterior view of right lateral caudal gill (31).

while searching for *P. autumnalis*, were *Libellago lineata* (BURM.), *Copera marginipes* (RAMB.), and *Pseudagrion pruinosum* (BURM.), which thrive among the silt and debris assembled between the fine rootlets. It was impossible to obtain them without stirring up the mud and disturbing the habitat.

Of many *autumnalis* secured in 1930 several were bred out, and after drawings had been made from live examples, some of the latter were preserved in spirit for future study.

*Notoneura moluccensis* (SELYS) (fig. 32-35).

Material. — Three ♂ (penult), Moluccas, Ambon I., stream near Tulehu, sea-level, 16.x.1949, M. A. LIEFTINCK.

These larvae are so similar structurally to the next described species, *N. fonticola*, and to *N. plagiata* discussed thereafter, that it will suffice to point out the differences, which are slight and probably only of specific value.

Though no full-grown larvae are available for comparison with *fonticola*, the body is evidently shorter and more compactly built than in that species, a feature corresponding with the general facies of the adult insect, both *moluccensis* and *plagiata* belonging to a different species-group than *fonticola*.

Head longer, with slightly more protuberant eyes and with the postocular lobes better developed, strongly convex posteriorly; proportions as shown in fig. 32. Shape of antennae and prothorax very similar to *fonticola*. Mentum with a pair of minute spike-like setae on each side near the border of the produced anterior portion of the middle lobe. One mental and two lateral setae. End-hook of lateral lobe deeply bifid, the outer hook much larger than the apex, both hooks curved and pointed. Movable hook considerably more slender and also shorter than in both *fonticola* and *plagiata*.

Legs as in the next two species, the three dark brown bands on femora and tibiae sharply delimited. Body-colouring brownish yellow variegated with dark brown and deep black as shown in fig. 32. Abdomen with the lateral carinae of terminal segments not terminating in acute apical spines and only the 10th segment carrying a row of fine spinules along posterior border.

Gizzard with 16 dental folds, clearly differentiated into major and minor folds, as described for *plagiata*; dentition also similar to that species.

Caudal gills (fig. 35) deeply pigmented, only little different in shape from those of *plagiata*; armature of mid-ribs and of dorsal and ventral margins as described for *fonticola* and as shown in the same figure.



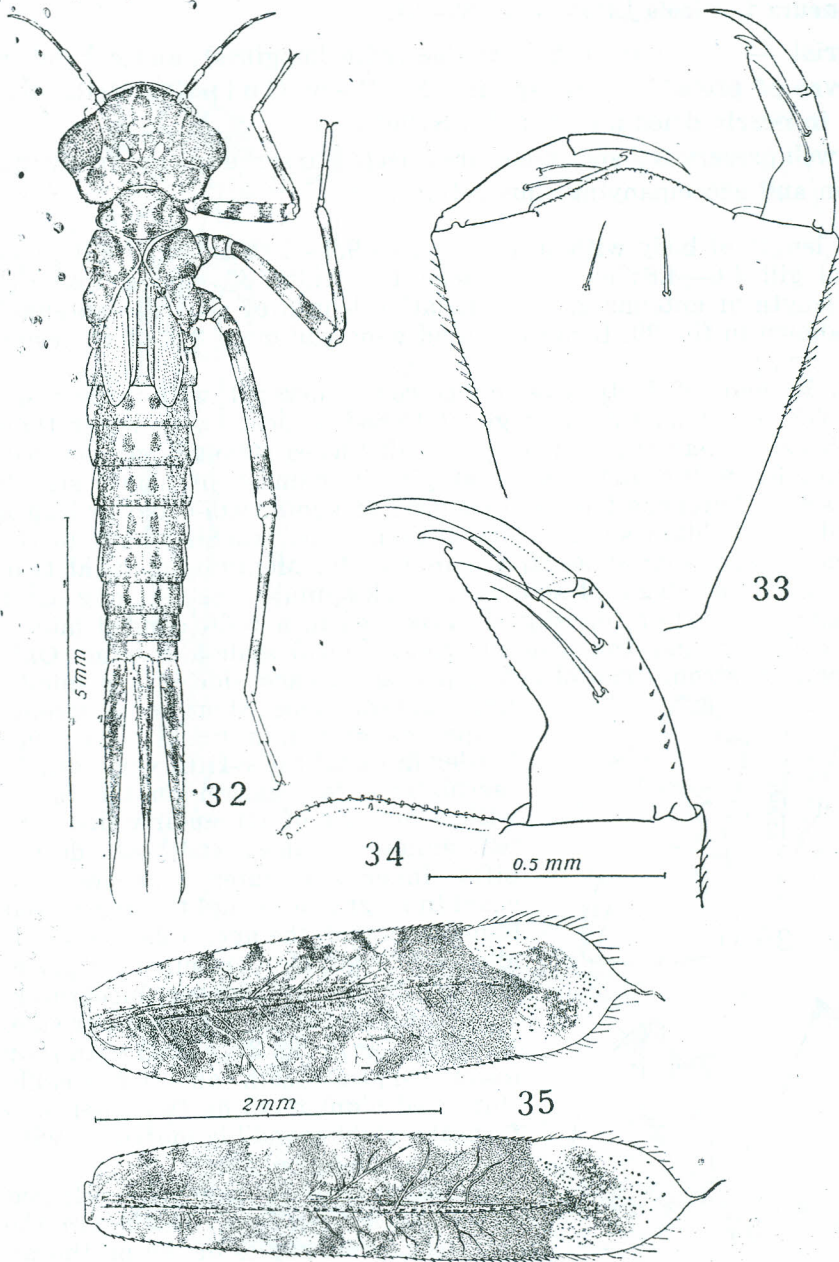


Fig. 32—35. Larval structures of *Notoneura moluccensis* (SELYS), from Ambon. Perult larva, freshly killed specimen (32), interior view of labium (33), right lateral lobe of labium (34), left side-view of median gill and exterior view of left lateral caudal gill (35).

**Notoneura fonticola** LIEFT. (fig. 37-43).

Material. — Two ♂ (ult), 2 ♀ exuviae (with imagines), and a number of ult larvae of probably same species, N. New Guinea, Hollandia, 17.i.1936; in nearly dried-up river, W. STÜBER.

Two well preserved ♂ specimens are selected to serve for the following description and accompanying illustrations.

Total length of body without caudal gills 9.9—10.2; median gill 4.0—4.2, lateral gill 4.6—4.8; length of head 1.4, width of same across the eyes 2.6; length of antenna 2.3 mm. Relative length of separate antennal joints as shown in fig. 39. Length of hind wing rudiment 3.3, of posterior femur 3.0 mm.

Ground-colour of body pale olive-brown, marked with brown, as shown in fig. 38. Head rather large, flattened, almost twice wider than long and broader than the thorax; postocular lobes strongly pronounced, the hind angles well-rounded and carrying a number of short, strong spinulose setae. Antennae long and slender, 2nd joint sub-equal in length to 3rd and 4th. Labium slightly longer than wide, reaching back to the base of mesocoxae, shaped as shown in fig. 40. Mentum in distal two-third with a row of about 24 short and thick spinulose setae along outer margin; anterior portion but slightly produced in a well-rounded middle lobe that carries a marginal row of microscopical scale-like setae. Only a single pair of strong mental setae, placed on each side of the middle

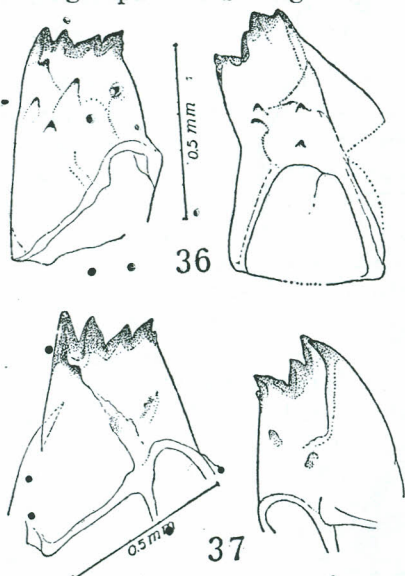


Fig. 36. Interior view of right and left mandibles of *Prodasineura autumnalis* (FRAS.), ult larva. Fig. 37. The same of *Notoneura fonticola* LIEFT.

line. Lateral lobe short and strong, shaped as shown in fig. 41, its inner border in distal three-fifths very weakly serrulate; outer margin on the inside with a number of irregularly distributed minute setulae; end-hook deeply bifid, inner and outer branches sub-equal in length, both slightly curved and bluntly pointed, the apex followed mesially by a triangular prominence; moveable hook long and slender, moderately curved. Lateral setae two on either side. Mandibles as in fig. 37, armed with four unequal apical teeth and 1-2 weakly chitinized blunt teeth on the inner surface, the right mandible moreover with a minute sub-apical tooth.

Prothorax and synthorax shaped much as described for *Prodasineura*, the rounded lateral angles of the prothorax slightly protuberant and raised. Wing-cases parallel, reaching as far back as the end of the fourth segment or a little further.

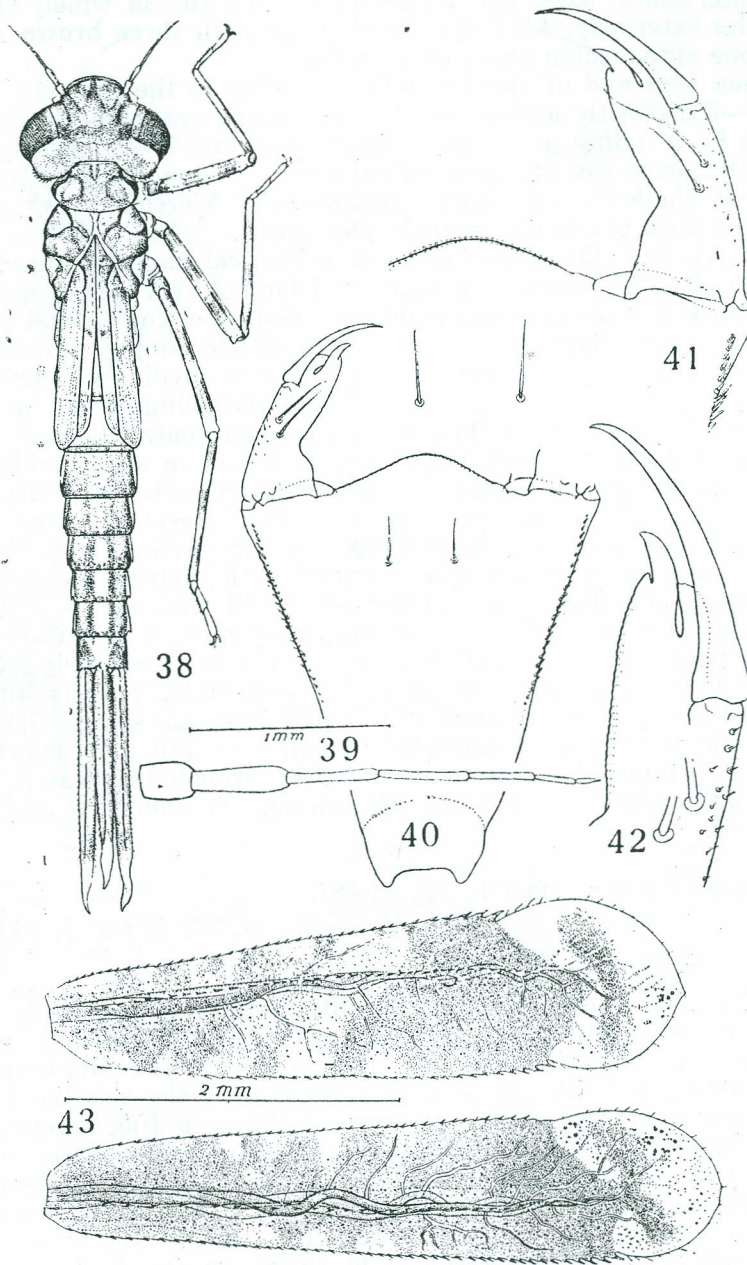


Fig. 38—43. Larval structures of *Notoneura fonticola* LIEFT., from Hollandia, N. New Guinea. Full-grown larva, spirit specimen (38), antenna (39), interior view of labium (40), right lateral lobe of labium (41), apex of lateral lobe more highly magnified (42), left side-view of median gill and extero-lateral view of left lateral caudal gill (43).

Legs long, almost bare, anterior femora with a row of widely spaced short spicules exteriorly. All femora and tibiae with three brown rings, one basal, one ante-median and one sub-apical.

Abdomen long and of slender build, tapering to the end, the basal segments 2—5 distinctly longer than the succeeding ones; lateral carinae of segments 8—9 ending in an acute apical spine, and 7—10 dorsally and laterally with a dense row of microscopical spinules along posterior border; 10th segment shallowly emarginate mid-dorsally. Cercoids very small.

Gizzard not examined (compare *N. plagiata*).

Caudal gills (fig. 43) of the "Subnodate Vertical Lamella" type, with the nodal line situated near the apex, the division not very clearly marked. Basal division not swollen, merging into the distal portion (apical blade) without definite boundary line. Tips of gills either simply rounded, as shown in the figure, or with a short apical filament. Median gill with two distinctly denticulate mid-ribs, right and left, extending from base up to about three-fourths of the gill-length; dorsal and ventral border of the gill carrying also a row of short spinulose setae set in strong chitinous bases, both extending about as far distad as the mid-ribs, thus marking the end of the original basal joint of the gill. Lateral gill similar to median gill, but asymmetrical and longer; inner surface very weakly concave and both sides of the gill provided with distinct, denticulate, median carinae; dorsal and ventral border of gill with a row of short spinulose setae similar to those along margin of median gill. Cuticle of both gills bare, margin of the blade posterior to the 'node' sparsely fringed with pencil hairs. Pigmentation of gills coenagrioid, purplish-brown, forming a definite pattern, as shown in fig. 43. Tracheal system distinct; main longitudinal tracheae apparently two in each gill, but sometimes an additional primary trachea in lateral gill; branch tracheae few in number, their course irregular, but all coming off obliquely from the main tracheae.

*Notoneura plagiata* (SELYS) (fig. 44-48).

Material. — Three ♂, 2 ♀ (ult), 2 penult, N. W. New Guinea, Sorong, 50 m, 29.viii.1948, forest-brook, M. A. LIEFTINCK.

Body short and stout as compared with *fonticola*. Head wider and eyes more protuberant, the proportions being shown in fig. 44. Side angles of prothorax projecting laterad, so as to form a more or less nipple-shaped tubercle on either side. Antennae only little longer, the relative length of the separate joints approximately equal to the preceding species, 2nd to 4th joint strongly pigmented (blackish-brown), except at the apices. Mentum with a pair of minute spike-like setae on each side near the border of the produced anterior portion of the middle lobe (absent in *fonticola*, but present also in *moluccensis*). One mental and two lateral setae. End-hook of lateral lobe deeply bifid, the two hooks slender, curved and acutely pointed (fig. 46).

Legs as in *moluccensis*, with three well defined dark brown bands on all femora and tibiae. Body-colouring brownish-yellow, mottled and

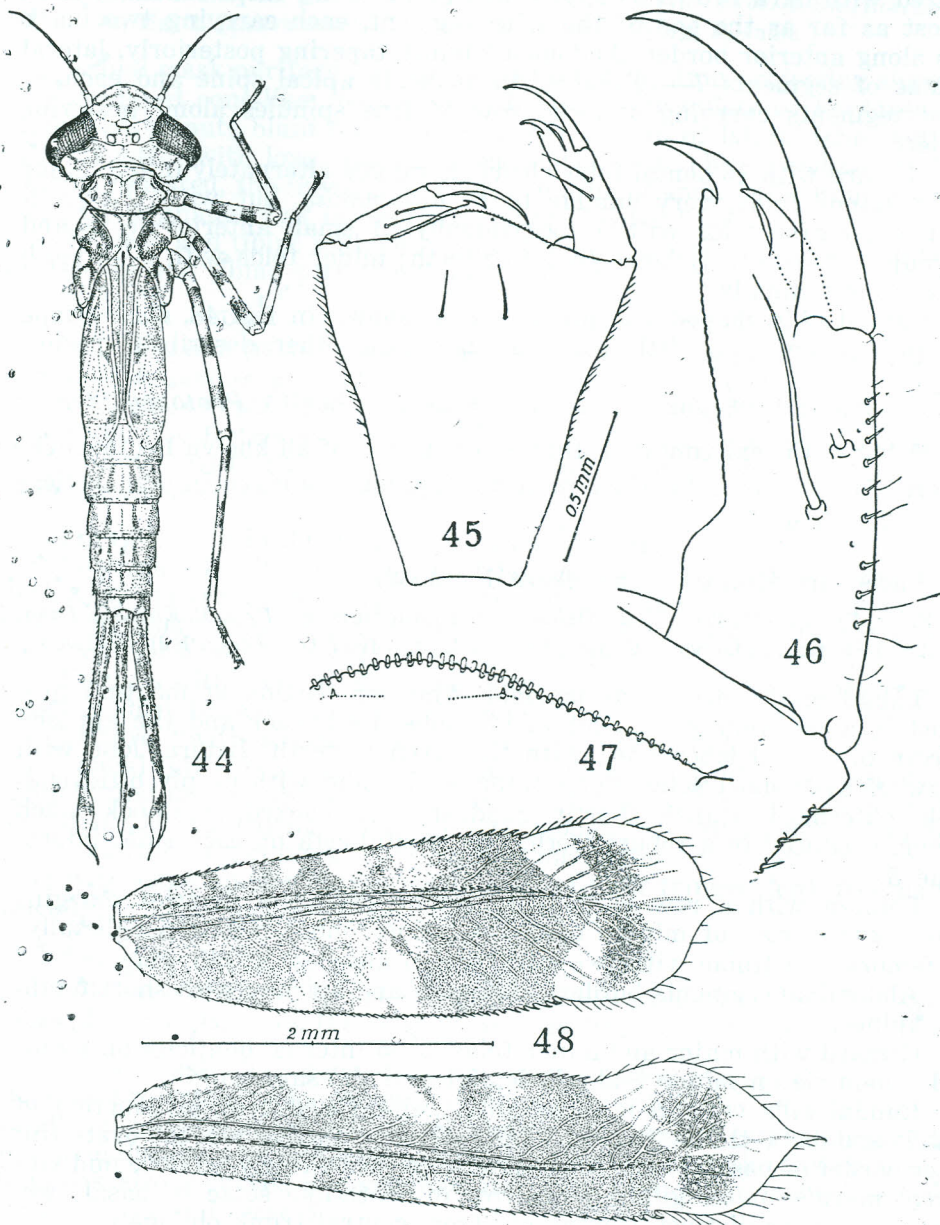


Fig. 44—48. Larval structures of *Notoneura plagiata* (SELYS), from Sorong, W. New Guinea. Full-grown larva, 'spirit specimen' (44), interior view of labium (45), right lateral lobe of labium (46), apex of median lobe, showing apical scale-like setae (47), left side-view of median gill and exterior view of left lateral caudal gill (48).

spotted with dark brown as shown in fig. 44. Wing cases reaching back almost as far as the end of the fifth segment, each carrying two black dots along anterior border. Abdomen slightly tapering posteriorly, lateral carinae of segments 7—10 ending in an acute apical spine and each of these segments carrying a dense row of fine spinules along posterior border.

Gizzard with 16 dental folds clearly arranged alternately into 8 major and 8 minor folds, very similar to *P. autumnalis*, but with the teeth stronger; major folds with 1 (occasionally 2) small anterior teeth and a group of 3 (rarely 4) large posterior teeth; minor folds with 1—2 teeth placed longitudinally.

Caudal gills shaped and pigmented as shown in fig. 48, their shape and proportions only little different from the other described species.

##### 5. SYNOPSIS OF THE KNOWN LARVAE IN THE FAMILY *Protoneuridae*

A list of the existing literature on the larvae of all known Protoneurid genera, followed by a brief characterization, may be given in alphabetical order, as follows :

###### *Caconeura* KIRBY (= *Indoneura* LAIDLAW)

F. C. FRASER (1943). New Oriental Odonate larvae. *Proc. R. Ent. Soc. Lond.* (B) 12: 84-86, fig. 3. [Larva of *C. gomphoides* (RAMB.), from the Nilgiri Hills, S. India.]

Labial mask normal, coenagrioid. Anterior portion of mentum produced in a not very prominent middle lobe, its border and the apposed margin of lateral lobes lined with tiny crenate teeth. Lateral lobe with a row of 8—9 short setae along outer border and with deeply bifid end-hook, outermost branch shortly quadrate and hooked, end-hook much longer, produced in a robust tooth. One mental seta on each side; lateral setae 3.

Femora with a row of 6—7 robust spines along exterior margin; tibiae with a row of minute coral-like spines, more closely set distally; all femora and tibiae with two dark brown annules.

Abdominal segments bordered laterally and apically with short tooth-like spines.

Gizzard with major and minor folds, 3—5 internal denticles on major and 1 denticle on minor fold, all denticles of the same size.

Caudal gills vertical lamellae with well-defined node at junction of middle and distal thirds, the latter abruptly expanded as a broad ovate fin; outer border of basal two-thirds of lateral gill with finely setulose mid-rib; dorsal margin of all gills with a row of tooth-like setae in basal two-thirds; tracheae distinct, coming off from central trunk obliquely.

###### *Disparoneura* SELYS (= *Chloroneura* LAIDLAW).

F. C. FRASER (1919). Descriptions of new Indian Odonate larvae and exuviae. *Rec. Ind. Mus.* 16: 466-467, pl. 36, fig. 3, pl. 37, fig. 4. [Larva of *D. quadrimaculata*

(RAMB.), [from India.] Id. (1943). New Oriental Odonate larvae. *Proc. R. Ent. Soc. Lond.* (B) 12: 84, fig. 2. [Larva of *D. apicalis* (FRAS.), from Coorg, S. India.]

Labial mask pyriform. Anterior portion of mentum projecting sharply and produced cone-like, deeply cupped, margin crenulate or bordered by closely set minute blunt teeth, the apposed margin of lateral lobes entire. Lateral lobe "with long movable hook and a short obtuse end-hook" (?), or "reduplicated, the inner part ending in a blunt spine" (?). Four mental setae in an oblique row on each side; lateral setae 6—7.

Femora and tibiae with two rows of very short, widely-spaced spines; all femora and tibiae with two dark brown annules.

#### *Iscsticta* SELYS.

R. J. TILLYARD (1917a). On the morphology of the caudal gills of the larvae of zygopterid dragonflies. pt. i-ii & iii-iv. *Proc. Linn. Soc. N. S. Wales*, 42: 38, 92-93, fig. 23, 624-625, 632, pl. 1, fig. 7 [Caudal gills of *I. simplex* MARTIN, from N. S. Wales] Id. (1917b). *The Biology of Dragonflies*: 195, fig. 8, 42, 84. [Larval structures of *I. simplex* MARTIN.] Id. (1926). *The Insects of Australia and New Zealand*, fig. F 11 A. [Larva & labium of *I. simplex* MARTIN.]

Larva undescribed (fig. 42C, TILLYARD, l.c. 1917b: 93), of slender build.

Labial mask with cleft median lobe, the anterior portion of mentum produced, apparently subtriangular in outline. Lateral lobe with deeply bifid end-hook, the outermost branch hook-like, but much shorter than the incurved end-hook. No mental seta; lateral setae 3.

Femora with four, tibiae apparently with three broad, sharply pointed, dark brown annules.

Gizzard "with sixteen generalized folds" (TILLYARD, l.c. 1917: 279).

Caudal gills constricted vertical lamellae, definitely two-jointed, opaque throughout and deeply pigmented; tracheal system similar to *Neosticta*; lateral carinae (mid-ribs) of probably all gills finely setulose; dorsal margin of median gill and ventral margin of lateral gill with a row of minute setae up to node; margin of distal joint fringed with fine hairs apically.

#### *Neoneura* SELYS.

J. G. NEEDHAM (1939). Nymph of the Protoneurine genus *Neoneura*. *Ent. News*, Philad., 50: 241-245, 6 figs. [Larva of *N. carnatica* SELYS, from Cuba.]

Labial mask shaped much as in *Disparoneura*. Anterior portion of mentum projecting strongly and produced in a broadly rounded entire middle lobe, the apposed margin of lateral lobes weakly serrulate. Lateral lobe with deeply bifid end-hook, outermost branch tooth-like and incurved, end-hook also incurved but much stouter and longer. One mental seta on each side; lateral setae 3.

Femora with dense row of minute sharp spinules along interior margin; tibiae and tarsi heavily fringed with long hairs on posterior margin and densely beset with sharp, short, spinulose setae on the inner surface toward the tip; femora with two, tibiae with only one dark brown annules at one-third their length.

Gizzard undescribed.

Caudal gills vertical lamellae, thick at base and tapering to thin lamellae at the tip, each with well-defined node, obliquely divided at two-fifths their length into two parts: a thick opaque, strongly pigmented basal segment, longest on its ventral margin, and a thin pointed apical leaf-like portion; outer border of basal three-fifths of lateral gill with finely setulose mid-rib; dorsal (and apparently also ventral) margin of all gills with a row of tooth-like setae up to node, and moreover fringed with longish hairs from near base to apex; tracheae probably as in *Caconeura*.

#### **Neosticta** TILLYARD.

R. J. TILLYARD (1917a). On the morphology of the caudal gills of the larvae of zygopterid dragonflies. pt. i-ii & iii-iv. *Proc. Linn. Soc. N. S. Wales*, 42: 37-39, 77-79, figs. 14-16 & 612-613, 621, 625, 632, fig. 39, pl. 1, fig. 6, pl. 3, fig. 21, pl. 4, fig. 28. [Caudal gills of *N. canescens* TILL., from N. S. Wales.] Id. (1917b). *The Biology of Dragonflies*: 192, 195, 199, fig. 2E, 42B, 84C. [Larval structures of *N. canescens* TILL.]

Larva undescribed (fig. 42B, TILLYARD, l.c. 1917b: 93), body short and thick-set.

Labial mask undescribed (similar to *Isosticta* and *Nososticta*?); "Mask flat, without setae". (TILLYARD, l.c. 1917b: 279).

Femora and tibiae with three sharply pronounced dark brown annules.

Gizzard, see *Isosticta*.

Caudal gills strongly inflated, constricted saccoid, the constriction very strongly marked; cuticle clear and unpigmented, hypodermal pigment confined to three transverse zones; main tracheal stems and branch tracheae simple, more or less visible.

#### **Nososticta** SELYS.

R. J. TILLYARD (1917a). On the morphology of the caudal gills of the larvae of zygopterid dragonflies. pt. i.ii & iii-iv. *Proc. Linn. Soc. N. S. Wales*, 42: 37-38, 79. [Notes on caudal gills of *N. solida* SELYS, from N. Queensland.] Id. (1917b). *The Biology of Dragonflies*: 192, 195. [Notes on same organs.]

Larva undescribed, apparently rather similar to that of *Neosticta*.

Labial mask and further details, see *Neosticta*.

Caudal gills "closely resembling those of *Neosticta* in size and shape, but may be distinguished, in common with the whole larva, by being of a more definite black-and-white banded pattern, the pattern in *Neosticta* being banded dark brown and pale yellowish-brown". (TILLYARD, l.c. 1917a: 79).

#### **Notoneura** TILLYARD.

Described in this paper (fig. 32-48).

Labial mask normal, coenagrioid. Anterior portion of mentum slightly produced, its border entire or feebly crenulate, with row of blunt scale-like setae, the apposed margin of lateral lobe weakly serrate. Lateral



lobe with deeply bifid apex, the branches sub-equal in length, both curved and pointed, the end-hook placed considerably more distad. One mental seta on each side; lateral setae 2.

Legs almost bare; femora with interior and exterior rows of extremely minute spinules; all femora and tibiae with three dark annules.

Abdominal segments 7-10 usually with short lateral spine at apex and with a row of short acute spinules along posterior border.

Gizzard with 8 major and 8 minor folds, dentition much as in *Prodasineura*.

Caudal gills vertical, subnodate, in the form of flattened lamellae, narrow, lanceolate, node situated near apex, the apical division usually slightly expanded, rounded or with short apical filament and with pubescent marginal hairs; mid-ribs and dorsal and ventral borders of all gills carrying a row of short, spinulose setae.

#### **Prodasineura COWLEY.**

Described in this paper (fig. 27-31, 36).

Labial mask normal, coenagrioid. Anterior portion of mentum and apposed margin of lateral lobe as described for *Notoneura*. Lateral lobe with deeply bifid apex, the outermost branch obliquely truncated, end-hook plated more distad, curved and pointed. One mental seta on each side; lateral setae 4.

Femora with exterior row of very short spinules and sparsely pubescent; tibiae and tarsi with longer pubescent hairs, thicker and more closely set distally on the inside; femora with three, tibiae with two dark annules.

Abdominal segments 8-9 laterally and 7-10 posteriorly with row of short acute spinules.

Gizzard with 8 major and 8 minor folds, 3-4 and 2-4 small denticles on major, 2 on minor fold.

Caudal gills slightly inflated, vertical, elongate-oval lamellae, well rounded apically; node absent; outer border of median gill on both sides with finely spinulose setae from base almost up to apex, outer border of lateral gill unarmed; dorsal and ventral margin of all gills with row of short spinulose setae; tracheae distinct, coming off from central stems obliquely.

#### **Selysioneura FÖRSTER.**

Described in this paper (fig. 20-26).

Head and prothorax of large size. Antennae long and very slender, third joint the longest. Labial mask normal, coenagrioid. Anterior portion of mentum strongly produced cone-like, but not deeply cupped, its margin distinctly serrulate but devoid of scale-like spinules, the apposed margin of lateral lobe also distinctly serrulate. Lateral lobe with very long and slender movable hook, the end-hook deeply bifid, its two branches hooked and pointed, the outermost branch the shortest. One short mental seta on each side; lateral setae 0 or (usually) 1.

Femora somewhat expanded and flattened, with interior row of widely spaced microscopical spicules; tibiae in apical half with row of longish pubescent hairs.

Abdominal segments almost bare, unarmed.

Gizzard with 16 generalized folds, the denticulation more or less differentiated alternately (see description).

Caudal gills considerably swollen, of the constricted saccus type, tapering, semi-transparent, unpigmented (see description); distal joint pointed, considerably smaller and shorter than basal joint; tracheal system difficult to follow, rather similar to *Isosticta*.

#### 6. SOME GENERAL REMARKS ON PROTONEURID LARVAE AND IMAGINES

##### Imaginal characters

Like other families, e.g. the Gomphidae, the diversity of forms and the wealth of species developed suggest that within limits the Protoneuridae are a modern and flourishing branch of the Order, though the habits and dwelling-places of its members do not tend to bring it into prominence. As indicated above, apparently various tendencies have been at work resulting in the formation of amplified and reduced groups of genera. In regard to venation, the Old World genera appear to show advancing specialization from west to east, reaching its maximum in the Australian region. On comparing those forms inhabiting the Indo-Australian area, we can distinguish two successful but entirely different groups of genera which, though branches of the same parent stock, are probably not derived from a single ancestral form. These are (1) an extreme western group, culminating in the large-sized and richly veined genera *Cacoreura* KIRBY and *Phylloneura* FRAS., both confined to peninsular India; and (2) an extreme eastern group, culminating in such highly reduced and strongly modified forms like *Selysioneura* FÖRST., *Tanymecosticta* LIEFT., and *Neosticta* TILL., all peculiar to the Australo-Papuan region. <sup>1)</sup> Both groups have followed their own lines of development, but while I am inclined to believe that the Indian cluster is only a luxuriant branch of a more generalized type like *Elattonneura*, the far eastern assemblage has reached a much higher grade of specialization and seems to stand alone. It would appear, then, that the ascent in the scale of development of these groups has gone in opposite directions, the former exemplifying specialization by amplification, the latter by reduction.

The more typical and most widely distributed members of the family, i.e. the Old World genera *Elattonneura* COWLEY, *Prodasineura* COWLEY, and *Notoneura* TILL., which at the same time include the largest number of

<sup>1)</sup> The position of the monotypic Australian *Nososticta* SELYS is at present obscure.

species, are intermediate forms connecting these two main lines of development. It is worth remarking that *Elattonneura* and *Notoneura*, each with a limited number of species, have penetrated into the Ethiopian region.

#### Larval characters

As has been pointed out by TILLYARD, in his valuable synthesis of the morphology of the caudal gills of the larvae of zygopterous dragonflies, the available evidence obtained from his studies would be in favour of the development of the Coenagriid-like form of Vertical Lamellate Gill-type from a two-jointed or constricted Saccoid Type, such as still exists in the Protoneurid genera *Neosticta*, *Nososticta* and — as shown in this paper — also in *Selysioneura*. TILLYARD also opined that the Constricted or two-jointed Lamella of *Isosticta* is clearly a direct development from the Constricted Saccus of *Neosticta*, these two genera being too closely allied to admit of any doubt on that point. The phylogenetic sequence *Neosticta-Selysioneura-Isosticta* being thus admitted by TILLYARD, he then thought there was a break, because the larvae of the Protoneuridae known at that time had reached no higher stage than that shown by *Isosticta*. The subsequent discovery of the larvae of several other Protoneurid genera, however, has brought to light that this is definitely not the case. Within the family it has now become possible to follow the phylogenetic sequence of gill-forms from the Constricted Saccus (*Neosticta*, *Nososticta*, *Selysioneura*) through the Constricted Lamella (*Isosticta*) to the Vertical Nodose (*Naoneura*, *Caconeura*), Subnodate (*Notoneura*) and even Denodate (*Elattonneura*) types. Apart from these, it is of considerable interest to note that even various intermediate stages in the evolution of the gills are present within the family, as is clearly demonstrated by the Triquetroquadrate type occurring in *Disparoneura*, and the curious aberrant Vertical Lamella existing in *Prodasineura*.

In one of his earlier chapters of his paper on this subject, TILLYARD (1917a) stated that, though all newly-hatched zygopterous larvae have filiform, one-jointed and hairy caudal gills, a condition generally admitted to be primitive, the one-jointed condition may not be taken as primitive because in the case of other organs (e.g. antennae, tarsi, etc.) the number of joints increases as the larva grows, and yet it is certain that the last and highest number of joints attained is the most primitive number. He therefore assumed that, in the case of a larva that develops two-jointed gills, such as *Neosticta*, the two-jointed condition is probably primitive. TILLYARD further declared that the Triquetroquadrate gill-type, as seen in its highest development in the Agriidae, is clearly a specialized deve-

development of the older Saccoid type. In the phylogenetic chapter, published a little later the same year, TILLYARD contradicts his previous statement by suspecting "that the original [Zygoptera] possessed only one-jointed gills, and that the two-jointed condition arose in the common ancestor of only those [families] still possessing it, and failing to become of any definite service to the larva, is now again reverting to the one-jointed form, by degradation through the Nodate, Subnodate, and finally Denodate stages" (*loc. cit.*: 621). In the writer's opinion, the first nor the last theory sound very convincing, because (1) the Constricted Saccus, or the most "primitive" type of gill, is found in such genera like *Selysioneura* and *Neosticta*, of which the imagines present a combination of venational and other morphological characters of so high a degree of specialization that they can hardly be equalled in their reduction by any other member of the Zygoptera; (2) the Triquetro-quadrata gill-type, which would be the next in primitiveness, occurs in the remotely allied Old World genus *Disparoneura* (= *Chloroneura olim*), which is admittedly one of the more generalized and archaic members of the group; and (3) the highly developed Subnodate and Denodate gill-types are found in such genera like *Notoneura*, *Elattonneura* and *Prodasineura*, which in the adult stage are by no means so highly specialized as *Isosticta* and *Selysioneura*. Or, when examining other features, we see that the larva of *Disparoneura* shows a highly specialized type of labial mask with a strongly produced middle lobe, and furnished with many mental and lateral setae, thus resembling that of the most advanced members of the Coenagriidae; the extremely reduced eastern *Selysioneura*, on the other hand, possesses a type of larva which has retained primitive features, its labium having an almost cleft middle lobe, carrying only a single pair of mental and lateral setae.

These two genera not only illustrate the two most divergent types of larva existing within the family, but also offer a striking example of the antithesis between larva and adult.