# THE AQUATIC LARVA AND THE PUPA OF CHORISTELLA PHILPOTTI TILLYARD, 1917 (Mecoptera: Nannochoristidae)

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Abstract : Four larval instars are described; the first three are apneustic and aquatic, living in fine mud in a slow-flowing stream. During the fourth stadium, the larva moves out of the water, becoming hemipneustic and undergoing other morphological changes, to enter a prepupal phase. Pupation usually occurs in very damp vegetation or soil. The larva is elongate, campodeiform, with a smooth, cylindrical body and only one pair of hook-bearing abdominal appendages. A pair of exsertile papillae arising above and below the anus contain extensions of two of the Malpighian tubules. A comparison is made with the larvae of other known Mecoptera. The external form of the pupa is similar to that of other Mecoptera.

#### Introduction

Among the Mecoptera, life histories are known, and descriptions of immature stages have been given, for members of the Panorpidae and Bittacidae; comparable data are also available for the Boreidae which are, however, sufficiently distinct to be now regarded as a separate order (Hinton 1958). Information on the Choristidae appears to be confined to brief remarks by Tillyard (1918, 1921, 1926 with illustrations) while nothing is known about immature stages in the Notiothaumidae and the Meropeidae. In those families for which information is published, it is clear that all the larval stages are terrestrial, and that pupation occurs in a cell in the soil. No certain data are reported for the small family Nannochoristidae occurring in Tasmania, South-east Australia, South America and New Zealand, and some statements in the literature require correction or amplification.

Essig (1942, p. 401) said "... it is thought that the immature stages of the Nannochoristidae are aquatic." This statement is unsubstantiated and is probably derived ultimately, but by erroneous inference, from Tillyard (1917, p. 289) who wrote on the Australian *Nannochorista* : "All we can be certain of is that the larval stage must be either aquatic or semi-aquatic, since the insects are confined to the neighborhood of water. The presence of cerci in the female suggests that the eggs are carefully placed, either upon moist ground, or upon the stems of plants fringing the water-courses or the borders of lakes." and (p. 297) "The habit [probable aquatic or semi-aquatic life-history] is still retained by *Nannochorista* ...". Later, Tillyard (1921, p. 529) wrote that the Nannochoristidae "... are aquatic in their larval stages." but there is no evidence that, in fact, even he was entitled to make such an assertion. Indeed in his book (Tillyard 1926,

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p. 331) he stated "The larvae (unknown) are almost certainly aquatic." [Italics mine]. If Tillyard had possessed or seen larvae of Nannochoristidae, he would certainly not have made the latter, inconclusive-and, for him, the final-remark on this subject. A later claim by Evans (1942) to have discovered the probable larva of Nannochorista is here refuted (see Discussion).

It is therefore of considerable interest that the immature stages of *Choristella philpotti* (Nannochoristidae), the only New Zealand Mecopteran, have been found, for the family represents an old but somewhat specialised one with close relations to the Diptera (Imms 1944). It was predicted by Martynova (1961) that "... the anatomy of the larva of such phylogenetic relics ... like ... Nannochoristidae is likely to differ drastically from the structure of Panorpidae ..."; the larva of *Choristella* is here shown to be so strikingly different from known Mecopteran larvae that it is not at first recognisable as belonging even to the order. As well as exhibiting structural differences, the larva contrasts with those of other Mecoptera in being aquatic.

A brief report of the discovery of the immature stages was made (Pilgrim 1962) when specimens were exhibited to a meeting of the New Zealand Entomological Society. Later references to the aquatic nature of the immature stages in the life history are Pilgrim (1969, 1970) and Williams (1968, p. 198). The aquatic habitat has subsequently been confirmed for species of the closely related *Nannochorista* in Australia (Riek 1970a, b; Williams 1968) and in South America (Edmunds, pers. comm.).

Larvae and pupae have been collected in this study over a period of 14 years from a wide distribution in the South Island of New Zealand. However, since the systematics of the genus have not been thoroughly studied and the (slight) possibility of several species remains, all the data in the present paper are derived from collections made in one locality. This is a small stream less than one metre wide with water 25-30 cm deep meandering slowly through river terraces in the Hawdon River valley at an altitude of *ca* 550 m [Map reference : N. Z. M. S. I, S. 59; 218245]. The region is heavilyforested, dominantly with *Nothofagus solandri* var. *cliffortioides*, and much of the bed of the stream is covered with silt, containing large amounts of organic debris, in which larval Chironomidae are abundant. The latter serve as the main food source of *Choristella* larvae which inhabit the silt.

#### Methods

Collections of larvae were made by washing silt from the bottom of pools and quiet stretches of the stream through two Endecott's test sieves, one of coarse mesh (# 5,3350  $\mu$ m) to exclude twigs, stones and other debris, and one of fine mesh (# 25, 600  $\mu$ m) to retain the larvae and associated fauna. The effectiveness of the latter sieve can be judged by the fact that it retained *Choristella* larvae down to 2.6 mm total length (first instar), as well as nymphs and larvae of associated insects, nematodes, molluscs, oligo-chaetes and occasional "Hydra."

Larvae of *Choristella* often made themselves evident by actively wriggling among the residues on the sieve as the water drained from it. These were picked out with fine forceps and transferred to water-filled containers for live examination and growth studies, or to Pampel's fluid for preservation. The whole of the residue in the sieve

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was also preserved in Pampel's fluid for further searching. In this fixative, *Choristella* larvae changed color from translucent dark grey to opaque brown-pink, losing most of their characteristic pattern from the meso- and metathorax and abdomen, and stood out among the debris. Being the only faunal element to do so, they were readily detected. This color change lasted for several days, after which the larvae turned and remained almost white. Larvae fixed in Pampel's fluid usually died in an extended, almost straight altitude with often one or both of the anal papillae extruded and the mandibles widely agape. Larvae so fixed were well suited for subsequent histological examination.

Live material was examined under a dissecting microscope. After preservation, specimens were either cleared and examined whole in clove oil or treated with KOH before preparing slide mounts of whole or part animals. Staining with Chlorazol Black E, Ziehl's Carbol Fuchsin, or Methylene Blue, was used to highlight features of the skeleton. Serial sections of larval abdomens, both transverse and longitudinal, were cut at  $7\mu$ m after softening in Petrunkevitch's solution, and stained in Mallory's triple

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Fig. 1-3. *Choristella philpotti*, photographed from freshly killed specimens: 1-2, early phase, fourth instar; 3, prepupal phase, fourth instar.

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stain. Polarised light microscopy was used to determine the attachments and course of certain muscles. Drawings were made either by tracing from photomicrographs, or by using a Leitz Drawing Attachment, at magnifications corresponding to two to three times the reproduced figures.

## Morphology of the larva

The description of the larva that follows is based on early fourth (final) instar specimens (fig. 1-2) of total body length, after preservation, of 11.4-21.2 mm (mean=17.35 mm, N=142). Elongate, cylindrical, campodeiform, with short but conspicuous antennae and large black eyespots; thoracic segments subequal, each with well developed legs; ten abdominal segments with no appendages except a pair of terminal hooks. General color in life, dark grey, shining; head capsule and its appendages, pronotum, and por-



Fig. 4-5. C. philpotti, early phase, fourth instar: 4, head and prothorax, dorsal view; 5, head, ventral view.

tions of legs brown; remainder of thorax and abdomen with translucent areas forming a regular pattern dorsally, less conspicuous ventrally. Head rounded oval (fig. 4-5), longer than broad, widest near the posterior angles; height about half overall length; prognathous. Dorsal surface smooth, shining, strongly convex, well sclerotised, epicranial suture well defined ; ventral surface almost flat, extensively membranous. No ocelli. Eves merely large black pigmented areas, roughly oval with irregular margins, the pigment dissolving completely in KOH leaving no trace of corneal lenses or any other sign of eye structure at the surface. Posterior margin of head drawn back into two marked postoccipital lobes covered by loose folds of cervical region. Head color : all sclerotised parts light brown, mandibles darker especially at tips; diffuse darker brown areas near center and posterior regions of head dorsally reaching almost black on postoccipital processes, posterior margin of head capsule and gular sclerites. (Newly-moulted specimens almost completely colorless, except tips of mandibles. Pigmentation develops from posterior region of head forwards during the stadium.) Tentorium strongly pigmented, showing darkly through head capsule. Clypeus large, trapezoidal; clypeolabral suture distinct. Labrum semicircular with pronounced median emargination, a projecting tooth-like seta at each antero-lateral corner together with a number of small marginal denticulations; beneath, several tooth-like setae (also some present on clypeus) and a row of large inwardly-curved setae near each posterolateral corner. Labrum, clypeus and dorsum of head bear small circular structures (sensory?) ca  $10\mu$ m, and all surfaces bear a few setae, some tufted. Antennae arise immediately mesad of mandibular ginglymus and project antero-laterally to a little beyond the mandibles. Scape arises from a fleshy mound which does not bear any visible sclerite and thus is interpreted as not being a segment; scape short and stout, pedicel long and cylindrical. third (terminal) segment cylindrical, slightly swollen towards the bluntly rounded tip which bears a few spinous setae. Ratio of scape, pedicel and terminal segment lengths -1:21, diameters -3:2:1. Distinct oval structures (sensory?), ca  $10\times6\mu$ m, arranged one near tip of terminal segment, two distally on pedicel.

Mandibles prominent, stout, curving evenly to a sharp apical tooth, inside which are three roughly triangular major teeth (fig. 6); mandibles normally symmetrical, although very occasional specimens have an additional tooth on one side; attached about midway along inner border of each mandible is a movable palmate lobe, the 'lacinia mobilis' (see below).

Maxillae (fig. 7) well developed; palp three-segmented, resembling a slightly smaller version of the antenna; first segment a short ring, the second slightly narrower, longer than wide, the third cylindrical, half as wide as the first two and twice as long as wide, with ovate setae at the tip.

Galea a short fleshy conical lobe bearing numerous long setae especially dorsally, and a dense tuft at the tip including some stout serrated setae.

Lacinia weakly projecting, with many long fine setae and a group of very stout setae forming a comb anteriorly; the medial margin beset with rows of blunt, almost pentagonal teeth.

Labium (fig. 8) a simple, rounded, undivided lobe, slightly projecting from ventral surface of the head; its only appendages are short two-segmented labial palps of which the first segment is very small and has a sclerotised ring, incomplete medially; second



Fig. 6-8. C. philpotti: 6, outlines of left mandibles, ventral view, drawn at slightly different orientations from slide-mounted material; A, first instar; B, second instar; C, second instar-pharate third instar; D, third instar; E, early phase, fourth instar; F, prepupal phase, fourth instar. 7, early phase, fourth instar; left maxilla, dorsal view. 8, early phase, fourth instar; labium and hypopharynx, ventral view.

segment  $3 \times$  as long as broad and ends bluntly with a few short stout setae; two tiny stout setae close to the anterior margin, and a pair of long tufted setae behind the palps; no sign of glossae or paraglossae. Hypopharynx a transversely triangular fleshy lobe lying in front of the labium.

The lacinia mobilis (so referred to here without prejudice to any considerations of homology with structures given this name in other groups) bears five sharp, roughly equal teeth and towards its base a soft swelling bearing numerous long setae (fig. 6); among the setae is a sharp denticulate lobe which does not appear to be separately articulated. The lacinia mobilis as a whole is articulated through extensive soft cuticle to the ventro-medial surface of the mandible, though there is an area on each side of the joint which is well sclerotised and which forms a firmer bearing surface and probably also restricts the movement of the lacinia to some extent. No muscles have been observed attached to the lacinia mobilis, either by dissection, by staining, or by polarised light microscopy, so that its operation must be a passive one, the structure moving indirectly according to the movements and disposition of the mandible itself. Like the mandibles, the laciniae are symmetrical, though an additional sixth tooth on one side was occasionally observed. The teeth of the mandible and of the lacinia mobilis are very sharp early in each stadium (especially in pale newly-moulted specimens) but later become blunted and even broken. This is particularly evident in the case of the teeth of the mandibles proper (fig. 6c).

As a whole, the mouth region, including the mouth parts and labrum, is beset with sharp teeth, stout spines and tufts of recurved setae. With its prognathous aspect it is admirably suited for capturing, impaling and ingesting struggling prey. Neck with two small cervical sclerites ventro-laterally on each side; the anterior a slender Y-shaped structure, the posterior oval, vertically elongated and lying close to the prothoracic coxa. Thoracic segments shorter than wide, prothorax smallest, meso- and metathorax about equal in size. Prothorax bears a strongly sclerotised pronotal shield, pigmented brown except for a median strip and some lighter pattern (fig. 4); hind margins especially dark. (As is the case with the head capsule, all this pigmentation develops from the posterior aspect after each moult, but it precedes that of the head.) Meso- and metathorax are grey and resemble the abdominal segments but with a different pattern of translucent areas. A few fine setae are present on all segments. The spiracular opening on the prothorax lies dorso-laterally in an unpigmented notch of the pronotal shield at the posterior 1/6 (fig. 4); it is circular or slightly oval (fig. 9a),  $35-40 \mu m$  in diameter, and consists of a well-sclerotised central scar with 12-16 openings and a narrow peritreme. On the metathorax is a minute ( $7\mu m$ ) stigmatic scar of a non-functional spiracle (fig. 9b), about mid-laterally close to the front margin of the segment. All legs



Fig. 9-10. *C. philpotti*, early phase, fourth instar: 9, spiracular openings, right side; A, on prothorax; B, on metathorax (stigmatic scar); C, on second abdominal segment. 10, tarsus and end of tibia, right prothoracic leg, anterior view.

similar in form and size; about as long as the meso- or metathorax. They arise ventrolaterally from the anterior fourth of their segments and project forwards and outwards. Each leg consists of five segments; coxa, borne on a slightly raised portion of the body wall, is short and broad and bears a few long setae. Femur is stout and conical and is the largest segment of the leg; it bears a few long setae, five stout lanceolate setae around the middle of the segment and a patch of short setae mid-ventrally. Tibia is long and slender, with a long apodeme extending well into the femur; at the distal end ventrally is a group of short setae, and dorso-laterally a group of large curved setae on the posterior face. Tarsus (fig. 10) consists of two segments, the distal slightly the longer. The proximal segment bears only a few short setae, the distal a large stout, almost semi-circular claw which bears four stout, curved articulating setae as long as the claw itself. One of these arises from the convex surface near the base, two are symmetrically placed on the sides and the fourth is on the posterior face. A fold of integument sometimes visible between coxa and femur may represent a trochanter, but there is no sclerotisation to make this segment clearly evident. The dorsal surfaces of coxa and tarsus are sclerotised, as is much of tibia including the apodeme; these sclerotisations and the claw complex are brown.

Abdomen cylindrical, with segments 8-10 tapering so that segment 10 is ca 1/3 diam-

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eter of segments 1-6; segment 1 is about as long as pro- + mesothorax, segments 2-7 each as long as meso- + metathorax, segments 8-10 successively slightly shorter. All segments smooth and shining, the surface being interrupted only by a shallow groove (marking the position of extensive apodemal invaginations) at *ca* the anterior 1/6, especially marked in segments 2-7. No surface ornamentation, projections or appendages of any kind apart from the terminal hooks on segment 10, and a few fine setae on segments 1-8, rather more numerous on segment 9 and more conspicuous on segment 10. Spiracular openings on segments 1-7, situated mid-laterally at the anterior 1/3; they are similar to those on the prothorax but smaller (*ca* 27  $\mu$ m in diameter) and have 9-14 openings (fig. 9c). In live specimens immersed in water, air-filled tracheae could be seen passing inwards from these openings.

Segment 10 (fig. 11) is conical and ends in two fleshy lobes directed postero-laterally, each bearing a terminal hook. The groove between the lobes leads to a deep cloaca at the inner end of which is the anus. Dorsally and ventrally near the inner end of the cloaca are two pouches, from each of which protrudes an anal papilla. The medial surface of the fleshy lobes and the lining of the cloaca for a short distance inwards bear numerous short spine-like setae oriented at a low angle to the surface cuticle and directed posteriorly.

The terminal hooks arise by a broad base from the fleshy lobes on segment 10. The





Fig. 11-12. C. philpotti, early phase, fourth instar. 11, end of abdomen, left lateral view, showing anal papillae (fully extended) and left terminal hook. 12, transverse, slightly oblique, sections of tenth abdominal segment to show disposition of partly retracted anal papillae: A, section through cloaca; dorsal papilla contains trachea and Malpighian tubule; ventral papilla contains trachea only at this level: B, more anterior section in which trachea and Malpighian tubule of dorsal papilla are free within the hemocoel and flanked by muscles operating the papilla; ventral papilla lies within its cloacal pouch.

ap-anal papilla, c-cloaca, cp-cloacal pouch, h-hemocoel, m-muscle, mt-Malpighian tubule, r-rectum, t-trachea.

hooks taper to a sharp tip curved through almost 90° and project obliquely backwards and downwards. Near the base is a pair of setae. The hooks are sclerotised and pale brown, darker at the tip. They are operated by two sets of muscles, dorsal and ventral, which run forward to the front of segment 10.

The anal papillae (fig. 11) are blunt, tapering, slightly curved, finger-like lobes, unpigmented and, in life, transparent; when fully extended they are a little more than half the length of segment 10 in a last instar larva, and about 9/10 its length in early instars. In living larvae, they show no movements beyond retraction and exsertion. Retraction is rapid and is accomplished by sets of dorsally and ventrally arranged muscles running from their inner ends to insert on apodemes at the front of segment 9. Retraction may be partial, or complete when the papillae are entirely enclosed within the cloaca, their anterior ends reaching to the anterior 1/5 of segment 10. Retraction is *not* by means of intussusception-there are no intrinsic muscles in the papillae and no folding or telescoping has been observed. The cloaca itself is provided with retractor muscles and their action may assist the withdrawal of the papillae. Exsertion is slowthere are no muscles directly involved in this process which is presumably carried out by hydrostatic pressure of the hemolymph, the lumen of the papilla being open to the hemocoel.

Retraction and exsertion of the two papillae are independently operable and, in life, either or both may be visible or hidden. Similarly, after preservation, both, either or neither may be exserted.

In life, the papillae can be seen to be lined with a single layer of large flattened hypodermal cells. The lumen contains hemolymph in which blood cells can be seen circulating, and a hollow, cellular core which extends about half way along the papilla where it ends bluntly with a few fibrous strands. This core has been traced both by dissection and by serial sectioning and is shown to be the end of a Malpighian tubule (fig. 12). From the gut in segment 6 there arise six symmetrically arranged Malpighian tubules, all histologically similar and with an outside diameter of 35-40  $\mu$ m, four of them looping around in the hemocoel closely applied to the gut and ending in segment 8. The remaining two are closely associated with the former, but continue through segment 10 where they straighten out and become arranged above and below the gut, then enter the cloacal pouches and terminate axially in the anal papillae. At entry they narrow to 20 µm in diameter in a papilla of 90 µm outside diameter. This arrangement, presumed when first observed to be due to accidental damage from compression of the larva in handling, is a completely constant feature in the anatomy of the papillae, the tubules remaining in position on retraction and exsertion of the latter. No separate muscles are attached to the tubules, but they appear to be loosely anchored inside the papillae by the terminal fibrous strands. No tracheal gills were observed in the anal papillae, which contain only fine branches of tracheal trunks arising near the junction between segments 9 and 10.

The cuticle over the abdomen differentiates, after using Mallory's triple stain, into an outer thin unstained layer which remains pale brown, a thicker red layer and an even thicker blue layer. Following the terminology of Taylor & Richards (1965) these are exo-, meso- and endocuticle respectively; immediately beneath the latter is the hypodermis. The exocuticle lines the cloaca at least as far inside as the regions bearing the spiny setae, but the mesocuticle does not extend beyond the outer rim of the cloaca; a thin extension of the endocuticle, however, lines the whole of the cloaca and covers the anal papillae in their entirety.

The larva is very active, wriggling violently when disturbed or as the water drains from a mud sample in the collecting sieve. The whole body is thrown into marked sinuous movements which, assisted by the legs, enable it to progress "eel-like" through the substratum. The terminal hooks may act as temporary anchors in the soft substratum or as attachments to plant debris or gravel therein; they are the only projections of the otherwise smooth abdomen which could be so used. When suspended in water, the larva sinks but the sinuations of the body allow it some progress in still water. It was never observed to attempt to rise in the water.

## Early instars

Analyses of total body length and of head capsule breadth (Table I) strongly suggest the existence of four instars. Of the two measurements, total body length is the less reliable since it is subject to variable amounts of contraction in preserved specimens. Head capsule breadth does not suffer from this (within the limits of measurement) and can be used with greater confidence. It is significant that the latter shows more clearly the separation into four groups without overlaps in their ranges. The suggestion of four instars is reinforced by observations of moulting in several specimens from one size group to the next, and by the examination of a number of pharate larvae.

Instar	Number of specimens	Total body length(mm)	Head capsule breadth(mm)
I	8	3.8 ( 2.6-4.5)	0. 22 (0. 22-0. 23)
II	44	6.0 ( 3.5-8.2)	0.31 (0.29-0.34)
III	95	10.0 ( 6.8-12.9)	0.45 (0.40-0.51)
IV early	163	17.4 (11.4-21.2)	0. 69 (0. 60-0. 77)
IV prepupa	14	16. 6 (15. 1-18. 7)	0. 71 (0. 63-0. 91)

Table I. Summary of size distribution of body length and head capsule breadth of larvae

Most of the features of the early fourth instar described above are present in the first three instars, the main differences being in size and proportion, and in coloration which is similar but paler overall. As well as these, in the first three instars *all* the spiracles are non-functional and are represented on the body surface by extremely small (*ca* 5  $\mu$ m) inconspicuous stigmatic scars only.

### Prepupa

This term will be applied to the larva in the later phase of the fourth stadium when it shows marked differences in morphology and behavior. Use of the term follows a definition in de la Torre-Bueno (1937 p. 230 "... an active but non-feeding stage in the larva of the Holometabola." At the inception of this phase the larva is *not* a pharate pupa, but the latter develops later. Prepupae (= Vorpuppen) have been referred to in the life history of *Panorpa* spp. (Byers 1963; Gassner 1963; Rottmar 1966; Yie 1951), *Harpobittacus* (Currie 1932) and *Bittacus* (Setty 1940), though the distinction is there made entirely on behavioral grounds, with only trifling changes in the morphology of the larva. Setty (p. 324) states that "... the [fully formed fourth instar] larva of *B. punctiger* soon casts its skin to form a prepupa.", thus implying that a further, separate, instar is involved, but this is not in accord with the situation in the other genera.

In gross appearance, the prepupa differs from the early fourth instar in that the color of the unsclerotised parts of the body are opaque cream, due to underlying fatty material, against which the spiracular openings now stand out conspicuously. Sclerotisation of the head and prothorax remain as before, but dorsally the mesothorax develops a pair of broad longitudinal areas (fig. 3), the metathorax a broad U-shaped area, and segments 1-9 of the abdomen a single median longitudinal stripe, broad anteriorly but becoming progressively narrower on the posterior segments. All these areas are diffuse edged and dark brown; they remain on the larval (prepupal) exuviae following ecdysis. The head preserves all its earlier features, details of the appendages being unaltered except for the mandibles which lose the lacinia mobilis. This is shed and the region of attachment is shown by a dark brown, almost black, scar on the now blunt-toothed mandible (fig. 6f). The thoracic segments are now opaque and, especially the meso- and metathoracic, become very swollen as the rudiments of wing- and leg-buds develop. This makes the larval legs very fat at the base and gives them a stubby appearance; nevertheless, they are still capable of providing locomotion. The rest of the abdomen is unchanged externally, and retains its terminal hooks and anal papillae.

The prepupa is no longer found in the stream mud but in very damp vegetation (moss, etc.), or in the underlying soil, or occasionally beneath the bark of rotting logs which are partly submerged in the stream. In all cases they are definitely above the water level, but usually within 10-20 cm of it, in situations of very high humidity. Prepupae are normally C-shaped when discovered and wriggle actively when disturbed. Those lying in the soil or beneath bark produce a cell by excavating the soil or underlying sodden wood, but those lying in moss do not appear to make a special cell. Of 18 prepupae examined in this study, only one was found in the stream mud. It had shed one of its laciniae and presumably was about to leave the water.

In contrast to that of the larva, the general appearance of the pupa (fig. 13-14) is much more recognisably like that of Mecopteran pupae already described (*Panorpa*, Byers 1963; Miyaké 1912; Yie 1951; *Bittacus*, Brauer 1871; Setty 1940; *Harpobittacus*, Currie 1932).

The pupa is strongly curved into a C and measures ca 5 mm. The terminal segments of the abdomen have never been observed upturned in either sex, as is commonly the case in other Mecopteran pupae, especially males. It should be pointed out, however, that in the adult male of *C. philpotti* and other Nannochoristidae these segments are not upturned either. The color is pale fawn early in the pupal stadium but develops gradually to a dark brown; the color is, however, entirely due to the enclosed pharate



Fig. 13-14. C. philpotti, pupae: 13,  $\sigma$ ; 14,  $\varphi$  end of abdomen.

adult, since the pupal exuviae are colorless when shed. The antennae are extended over the eye to about mid-wing length; the mouth parts, with large sharp mandibles, lie between the wing bases. The wings are free and extend to about the third abdominal segment. The legs, which are long and end in a pair of minute recurved hooks, are doubled up and partly held between the wings but extend further along the ventral side of the abdomen. Large setae, mostly arising from small hillocks on the body surface, occur sparsely on the head and all segments of the thorax and abdomen; a few also occur on

the appendages, at the distal ends of all tibiae and of the fore and mid femora, on the pedicel of the antenna and on the fore wing base. These setae probably function by keeping the pupa from making extensive body contact with the surroundings; if this is so, it is probably significant that the hind leg, which is the most concealed between the wings and abdomen, lacks the femoral seta and its tibial seta is quite short and sometimes lacking. Spiracular openings occur on the prothorax and on segments 1–7 of the abdomen, in positions approximately corresponding to those of the larva; a stigmatic scar on the metathorax lies just anterior to the hind wing base. Sexual dimorphism is very obvious in the terminal segment of the abdomen from an early stage; indeed, it can readily be detected even in pharate pupae in the prepupal phase.

The pupa is active when disturbed, especially so towards the end of the pupal period when activity is clearly ascribable to the pharate adult; spontaneous, vigorous, wriggling occurs more and more frequently, finally leading to rupture of the pupal exuviae and to emergence. The split in the exuviae is along the mid-line from the posterior end of the metathorax to the head, whence it follwos one arm of Y-shaped epicranial suture to the base of the corresponding antenna and thence to the labrum.

# Discussion

The present statement that the immature stages herein described are those of *Choristella philpotti* requires some justification in view of the claim by Evans (1942) to have discovered the "probable" larva of *Nannochorista*, the only other genus in the Nannochoristidae and one in which the adult is extremely similar to *Choristella*. Evans' larvae are grossly different from those described here; their "probable" generic origin relies on equivocal, circumstantial evidence<sup>2</sup>, and his description leaves no doubt that his two

<sup>2. &</sup>quot;In some spirit material ... collected in moss on Mt Wellington ... It is probable that these are the larvae of a *Nannochorista* and not of *A*. [*pteropanorpa*] *tasmanica*, because the moss was from an environment frequented by *N*. *dipteroides*." (Evans 1942, p. 31).

specimens are the larvae of another, more orthodox, Mecopteran. Apteropanorpa tasmanica also occurs in the vicinity of Mt Wellington (Carpenter 1941) from which his specimens were collected, and it seems likely that the larvae are, in fact, of this genus. This view is supported by Riek (1970a). Evans' description is not inconsistent with those of already described Panorpid larvae (Brauer 1863; Byers 1963; Felt 1896; Miyaké 1912; Yie 1951), though Byers (1965) has suggested that Apteropanorpa is perhaps not suitably included in the Panorpidae s. str. The only other Mecopteran known from Tasmania (Riek 1954) is Harpobittacus australis australis, and its larva is known (Currie 1932; described as H. tillyardi, but actually H. a. australis according to Riek 1954), and is quite different from those described by Evans.

The present study is based on examination of more than 300 larvae and of 40 pupae collected during 1957-70, from within a few hundred metres in one small stream. Proof of correct association of the immature stages, and of their identity as *Choristella philpotti*, was obtained from the following transformations which occurred in the laboratory: larva-larva-1; prepupa-pupa-  $6 \ Q \ Q$ ; pupa-adult - 7  $\ D \ Q$ , 3  $\ Q \ Q$ ; prepupa-pupa-adult - 2  $\ Q \ Q$ ; these adults proved identical with those collected in the field, with authenticated museum specimens, and with the original description.<sup>3</sup> Additional confirmation was afforded by observations of pharate specimens, viz.: larva-pharate larva - 11; prepupa-pharate adult - 20  $\ D \ Q \ Q$ .

In order to discuss the immature stages of *Choristella philpotti* in relation to those of other Mecoptera, it is necessary to review the position of the Nannochoristidae within the order. The Boreidae, in which life-histories are known and of which the larvae are distinctive (Brauer 1855, 1857, 1863) have been removed to a separate sub-order Neomecoptera (Crampton 1930); this was raised to ordinal rank by Hinton (1958), though the validity of this move has been questioned by Martynova (1961) and by Hepburn (1970). The rare Meropeidae and Notiothaumidae, in neither of which immature stages are known, together form the sub-order Protomecoptera (Tillyard 1917) and the remaining extant families constitute the sub-order Eumecoptera (Tillyard 1917); these are the long-established Bittacidae and Panorpidae and the more recently established Panorpodidae and Apteropanorpidae (Byers 1965).

The family Nannochoristidae was erected by Tillyard (1917), while the Choristidae was raised to family status by him (Tillyard 1926). Both these families have been commonly included, especially by northern hemisphere writers, within the Panorpidae, the two being regarded as "... much less distinct from the Panorpidae than are the other families." (Imms 1957, p. 509). However, separation of these two groups as families in their own right is defensible on many grounds, and is maintained by Riek (1954, 1970a) and Martynova (1959), while Imms himself (1944) showed that the adult characters of the Nannochoristidae are sufficiently remarkable to regard them as distinct. Comparison of *C. philpotti* larvae and pupae can most profitably be made, therefore, with members

<sup>3.</sup> One difference noticed from Tillyard's description concerns his inclusion (1917, Text-fig. 3) of a cross vein in the hind wing between  $R_1$  and  $R_{2+3}$ , continuing from that between C and  $R_1$ ; this is not present in any specimen in the writer's material, nor is it present in the type specimens. Tillyard's illustration is therefore in error in this respect. Some other variations occur sporadically among the more posterior cross veins, but these are not systematic or correlated in any way and are here regarded as trivial, normal, variants.

of other Eumecoptera.

Larvae of Panorpidae, Bittacidae and Choristidae are eruciform; they possess welldefined eyes with corneal lenses, abdominal prolegs on segments  $1-8^4$ , a sucker at the end of the abdomen, and segmentally-arranged annulated or clubbed setae or complexly branched processes dorsally and laterally on the abdomen and, in some cases, on the thorax.

The larva of C. *philpotti* differs from the foregoing in the following structural features: it is campodeiform with prognathous mouth parts including a lacinia mobilis on the mandible; eyes are represented merely by internal pigment spots without any surface specialisation; the abdomen bears only one pair of appendages (terminal hooks, on segment 10) and has a pair of papillae exsertable from cloacal invaginations. Both thorax and abdomen are devoid of processes and of any but simple setae. The respiratory system is apneustic in the first three instars. In its habits, the larva of C. *philpotti* differs from the terrestrial larvae of other families in being fully aquatic until part way through the fourth stadium. These differences in the larval stages alone might be considered sufficient to justify the recognition of Nannochoristidae as a distinct family.

As was stated earlier, the term *lacinia mobilis* is used here "... without prejudice to any considerations of homology with structures given this name in other groups." With this in mind, it is nevertheless interesting to find that Hansen (1930), in his survey of the insect mandible, recorded a lacinia mobilis in very few of the Endopterygota and, specifically, his Neuroptera which included the Panorpatae are quoted as being "... always without lacinia mobilis." (p. 179). At least it is certain that a movable toothed lobe on the mandible is, so far, unique among Mecoptera.

Spiracles.

The arrangement of the external openings of the tracheal system develops as follows (using the terminology of Keilin 1944, where S = functional, and N = non-functional, spiracle) :

Instars I–III	$N_{I,III}N_{1-7}$
Instar IV	$S_I N_{III} S_{1-7}$
Pupa	$S_I N_{III} S_{1-7}$
Adult	$S_{I,III}S_{1-7}$

No trace was observed of even a non-functional spiracle on the eighth segment of the abdomen in any stadium, so that the system is hypopneustic at best.

In other Mecopteran genera, as far as can be ascertained from the literature, all the spiracles present are open (functional) throughout all instars. Indeed, several writers use spiracle dimensions, and/or number of spiracular openings, to substantiate instar separation (Gassner 1963; Miyaké 1912; Yie 1951). One thoracic and eight abdominal spiracles are reported in *Panorpa* (Byers 1963; Felt 1896), *Bittacus* (Setty 1939, 1940, 1941), *Harpobittacus* (Currie 1932) and *Chorista* (Tillyard 1926, Fig. V5). No mention is made in these accounts of a non-functional spiracle on the metathorax but, since

<sup>4.</sup> Segments 1-9 in *Bittacus stigmaterus* Say, according to Setty (1931, p. 477 and fig. 6), but this is evidently an error since no reference is made to the anomaly in later work (Setty 1940).

this is probably extremely small, it may have been overlooked by the authors mentioned. In those genera outside the Nannochoristidae, therefore, the arrangement is peripneustic, or  $S_1N?_{III}S_{1-8}$ , and is constant throughout larval life. These larvae are terrestrial and air-breathing in all stadia. In *Choristella*, the first three instars are apneustic and fully aquatic, their respiratory needs evidently being satisfied by extraction of oxygen from the water. The fourth instar is hemipneustic with eight pairs of functional spiracles, and it is to be recalled that the later, prepupal, phase of this instar is terrestrial, the respiratory arrangement presaging the pupal and adult conditions and their requirements. Further development of another functional spiracle ( $S_{III}$ ) on the metathorax in the adult is in accord with the situation in most other holometabolous insects (Hinton 1947, p. 465).

The great majority of Mecopteran larvae are terrestrial and the aquatic habit of *Choristella* (and other Nannochoristidae) must be regarded as a secondary development, the apneustic instars being an adaptation to this mode of life. The pattern of development of functional spiracles in *Choristella* conforms with generalisations (1)-(4) formulated by Hinton (1947, p. 459) in relation to aquatic holometabolous larvae. There is also complete accord with Hinton's statements (1947, p. 462) "... the instars which have the greatest number of spiracles must be better adapted to an aerial life than those which have fewer functional spiracles. A difference in the number of functional spiracles between two larval instars of the same species implies a difference in the number of functional spiracles nearly always occurs in the final instar, is a plain indication that the final instar is not as strictly aquatic as the early instars, and the retention of a greater number of functional spiracles in this instar is an adaptation to passing at least some of its life out of water."

Anal papillae.

The anal papillae are curious structures and are also unique to the Nannochoristidae. Riek (1970a Fig. 32.8C) refers to them as "eversible anal gills", but there is no evidence to support the view that they are in any way especially significant in respiration. The absence of all but minute tracheal branches argues against this activity, and a quite different function is suggested here. The papillae are very thin walled and it is postulated that they serve as sites for the exchange (uptake?) of solutes with the environment. They resemble, morphologically, the anal papillae of other aquatic insect larvae (e.g. Nematocera), where they have been shown to function in this manner (Wigglesworth 1950). If an inflow of water should occur through their surface, the presence of axially disposed Malpighian tubules within them would suggest that a flushing of the tubules could occur in relation to this flow. The Malpighian tubules themselves are similar to those described elsewhere; there are six as in *Panorpa* [and in *Boreus*] (Potter 1938) and their histological structure is like that of *Panorpa* (Grell 1938).

With regard to the homology of the anal papillae, it is possible that they can be equated with the "rectal processes" of  $Panorpa^5$  (Potter 1938, p. 121); these "... can be evaginated through the anus," and constitute the four-lobed anal sucker of *Panorpa* (Brauer

<sup>5.</sup> According to Potter, Shiperovitsh (1925) suggested that the processes have a respiratory function.

1863; Byers 1963; Gassner 1963; Miyaké 1912). In *Bittacus* (Setty 1940) the anal sucker appears to be less conspicuously lobed, and in *Harpobittacus* it is tri-lobed (Currie 1932). In *Chorista*, the anal sucker is fleshy and indistinctly four-lobed (personal observation on preserved material). In all these genera, the anal sucker has been observed to be used in locomotion, which is terrestrial on soil or among vegetation. *Choristella*, living in very soft mud, would not be able to utilise such a sucker. The smooth, elongated, slender body is well suited for movement through the habitat, while the terminal hooks may serve to attach the animal temporarily to a firmer substrate or even to anchor it within the mud. In these respects they would be much more effective than the anal sucker of the terrestrial forms.

Acknowledgements: I am indebted to Mr J. I. Townsend for checking the wing venation of the type specimens of Choristella philpotti. Mr E. F. Riek kindly provided four larvae of Chorista australis luteola for examination, and a translation of Martynova's paper (1959). Both Professor H. E. Hinton and Mr Riek gave helpful discussion and encouragement during this study. I am grateful to numerous colleagues who assisted in field collecting of the material, and to Dr M. J. Winterbourn for a critical reading of the draft manuscript.

## REFERENCES

- Brauer, F. 1855. Beiträge zur Kenntniss des inneren Baues und der Verwandlung der Neuropteren. Verhandl. zool.-bot. Ver. Wien 5: 701-26.
  - 1857. Beiträge zur Kenntniss der Verwandlung der Neuropteren. Verhandl. zool.-bot. Ver. Wien 7: 69-70.
  - 1863. Beiträge zur Kenntniss der Panorpiden-Larven. Verhandl. k.-k. zool.-bot. Ges. Wien 13: 307-24.
  - 1871. Beiträge zur Kenntniss der Lebensweise und Verwandlung der Neuropteren (Micromus variegatus Fabr., Panorpa communis L., Bittacus italicus Klg. und Bittacus hagenii Brau.). Verhandl. k.-k. zool.-bot. Ges. Wien 21: 107-16.
- Byers, G. W. 1963. The life history of *Panorpa nuptialis* (Mecoptera : Panorpidae). Ann. Ent. Soc. Amer. 56 (2) : 142-9.
- 1965. Families and genera of Mecoptera. Proc. XII Intern. Congr. Ent., Sect. 1, Systematics. p. 123.
- Carpenter, F. M. 1941. A new genus of Mecoptera from Tasmania. Pap. Proc. Roy. Soc. Tasmania (1940): 51-4.
- Crampton, G. C. 1930. The wings of the remarkable archaic mecopteron Notiothauma reedi Mc-Lachlan with remarks on their protoblattoid affinities. Psyche 37 (1): 83-103.
- Currie, G. A. 1932. Some notes on the biology and morphology of the immature stages of Harpobittacus tillyardi (Order Mecoptera). Proc. Linn. Soc. N. S. Wales 57 (3-4): 116-22.
- de la Torre-Bueno, J. R. 1937. A Glossary of Entomology. Brooklyn: Entomological Society. (Third Printing, and Supplement A; 1962).
- Essig, E. O. 1942. College entomology. MacMillan, New York.
- Evans, J. W. 1942. A mecopterous larva from Tasmania and notes on the morphology of the insect head. *Pap. Proc. Roy. Soc. Tasmania* (1941): 31-5.
- Felt, E. P. 1896. The scorpion-flies. Tenth Rep. N. Y. State Entomol. for 1894: 463-80.
- Gassner, G. 1963. Notes on the biology and immature stages of *Panorpa nuptialis* Gerstaecker (Mecoptera : Panorpidae). *Texas J. Sci.* 15 (2) : 142-54.
- Grell, K. G. 1938. Der Darmtraktus von Panorpa communis L. und seine Anhänge bei Larve

und Imago. Zool. Jahrb., Anat. 64(1): 1-86.

- Hansen, H. J. 1930. Studies on Arthropoda III. On the comparative morphology of the appendages in the Arthropoda. B. Crustacea (Supplement), Insecta, Myriapoda, and Arachnida. Gyldendalske Boghandel, Copenhagen. 1-376, Plates I-XVI.
- Hepburn, H. R. 1970. The skeleto-muscular system of Mecoptera : the thorax. Univ. Kansas Sci. Bull. 48 (21) : 801-44.
- Hinton, H. E. 1947. On the reduction of functional spiracles in the aquatic larvae of the Holometabola, with notes on the moulting process of spiracles. Trans. Roy. Ent. Soc. Lond. 98: 449-73.

1958. The phylogeny of the Panorpoid orders. Ann. Rev. Ent. 3: 181-206.

- Imms, A. D. 1944. On the constitution of the maxillae and labium in Mecoptera and Diptera. *Quart. J. micros. Sci.* 85 (1): 73-96.
  - 1957. A general textbook of entomology. 9th edition revised by O. W. Richards & R. G. Davies. Methuen, London.
- Keilin, D. 1944. Respiratory systems and respiratory adaptations in larvae and pupae of Diptera. *Parasitol.* 36 (1-2): 1-66.

Martynova, O. 1959. Filogeneticheskie vzaimootnosheniya nasekomykh mekopteroidnogo kompleksa. *Trudy Inst. Morfol. Zhiv. Severtsova.* 27: 221-30.

1961. Palaeoentomology. Ann. Rev. Ent. 6: 285-94.

- Miyaké, T. 1912. The life-history of *Panorpa klugi* M'Lachlan. J. Coll. Agric. Tokyo 4(2): 117-39.
- **Pilgrim**, R. L. C. 1962. The late larva and pupa of *Choristella philpotti* Tillyard, (Mecoptera). *Proc. Ent. Soc. New Zealand*. (In *New Zealand Ent.* 3(1): 2 [Title only])
  - 1969. Mecoptera (Scorpion-files). In: The Natural History of Canterbury. A. H. & A. W. Reed, Wellington. p. 480.

1970. Knowledge of New Zealand Mecoptera, Mallophaga, Anoplura and Siphonaptera. New Zealand Ent. 4 (3): 72-9.

- Potter, E. 1938. The internal anatomy of the larvae of *Panorpa* and *Boreus* (Mecoptera). *Proc. Roy. Ent. Soc. Lond. A.* 13 (7-9): 117-30.
- Riek, E. F. 1954. The Australian Mecoptera or scorpion-flies. Austr. J. Zool. 2(1): 143-68.
- 1970a. Mecoptera. Chapter 32 in The Insects of Australia. Melbourne University Press, Melbourne.
- 1970b. Endemism in the Australian insect fauna. Proc. Roy. Ent. Soc. Lond. C 35 (5): 17 [Abstract].
- Rottmar, B. 1966. Über Züchtung, Diapause und Postembryonale Entwicklung von Panorpa communis L. Zool. Jahrb., Anat. 83: 497-570.
- Setty, L. R. 1931. The biology of Bittacus stigmaterus Say (Mecoptera, Bittacusidae). Ann. Ent. Soc. Amer. 24 (3): 467-84.
  - 1939. The life history of *Bittacus strigosus* with a description of the larva. J. Kansas Ent. Soc. 12 (4): 126-7.
  - 1940. Biology and morphology of some North American Bittacidae (Order Mecoptera). Amer. Midl. Nat. 23 (2): 257-353.

1941. Description of the larva of *Bittacus apicalis* and a key to Bittacid larvae (Mecoptera). J. Kansas Ent. Soc. 14 (2): 64-5.

- Shiperovitsh, V. J. 1925. Biologie und Lebenszyklus von Panorpa communis L. Rev. Russe Ent. 79: 27-37 (Not seen; cited by Potter, 1938).
- Taylor, R. L. & A. G. Richards. 1965. Integumentary changes during moulting of arthropods with special reference to the subcuticle and ecdysial membrane. J. Morph. 116 (1): 1-22.
- Tillyard, R. J. 1917. Studies in Australian *Mecoptera*. No.i. The new family Nannochoristidae, with descriptions of a new genus and four new species: and an appendix descriptive of a new genus and species from New Zealand. *Proc. Linn. Soc. N. S. Wales* 42 (2): 284-301.

- 1918. Studies in Australian Mecoptera. No. ii. The wing-venation of Chorista australis Klug. Proc. Linn. Soc. N. S. Wales 43 (2): 395-408.
- 1921. On some interesting archaic insects (with exhibitions). Proc. Hawaii. Ent. Soc. 4(3): 525-30.

1926. The insects of Australia and New Zealand. Angus & Robertson, Sydney.

Wigglesworth, V. B. 1950. The principles of insect physiology. 4th edition. Methuen, London. Williams, W. D. 1968. Australian freshwater life. Sun Books, Melbourne.

Yie, Shi-Tao. 1951. The biology of Formosan Panorpidae and morphology of eleven species of their immature stages. *Mem. Coll. Agric. Nat. Taiwan Univ.* 2 (4): 1-111.