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A Taxonomic Revision of New Zealand Blepharoceridae and the
Origin and Evolution of the Australasian Blepharoceridae
(Diptera: Nematocera)*

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Abstract

LITERATURE pertaining to New Zealand Blepharoceridae is reviewed. Materials, methods and terminology are described. Keys are provided for the Australasian genera and subgenera of Blepharoceridae, and for the adults and larval instars of New Zealand *Neocurupira* and *Peritheates*.

New blepharocerids from the south of the South Island, New Zealand, are described as *Neocurupira rotalapisculus* n.sp. and Forms A, B and C, and are placed with *Neocurupira hudsoni* in a *hudsoni*-complex. Because these new blepharocerids possess dichoptic males the subgenus *Paracurupira* has been synonymised with *Neocurupira*. As *Neocurupira tonnoiri* and *Neocurupira chiltoni* are distinct from the other New Zealand *Neocurupira* and are similar to each other, they are placed in a *tonnoiri*-complex.

Nothohoraia n.gen. is erected for new blepharocerid material from Westland, New Zealand. This genus shows morphological affinities to *Neocurupira*, *Apistomyia* and *Horaia*, and possesses highly specialised larvae. *Peritheates intermedius* is placed in synonymy with *P. turriter*. Larval teratology is discussed.

The phylogeny of the Indo-Australasian Apistomyiinae is discussed and it is concluded that apistomyids probably arose from a *Neocurupira*-like ancestor. The zoogeography of the Australasian Blepharoceridae is considered and it is believed that *Edwardsina* arrived in Australia during the Cretaceous, either from the south or more probably the north. Later in the Cretaceous blepharocerids entered New Zealand from the north. During the Miocene *Apistomyia* and *Neocurupira* (*Austrocurupira*) entered Australia. The distribution of New Zealand blepharocerids is interpreted in the light of past geological and climatic changes and the possibility of refugia is discussed.

INTRODUCTION

ALTHOUGH blepharocerid adults were originally described by Westwood in 1842 and were associated with larvae and pupae by Müller (1879 and 1881), it is surprising that they were not discovered in New Zealand until 1900, for all stages are particularly numerous and widespread in the South Island.

Chilton (1906) reported the discovery of blepharocerid larvae in 1900 by G. R. Marriner at Lake Coleridge, Canterbury, and his own discovery in 1903 of

* This work is based on a portion of the author's Ph.D. Thesis.

blepharocerid larvae at Akaroa, Banks Peninsula. Because the Banks Peninsula larvae showed similarities to the South American genus *Curupira*, Chilton designated them as "? *Curupira*". From material collected at Arthur's Pass by G. V. Hudon, Lamb (1912) erected two new genera, *Neocurupira* and *Peritheates*, designating *N. hudsoni* and *P. turriifer* respectively as type species. Bezzi (1914) provided descriptions of three forms of larva collected by Chilton at Akaroa.

Campbell (1921) made a detailed study of the Banks Peninsula blepharocerid which he named *Curupira chiltoni*. He also attempted to identify the three forms of larva supplied to Bezzi by Chilton, but in the process produced a considerable amount of confusion. Later (1923) Campbell showed that the three forms of larva described by Bezzi were larval instars of *Curupira chiltoni*. In addition Campbell (1921) described and named new blepharocerid adults and larvae from Oha-kune, North Island, as *Apistomyia harrisi* and reported the occurrence of blepharocerids at Dunedin and Queenstown in the South Island.

Tillyard (1922a), in a revision of the New Zealand Blepharoceridae, described a new species, *Peritheates intermedius* and transferred *Apistomyia harrisi* Campbell to *Peritheates*. He also transferred *Curupira chiltoni* to a new genus *Paracurupira* on the basis of the dichoptic males of *C. chiltoni* and the holoptic males of *Neocurupira hudsoni*. Edwards (1929), in discussing the general classification of Blepharoceridae, relegated *Paracurupira* to subgeneric rank. Kitakami (1950), Alexander (1958) and Dumbleton (1963a) also consider *Paracurupira* to be subgeneric.

Tonnoir (1923a, 1923b and 1930b) discussed the rearing of blepharocerid larvae, described the pupation of *Peritheates intermedius* Tillyard, and mentioned a new form of *Neocurupira* larva but did not provide a description. Dumbleton (1963a) described two new species, *Neocurupira (Paracurupira) tonnoiri* (which was the form mentioned by Tonnoir, 1923b) and *Neocurupira (P.) campbelli*. As well as erecting a new subgenus, *Austrocurupira*, for the Australian species *N. nicholsoni* Tillyard, he presented keys to the known adults and the 4th instar larvae of New Zealand blepharocerids and discussed the affinities and some biology of New Zealand species of blepharocerid.

In this paper full descriptions are given for new and previously undescribed material with only the main diagnostic characters given for material described elsewhere.

The possible origins and evolution of New Zealand and Australian Blepharoceridae are discussed.

MATERIAL AND METHODS

Material

Descriptions are based on specimens preserved in Andre's Fluid or, more rarely, in 70 per cent alcohol. The storage of all stages of blepharocerid material in fluid is recommended, as it prevents the shrinkage of taxonomically important genitalia and head structures that is often met with on pinned specimens.

The amount of material available for measurement varied greatly with species. However, large numbers of certain instars of *Neocurupira campbelli*, *N. chiltoni*, *N. hudsoni* and *Peritheates turriifer* were available for measurement from an ecological study on blepharocerids (Craig, 1966).

In the locality records the following abbreviations indicate the institution in which New Zealand blepharocerid material is housed.

AMS—Australian Museum, Sydney, Australia.

AM—Auckland Museum, Auckland, New Zealand.

BM—British Museum (Natural History), England.

CM—Canterbury Museum, Christchurch, New Zealand.

CMB—Cambridge Museum, England.

DM—Dominion Museum, Wellington, New Zealand.

EDL—Entomology Division, Department of Scientific and Industrial Research, Lincoln, New Zealand.

EDN—Entomology Division, Department of Scientific and Industrial Research, Nelson, New Zealand.

UA—University of Auckland, Department of Zoology, Auckland, New Zealand.

UC—University of Canterbury, Zoology Department, Christchurch, New Zealand.

(Misc.) following locations indicates that the sample is housed in the Miscellaneous Freshwater Collection, Zoology Department, University of Canterbury.

Numbers in parentheses following locations, e.g., (23), indicate the number of the sample in the Freshwater Collection, Zoology Department, University of Canterbury. Numbers in italics, e.g., 23, indicate samples housed in the private collection of Dr V. M. Stout, Zoology Department, University of Canterbury.

The following initials are used to indicate major collectors:

D.A.C.—D. A. Craig.

L.J.D.—L. J. Dumbleton.

V.M.S.—V. M. Stout.

The letters L, P and A indicate a positive identification to species of larvae, pupae and adults in the sample. A query, e.g., L?, indicates a doubtful identification.

Locations cited are arranged in approximate order of North to South and East to West. Map references following locations refer to Department of Lands and Survey 1 inch to 1 mile Topographical Maps (N.Z.M.S.I.).

Species criteria

Decisions on the categorical rank of New Zealand blepharocerids are in most cases based on clear morphological differences. Evidence of reproductive isolation of species is available from the microsympatric distributions of the following species: *Neocurupira hudsoni* Lamb, *N. tonnoiri* Dumbleton, *N. campbelli* Dumbleton, *Nothohoraia micrognathia* n.gen. et sp., *Peritheates turriifer* Lamb, *P. harrisi* (Campbell). *Neocurupira chiltoni* (Campbell) though isolated from other New Zealand blepharocerids can on good morphological grounds be considered a species.

In the south of the South Island there occur a number of blepharocerids that differ in eye structure from *N. hudsoni* but in larval, pupal and genital characteristics are morphologically indistinct from those of *Neocurupira hudsoni*. Furthermore there is evidence of interbreeding between one of these "southern" forms and *N. hudsoni* where the distributions overlap. According to Mayr (1963) any interbreeding would indicate that *N. hudsoni* and the "southern" form were conspecific. However, Bigelow (1965) maintains that interbreeding does not necessarily mean conspecificity, for if the gene flow is restricted no merging of the populations will take place.

Because reproductive isolation of *N. hudsoni* and the "southern" form is not clear, the "southern" form though described, has, according to custom (Tonnoir, 1930b; and Stuckenberg, 1958) only been assigned an arbitrary letter and placed in the *hudsoni*-complex.

Terminology

Adult

Head. Previously the relationship between the estimated areas of the upper and lower eyes was used as a diagnostic character. As this ratio is not sufficiently accurate to demonstrate variation in the eye structure of new material

described here, a more accurate ratio describing the relationship of the upper eye to the lower eye has been devised. This ratio, called the *eye ratio*, is calculated using measurements taken from the eyes as indicated in Figure 2.

Male eye ratios vary from 1:0.5 (holoptic *Neocurupira hudsoni*) to 1:2.1 (dichoptic *Neocurupira tonnoiri*). The main disadvantage of the eye ratio is that it often necessitates the removal of the insect's head to allow a full-face view, as in Figure 2, to be obtained.

The head depth to head width ratio is also used in descriptions of new material and has been calculated for existing species (Fig. 2).

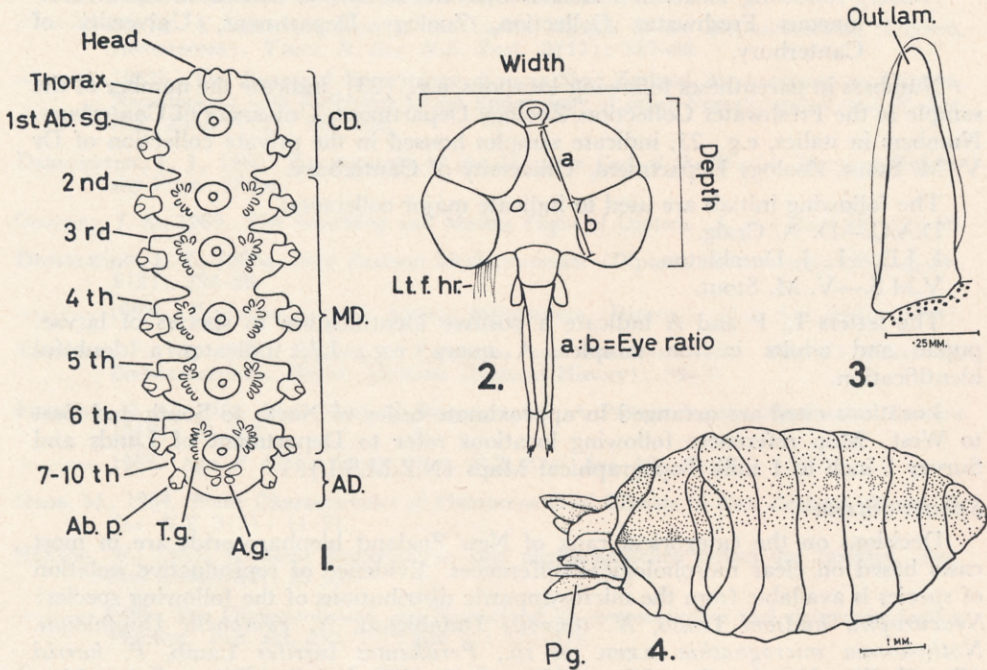


FIG. 1.—Diagram of fourth instar blepharocerid larva showing the relationship of divisions to body segments. FIG. 2.—Diagram of frontal view of male adult blepharocerid head, illustrating ratios used in descriptions. FIG. 3.—Anterior lamellae of Form C pupal gill. FIG. 4.—Dorsal view of *Neocurupira* pupa.

Lettering for all figs: A.g., Anal gills; Ab.p., Abdominal prolegs; AD, Anal division; Ant., Antenna; Bst., Basistyle; Cer., Cercus; CD., Cephalic division; C.s., Cephalic sclerites; Dst., Dististyle; Eg.b., Egg burster; G., Galea; Lb.P., Labial Palp.; Lt.f.hr., Lateral facial hairs; Lr., Labrum; MD, Median divisions; Mg.8th.t., Margin of 8th tergite; Mx.p., Maxillary palp.; Out.lam., Outer lamella; Ovt., Oviscapt; P.g., Pupal gills; Scl., Scales; Set., Setae; Sp., Spines; Tg., Tracheal gills; 1st.Ab.seg., First abdominal segment; 2nd–10th., Second to tenth abdominal segments; 9th.t., ninth tergite.

Genitalia. Although Snodgrass (1957) showed that the male genital forceps of nematocerous insects were probably the parameres (in the strict sense), to prevent confusion the terms *dististyle* and *basistyle* are still used here (Kitakami, 1950; Stuckenberg, 1958; and Alexander, 1963) in preference to clasper and basicoxite (Dumbleton, 1963a). The term *cercus* (Stuckenberg, 1958) is used for the bilobed extremity of the 9th tergite, rather than superior process (Dumbleton, 1963a) (Fig. 22).

Because Stuckenberg (1958) apparently provided the first adequate account of the female genitalia of the Blepharoceridae and his terminology was used by Alex-

ander (1963), his terms are used here whenever applicable, i.e., *oviscapt* rather than subgenital plate (Dumbleton, 1963a).

Pupa

The pupae of New Zealand blepharocerids, with the exception of *Nothohoraia micragnathia* (Figs. 56 and 57), are in appearance similar to Figure 4 and do not show any great generic or specific differences. Dumbleton (1963a), however, used the ratio of the basal width to the length of the outer gill lamellae to assist in identification (Fig. 3). This practice is continued here, but many pupae remain unidentified as the pupal gills are often too damaged by natural causes to be measured.

Larva

The arbitrary terms used here to designate the body segments of blepharocerid larvae (Fig. 1) are the same as those used by Tonnoir (1923c), Stuckenberg (1958) and Dumbleton (1963a). The *cephalic division* includes the cephalic region, the three thoracic segments and the first abdominal segment and bears ventrally one sucker. The *median divisions*, five in number, represent single abdominal segments and bear suckers ventrally. The fifth median division (true sixth abdominal segment) is often almost completely fused to the anal division except for a lateral constriction. The *anal division* consists of four fused abdominal segments. Some of the confusion that existed over the number of segments fused into the cephalic and anal divisions is discussed by Craig (1967b).

The embryonic development of blepharocerid larval appendages shows that the lateral abdominal projections of the larva are probably homologous with the embryonic thoracic prolegs (Craig, 1967b). Therefore the term *abdominal proleg* is used for such structures (Fig. 1), rather than the terms claw or fulcrum (Kitakami, 1950), lateral process (Campbell, 1923; Dumbleton, 1963a), ambulatory process (Tonnoir, 1930b) or pseudopod (Johannsen, 1934; Stuckenberg, 1958; and Alexander, 1963).

The term *seta*, defined by Stuckenberg (1958) as a "more or less flexible, slender, pale, hair-like structure", is used here to describe small, clear, lanceolate structures on the dorsal armature and on the ventral surface of the posterior margin of the larva (Fig. 37). The term *spine* as defined by Stuckenberg (1958) and as used by Dumbleton (1963a) for a short, dark, rigid, hair-like structure on the larva is also used here (Fig. 61). The term *scale* is used for the clear, fan-shaped structures that make up the marginal armature of *Neocurupira* larvae (Fig. 37), and *hair* is used for long, thin, flexible structures on the adult head, larval posterior body margins and prolegs.

Because growth, which takes place during each larval instar, results in considerable changes in the shape of the cephalic, median and anal divisions (e.g., first instar Figs. 46 and 47), descriptions are normally made from late larvae. The number of antennal articles, the shape of the abdominal prolegs, number of tracheal gills, hair length and sucker size are all useful as diagnostic characters, for as Kitakami (1950) pointed out they remain constant throughout any one instar.

The sucker approximately doubles in size with each ecdysis and in New Zealand blepharocerids can be used to identify instars. The differences in size of suckers during any one instar can be used to some extent to identify the species of a larva.

As fixation of the larva causes the suckers to become slightly oval in shape, the *sucker width* is taken as the greatest measurement across the sucker (normally at right angles to the long axis of the larva).

Colour

Colour descriptions of larvae and adults are based on the Munsell Book of Color, with the specimen under liquid and illuminated obliquely.

Measurements

Measurements of whole specimens were made to the nearest 0.05mm. Smaller material, such as the genitalia was mounted on slides and measured to the nearest 0.01mm.

Illustrations

All drawings were made with the help of a squared ocular.

CLASSIFICATION

At present the family Blepharoceridae is divided into four subfamilies (Kitakami, 1950; Alexander, 1958 and 1963); Edwardsiniinae Edwards, 1929, Blepharocerinae Bezzi, 1912, Paltostominae Bezzi, 1912 and Apistomyiinae Bezzie, 1912. This division, which is used here, is based primarily on the wing venation and head structure of adults.

Stuckenburg (1958) believes that the family should be primarily divided into Edwardsiniinae and Blepharocerinae, and that because the present Blepharocerinae, Paltostominae and Apistomyiinae are not of equal rank either one with another, or with the Edwardsiniinae, they should be reduced to the status of tribes within the Blepharocerinae.

On the basis of wing venation (M_3 and m-cu both absent) and the mouthparts (labial palpi long and slender) all known New Zealand Blepharoceridae, with the exception of *Neocurupira campbelli* and *Nothohoraia micrognathia*, undoubtedly belong to the subfamily Apistomyiinae.

Neocurupira campbelli and *Nothohoraia micrognathia* both possess short labial palpi but the pupal sheaths of these palpi are long. Dumbleton (1963a) considered that in *N. campbelli* this indicated a relatively recent reduction of the labial palpi. The same is probably true for *N. micrognathia*. For this reason both these blepharocerids are considered to belong to the Apistomyiinae and not the Paltostominae.

New genera and species of Blepharoceridae are usually based on adult characteristics (Alexander, 1958) with little importance assigned to the larval or pupal instars. Tonnoir (1923c) believed that larval characteristics of blepharocerids were unreliable taxonomically, but Edwards (1929) considered larval and adult characteristics to be of the same importance in taxonomy. Van Emden (1957) reviewed the general principles involved in the use of larval characteristics in taxonomy and came to a conclusion similar to that of Edwards. Using the principles outlined by Van Emden and those of Hennig (1953), Stuckenburg (1958) analysed the relationship of *Paulianina* to *Edwardsina*.

In this paper equal taxonomic importance is given to larvae, pupae and adults, and diagnostic characters for all three stages are provided in the key to the Australasian Genera and Subgenera of Blepharoceridae.

KEYS

To minimise confusion the following keys are similar to those of Dumbleton (1963a).

KEY TO THE AUSTRALASIAN GENERA AND SUBGENERA OF BLEPHAROCERIDAE

1. Adult maxillary palpus 4-5 segmented; eye not divided, dichoptic in both sexes; wing with veins R_s and M three-branched. Pupal gills complex and with more than 4 lamellae. Larval head capsule projecting from cephalothorax; prolegs not distinct; body divisions separated by intercalary regions; tracheal gills on intercalary regions.

Edwardsina Alexander.

— Adult maxillary palpus 1-2 segmented; eye divided, holoptic or dichoptic in males, dichoptic in females; wing with vein Rs forked or simple, median vein with only M1 and M4 present. Pupal gills of 4 lamellae. Larval head capsule sunken into cephalothorax; prolegs well developed; no intercalary regions; tracheal gills near suckers.	2
2. Vein Rs forked. Larvae with or without marginal armature of scales, dorsal armature of clear spines or tubercles.	3
— Vein Rs simple. Larvae with marginal armature of spines, dorsal armature of small blunt spines.	4
3. Adult labial palpi subequal to or longer than head depth; antenna of 11, 12 or 14 articles, females either macropterous or brachypterous. Pupae with dorsum highly convex; gills positioned anterolaterally, lamellae long and complete. Larvae with marginal armature of scales, dorsal armature of spines; cephalic sclerites not produced anterolaterally; antennae prominent; dorsum convex; prolegs projecting beyond lateral margins.	<i>Neocurupira</i> Lamb 5
— Adult labial palpi shorter than head depth; antenna of 14 articles in both sexes. Pupae flattened; gills positioned anteromedially, lamellae short and notched. Larvae with no marginal armature, dorsal armature of clear tubercles; cephalic sclerites projecting prominently anterolaterally; antennae small and recessed; body flattened, compressed anteroposteriorly; prolegs obscured by lateral margin.	<i>Nothohoraia micrognathia</i> n.gen. et sp.
4. Vein Rs nearly straight, ending just above wing apex; male dichoptic. Pupal gills positioned anterolaterally, lamellae long. Larval anal division well developed, posterior edge angular; prolegs bearing long hairs.	<i>Peritheates</i> Lamb
— Vein Rs curving upwards, ending close to R1; male holoptic. Pupal gills positioned anteromedially, lamellae small. Larval anal division reduced, posterior edge rounded; prolegs bearing short spines only.	<i>Apistomyia</i> Bigot
5. Adult ocellar turret prominent; antenna of 11-14 articles; maxillary palpus short. Larval marginal armature of scales; anal division well developed; 7th proleg present. (New Zealand.)	subgenus <i>Neocurupira</i> Lamb
— Adult ocellar turret small; antenna of 12 articles; maxillary palpus elongate. Larval marginal armature of spines; anal division reduced; 7th abdominal proleg reduced to long hair. (Australia.)	subgenus <i>Austrocurupira</i> Dumbleton

KEY TO ADULTS OF NEW ZEALAND *Neocurupira*

1. Labial palpi short in both sexes, subequal to head depth; antenna of 11-12 articles, distal segments wider than long; microtrichia dense, female wings brachypterous or macropterous; internal process of oviscapt conical; male dichoptic, eye ratio 1:2.0 (Figs. 27-30).	<i>N. campbelli</i> Dumbleton
— Labial palpi long in both sexes, 1.5-2.0 times as long as head depth; antenna of 14-15 articles, moniliform; wings clear, female always macropterous; internal process of oviscapt conical or truncate; male holotypic or dichoptic.	2

2. Antenna of 14 articles; male holoptic or dichoptic, eye ratios from 1:1.4–1:0.5; dististyles widest at midlength; posterior margin of cercus notched basally; internal process of oviscapt truncate, apex concave.	<i>hudsoni</i> -complex	3
— Antenna of 15 articles; male dichoptic, eye ratio 1:2.1 or 1:1.0; dististyles not widest at midlength; posterior margin of cercus deeply or broadly concave; internal process of oviscapt conical.	<i>tonnoiri</i> -complex	6
3. Male holoptic, eye ratio 1:0.5.	4
— Male dichoptic, eye ratio 1:1.4–1:0.9.	5
4. Mouthparts twice as long as head depth (Fig. 9).	<i>N. hudsoni</i> Lamb	
— Mouthparts less than twice as long as head depth.	Form A	
5. Male eye ratio 1:0.9; vein Rs arising from wing base (Figs. 6, 17 and 18).	<i>N. rotalapisculus</i> nov.sp.	
— Male eye ratio not as above; vein Rs arising from vein R1 (Figs. 7, 10, 19 and 20).	Forms B and C	
6. Male eye ratio 1:1.0; anal angle of wing approximately 120°, vein 1A not reaching wing margin; internal process of oviscapt conical, constricted apically, oviscapt lobes bearing fine pale spines subapically (Figs. 44, 45 and 50).	<i>N. chiltoni</i> (Campbell)	
— Male eye ratio 1:2.1; anal angle of wing approximately 110°, vein 1A reaching wing margin; internal process of oviscapt conical, oviscapt lobes bearing short dark spines subapically (Figs. 40, 48 and 49).	<i>N. tonnoiri</i> Dumbleton	

KEY TO THE ADULTS OF NEW ZEALAND *Peritheates*

1. Male ocellar turret rounded; wing length approximately 8mm; cercus wide with shallow median concavity; female with interior process of oviscapt truncate, slightly concave apically, oviscapt lobes bearing 8–10 clear spines subapically (Figs. 65a and 66).	<i>P. harrisi</i> (Campbell)
— Male ocellar turret constricted or diverging basally; wing length approximately 6mm; cercus with slight lateral flattening, median concavity rounded; female with interior process of oviscapt round apically, oviscapt lobes bearing 5–13 black spines subapically and at approximately midlength. (Figs. 65b and c, and 67.)	<i>P. turriifer</i> Lamb

KEY TO LARVAL INSTARS OF NEW ZEALAND BLEPHAROCERIDAE

The method utilised by Campbell (1921 and 1923) and Dumbleton (1963a) to distinguish the larval instars of *N. chiltoni* can be used with suitable modifications for all known New Zealand blepharocerids:

1. Tracheal gill filaments absent; antenna of one article; egg-burster on cephalic sclerites; sucker width 0.057–0.067mm (Figs. 46 and 47).	First Instar
— Tracheal gill filaments present; antenna of 2 articles; no egg-burster. 2
2. Two tracheal gill filaments per body division; sucker width 0.14–0.24mm (Figs. 43 and 63).	Second Instar
— More than 2 tracheal gill filaments per body division. 3
3. Six or 8 tracheal gill filaments per body division; sucker width 0.20–0.44mm (Figs. 42 and 62).	Third Instar
— Ten or 14 tracheal gill filaments per body division; sucker width 0.36–0.83mm (Figs. 41, 58 and 61).	Fourth Instar

KEY TO FOURTH INSTAR LARVAE OF NEW ZEALAND BLEPHAROCERIDAE

<p>1. Body flattened dorsoventrally; cephalic region produced anterolaterally; lateral margins thick; no marginal armature; ventral posterior margin of anal division heavily sclerotised; prolegs not extending beyond lateral margins; 10 tracheal gills per body division; 7th proleg very inconspicuous (Figs. 58 and 59).</p>	<p><i>Nothohoraia micrognathia</i></p>	<p>..... 2</p>
<p>— Body convex; cephalic region not produced anterolaterally; lateral margins acute or rounded; marginal armature of scales or spines; prolegs extending beyond lateral margins; 14 tracheal gills per body division; 7th proleg obvious.</p>		
<p>2. Marginal armature of scales, dorsal armature with or without spines, if present very large; prolegs with pale hairs only; posterior margin of anal division broadly rounded, bearing 6-30 hairs, row of short setae ventral to margin (Figs. 14, 31, 37 and 41).</p>	<p><i>Neocurupira</i></p>	<p>..... 3</p>
<p>— Marginal armature of irregular dark pointed spines, dorsal armature of small blunt spines; prolegs with 1-3 short dark spines dorsally among paler hairs; posterior margin of anal division rounded medially, constricted and angulate laterally, bearing 1-6 hairs medially, without row of short setae ventral to margin (Figs. 61 and 68).</p>	<p><i>Peritheates</i></p>	<p>..... 6</p>
<p>3. Prolegs pointed apically, angulate laterally, constricted basally; anal division separated laterally from 5th median division by acute angulate constriction, posterior margin thin.</p>	<p><i>tonnoiri</i>-complex</p>	<p>..... 4</p>
<p>— Prolegs rounded apically, not angulate laterally, not constricted basally, with slight medial constriction; anal division separated laterally from 5th median division by non-angulate constriction, posterior margin thicker.</p>		<p>..... 5</p>
<p>4. Dorsal armature of regularly arranged large black spines; 7th abdominal proleg pointed apically, 2-4 dark hairs dorsally; sucker width 0.60-0.65mm (Fig. 41).</p>	<p><i>N. chiltoni</i></p>	
<p>— Dorsal armature without large spines; 7th abdominal proleg rounded apically, without dark hairs dorsally; sucker width 0.54-0.64mm (Fig. 37).</p>	<p><i>N. tonnoiri</i></p>	
<p>5. Posterior margin of anal division bearing approximately 30 hairs; anal division separated laterally from 5th median division by shallow constriction; colour varying from uniform light brown to highly patterned (Plate 1a); sucker width 0.60-0.83mm.</p>	<p><i>hudsoni</i>-complex</p>	
<p>— Posterior margin of anal division bearing 6-8 black hairs; anal division separated laterally from 5th median division by very shallow constriction; colour uniformly dusky yellowish brown; sucker width 0.48-0.59mm (Fig. 31).</p>	<p><i>N. campbelli</i></p>	
<p>6. Posterior margin of anal division crenulate, bearing 6-8 hairs medially, hair bases inset; prolegs rounded apically, slightly constricted medially; 7th proleg longer than basal width; sucker width 0.47-0.54mm (Fig. 68).</p>	<p><i>Peritheates harrisi</i></p>	
<p>— Posterior margin of anal division bearing 2 hairs at junctions of rounded median and angulate lateral edges, hair bases not inset; prolegs bluntly pointed apically, constricted medially; 7th proleg shorter than basal width; sucker width 0.45-0.54mm (Fig. 61).</p>	<p><i>P. turrifer</i></p>	

KEY TO THIRD INSTAR LARVAE OF NEW ZEALAND BLEPHAROCERIDAE

1. Body flattened dorsoventrally; cephalic region produced anterolaterally; lateral margins thick; no marginal armature; ventral posterior margin of anal division heavily sclerotised; prolegs not extending beyond lateral margins; 6 tracheal gills per body division; 7th proleg inconspicuous.	<i>Nothohoraia micrognathia</i>	
— Body convex; cephalic region not produced anterolaterally; lateral margins acute or rounded; marginal armature of scales or spines; prolegs extending beyond lateral margin; 8 tracheal gills per body division; 7th proleg obvious.	2
2. Marginal armature of scales (Fig. 37).	<i>Neocurupira</i>	3
— Marginal armature of dark pointed spines (Fig. 61).	<i>Peritheates</i>	6
3. Prolegs constricted medially, angulate laterally; 7th proleg longer than basal width; posterior margin of anal division bearing 18–23 strong dark hairs.	<i>tonnoiri-complex</i>	4
— Prolegs only slightly constricted medially, not angulate laterally; 7th proleg shorter than basal width; posterior margin of anal division bearing 6–8 hairs.	5
4. Seventh proleg inset basally, roundly truncate apically; anal division separated laterally from 5th median division by deep angulate constriction; sucker width 0.26–0.32mm (Fig. 38).	<i>N. tonnoiri</i>	
— Seventh proleg not inset basally, cone shaped; anal division separated laterally from 5th median division by shallow angulate constriction; sucker width 0.30–0.36mm (Fig. 42).	<i>N. chiltoni</i>	
5. Prolegs rounded apically; anterior filaments of anal gills larger than posterior filaments and curving around 6th sucker; anal division separated laterally from 5th median division by deep subangulate constriction; sucker width 0.35–0.44mm (Fig. 15).	<i>hudsoni-complex</i>	
— Prolegs slightly pointed apically; anterior and posterior anal gill filaments subequal in size; anal division separated laterally from 5th median division by very shallow constriction; sucker width 0.30–0.36mm (Fig. 32).	<i>N. campbelli</i>	
6. Posterior margin of anal division broadly rounded medially, slightly concave laterally, bearing 8–12 hairs; 7th proleg rounded apically; anterior and posterior anal gill filaments subequal in size; sucker width 0.35mm (Fig. 69).	<i>Peritheates harrisi</i>	
— Posterior margin of anal division only slightly rounded medially, slightly concave laterally, bearing 2–4 hairs; 7th proleg conical, pointed apically; anterior anal gill filaments larger than posterior filaments; sucker width 0.26–0.33mm (Fig. 62).	<i>P. turrifer.</i>	

KEY TO SECOND INSTAR LARVAE OF NEW ZEALAND BLEPHAROCERIDAE

1. Body slightly convex; lateral margins sharply defined and crenulate; ventral posterior margin of anal division heavily sclerotised; prolegs not extending beyond lateral margins.	<i>Nothohoraia micrognathia</i>	
— Body convex; lateral margins rounded; prolegs extending beyond lateral margins.	2
2. Posterior margin of anal division bearing 8–22 hairs; prolegs robust; marginal armature if present of scales.	<i>Neocurupira</i>	3

<p>— Posterior margin of anal division bearing 2 hairs; prolegs thin, constricted medially; marginal armature of dark, sharp spines.</p> <p>3. Sixth proleg slightly constricted medially, curving posteriorly; posterior margin of anal division bearing 16–22 hairs; marginal armature prominent.</p> <p>— Sixth proleg not constricted medially, not curved, cone shaped; posterior margin of anal division bearing 7–14 hairs; marginal armature small or absent.</p> <p>4. Sixth proleg twice as long as basal width; 7th proleg hemispherical; posterior margin of anal division flattened laterally, very slightly pointed medially; anal division separated laterally from 5th median division by deep angulate constriction, close to base of 6th proleg; sucker width 0.18–0.19mm (Fig. 43).</p> <p>— Sixth proleg $\frac{1}{3}$ as long as basal width; 7th proleg conical; posterior margin of anal division broadly rounded; anal division separated laterally from 5th median division by subangulate constriction not close to base of 6th proleg; sucker width 0.14–0.18mm (Fig. 39).</p> <p>5. Posterior margin of anal division rounded apically, slightly concave laterally, bearing 12–14 long hairs; 6th proleg as long as basal width, rounded apically; 7th proleg conical, not prominent; posterior anal gill filaments $\frac{1}{3}$–$\frac{1}{2}$ as long as anterior filaments; anal division separated laterally from 5th median division by subangulate constriction; sucker width 0.20–0.24mm (Fig. 16).</p> <p>— Posterior margin of anal division broadly rounded, continuing anteriorly beyond 6th proleg, bearing 7–9 short black hairs; 6th proleg as long as basal width, conical, sharply rounded apically; 7th proleg conical, prominent; posterior anal gill filaments $\frac{2}{3}$ as long as anterior filaments; sucker width 0.17–0.18mm (Fig. 33).</p> <p>6. Marginal armature of short dark spines only on anal division; 7th proleg conical, bearing a single clear hair; prolegs 2.5 times as long as basal width, constricted laterally; sucker width 0.15–0.18mm (Fig. 63).</p> <p>— Second instar material of <i>P. harrisi</i> not available.</p>	<p><i>Peritheates</i> 6</p> <p><i>tonnoiri</i>-complex 4</p> <p>..... 5</p> <p><i>N. chiltoni</i></p> <p><i>N. tonnoiri</i></p> <p><i>hudsoni</i>-complex</p> <p><i>N. campbelli</i></p> <p><i>Peritheates turifer</i></p>
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THE NEW ZEALAND TAXA OF THE FAMILY BLEPHAROCERIDAE

Neocurupira Lamb, 1912

Neocurupira Lamb, 1912. (New Zealand.)

TYPE SPECIES: *Neocurupira hudsoni* Lamb, 1912.

Neocurupira (*Neocurupira*), Edwards, 1929; Alexander, 1958; Dumbleton, 1963a.

Paracurupira Tillyard, 1922. (As a genus.)

TYPE SPECIES: *Curupira chiltoni* Campbell, 1921.

Neocurupira (*Paracurupira*) Edwards, 1929. (As subgenus.) Alexander, 1958; Dumbleton, 1963a. New Synonymy.

Diagnosis

Previously *Neocurupira* was separated from the other Apistomyiinae on the basis of its forked vein Rs. However, because of the discovery of *Nothohoraia micrognathia* n.gen. et sp. it is now necessary to include pupal and larval characters in the generic diagnosis. The distinction now, between *Neocurupira* and the other genera of the Apistomyiinae, is made clear in the Key to the Australasian Genera and Subgenera of Blepharoceridae.

Description

Adult: Eye divided, male dichoptic or holoptic; antenna of 11–15 articles; labial palpus long and slender or if short, pupal sheath long, maxillary palpus short, 1–2 segments, distal segment usually truncate and wider distally; vein Rs forked; male dististyles widest at midlength or subapically, median concavity of cercus variable. *Pupa*: Gills positioned anterolaterally, lamellae at least three times as long as wide; dorsum highly arched. *Larvae*: Anal division well developed; marginal armature of scales, dorsal armature of large black spines or clear setae; prolegs bearing hairs only.

Remarks

Dumbleton (1963a) recognised three subgenera within *Neocurupira*; *Austrocurupira* Dumbleton, 1963a; *Neocurupira* Lamb, 1912, and *Paracurupira* Tillyard, 1922a. The erection of *Austrocurupira* was deemed necessary by Dumbleton because of the diversity within *Neocurupira* and because he retained the two other subgenera. Although *Paracurupira* is here synonymised with *Neocurupira*, *Austrocurupira* is still retained as a subgenus, though for reasons somewhat different from those of Dumbleton (p. 146).

With the discovery, in the south of the South Island, of new blepharocerids possessing dichoptic males, the status of the subgenus *Paracurupira* needed re-examination. Previously the new "southern" blepharocerids would have been placed in the subgenus *Paracurupira* on the basis of the dichoptic males. However, these "southern" blepharocerids are very closely related to *Neocurupira* (*N.*) *hudsoni*, showing similarities in larval, pupal, genital and wing morphology, a relationship which is much closer than that of a subgenus. Variation in male eye structure within the "southern" blepharocerids and the remainder of New Zealand *Neocurupira* is comparable to the intrageneric eye variation in the South African *Elporia* (Stuckenberg, 1955). Because dichoptic males of "southern" blepharocerids and holoptic males of *Neocurupira hudsoni* show a very close relationship, the separation of *Neocurupira* into subgenera *Neocurupira* and *Paracurupira* on the basis of holoptic males in *Neocurupira* and dichoptic males in *Paracurupira* is considered unwarranted. *Paracurupira* is now synonymised with *Neocurupira*.

THE *hudsoni*-COMPLEX

Diagnosis

Antenna of 14 articles; posterior margin of male cercus notched basally; internal process of oviscapt truncate, concave apically; posterior margin of anal division of fourth instar larva bearing 30 hairs; sucker width 0.60–0.83mm.

Remarks

The known distribution of *Neocurupira hudsoni*, based on collections of holoptic males, extends from Marlborough Sounds in the north of the South Island, southwards along the Southern Alps to a boundary which extends east from Lake Wanaka through the Nevis River Gorge and across the Umbrella Mountain Range to near Roxburgh (Fig. 26A). Throughout this area of distribution there is no significant morphological variation in either adults, pupae or larvae.

Blepharocerids found to the south of the area of distribution of *N. hudsoni* are in the larval and pupal stages, morphologically indistinguishable from *N. hudsoni* but adult males possess dichoptic eyes. These blepharocerids will be referred to as "southern", and are described as *Neocurupira rotalapisculus* and Forms A, B and C; for reasons discussed later they are here placed along with *N. hudsoni* in a *hudsoni*-complex but the Forms are not given any further taxonomic status.

Blepharocerid larvae, probably of *N. rotalapisculus* and Form C, were first reported from Dunedin and Queenstown by Campbell (1921) who figured dorsal views of Queenstown larvae. He later (1923) figured more Queenstown larvae showing a range of colour patterning similar to that of the patterned *N. hudsoni* larvae. Dumbleton (1963a) described the colour of the fourth instar larva of *N. hudsoni* as "uniform dark brown" but mentions finding patterned *N. hudsoni* larvae. On this basis he suggested that the Dunedin and Queenstown larvae described by Campbell be referred to *N. hudsoni*. Morphologically differences between larvae of New Zealand blepharocerid species are such that the larval differences between members of the *hudsoni*-complex indicates that these blepharocerids are conspecific.

The commensal chironomid *Dactylocladius commensalis* Tonnoir (1923b), often associated with *N. hudsoni* larvae, also occurs with Form C larvae. Tonnoir believed the association to be specific to *N. hudsoni* but *D. commensalis* does occur, though rarely, with larvae of *N. campbelli*. The abundance of *D. commensalis* on both *N. hudsoni* and Form C larvae is believed to indicate a very close relationship between these two blepharocerids. The rare occurrence of the commensal on *N. campbelli* larvae may indicate a relationship to the *hudsoni*-complex and is considered later (p. 148).

The pupae of *N. rotalapisculus* and Form C are similar in all respects to *N. hudsoni* pupae (Fig. 4) except for a slight difference in the shape and basal width length ratio of the outer lamella of the pupal gill. Pupal characters (with one exception, that of *Nothohoraia*), are not sufficiently distinct to provide positive identification of any New Zealand blepharocerid, so that the difference shown by "southern" pupae will not be considered further.

Campbell (1923) mentioned that the adults associated with the patterned Queenstown larvae showed wing venation similar to that of *N. chiltoni* and that the males were dichoptic. However, the venation of Form C is shown here (Figs. 5 and 7) to be more similar to that of *N. hudsoni* than to that of *N. chiltoni* (Fig. 50). Differences in wing shape and venation between the New Zealand *Neocurupira* species are sufficient for the similarities in wing shape and venation of *N. hudsoni* and Form C to indicate conspecificity. Wing shape and venation of *N. rotalapisculus* (Fig. 6) differ considerably from those of *N. hudsoni* and Form C.

Compared with the other species of New Zealand *Neocurupira*, members of the *hudsoni*-complex are uniform in genitalia. This is interpreted as indicating a close relationship between members of the complex. However, within the complex the genitalia of *N. rotalapisculus* show differences that separate it from the other members (compare Figs. 11 and 13 with 12, and 21 and 23 with 22).

Head structure of Form C females (Fig. 20) is very similar to that of *N. hudsoni* females; but, head structure of *N. rotalapisculus* females (Fig. 18) differs considerably, and in the width of the vertex area resembles *N. campbelli* females (Figs. 27 and 28).

Even though the adults of Form B and C are fully dichoptic, the similarities of their larvae, genitalia, wing shape, venation and shape of female head to those of *N. hudsoni*, suggests that Forms B and C are conspecific with *N. hudsoni*. *N. rotalapisculus*, though possessing morphologically similar larvae to those of *N. hudsoni*, shows considerable differences in the structure of the female head, in the

shape and venation of the wing, and the genitalia of both sexes. For these reasons this blepharocerid has been given species rank.

Form B is known from only a few specimens collected from the Matukituki Valley, Lake Wanaka. Form C and *N. hudsoni* have also been collected from this habitat and as Form B shows morphological similarities to these blepharocerids it is considered to be their hybrid. If Form B is indeed a hybrid, then according to Mayr's (1963) species definition, Form C and *N. hudsoni* are conspecific, a conclusion reached on morphological grounds. However, Bigelow (1965) has pointed out that hybridisation does not necessarily mean conspecificity if the hybrid zone has been maintained for long periods of time, for this indicates a restricted gene flow. If the gene flow was unrestricted, the hybrid zone would not be evident and perhaps a cline of variation or a homogeneous population would result. Bigelow maintains that the presence of the two parent forms in the hybrid zone indicates a highly restricted gene flow and that the two parent taxa are still to be considered as species, since the gene flow will never result in conspecificity.

As far as is known the overlap between Form C and *N. hudsoni* populations is very narrow (Fig. 26a) and Bigelow's hypothesis is applicable to the situation.

Further collections from the Lake Wanaka region would enable more authoritative conclusions to be reached concerning the reproductive isolation of *N. hudsoni* and Form C. Therefore Form C is not given definite taxonomic rank.

Neocurupira (Neocurupira) hudsoni Lamb.

Neocurupira hudsoni Lamb, 1912; Campbell, 1921.

Neocurupira (Neocurupira) hudsoni, Tillyard, 1922; Dumbleton, 1963a.

TYPE MATERIAL: BM. TYPE LOCALITY: Bealey River, Canterbury.

Diagnosis

N. hudsoni is the largest and most spectacular of the known New Zealand blepharocerids. Male holoptic, eye ratio 1:0.5; body length 9.5–11.0mm.

Description

Adult

Male (61 specimens). Body length 9.5–11.0mm. *Head* (Fig. 9). Depth width ratio 1:1.3; holoptic, eye ratio 1:0.5, upper facets large; labial palpus twice as long as head depth; 10–11 lateral facial hairs. *Normal wing* (Fig. 5). Length 7.2–10.0mm. *Brachypterous male wing* (Fig. 8). Length 2.5mm (one specimen). *Genitalia* (Figs. 21 and 24). Median concavity of cercus variable but notched basally, lateral lobes variable; dististyles broad basally, widest at midlength.

Female (32 specimens). Body length 5.5–8.0mm. *Head*. Depth width ratio 1:1.3; dichoptic, eye ratio 1:1.6; labial palpus 1.5 times as long as head depth; vertex area keel-like and 0.25 times as wide as head width. *Wing*. More membranous than male wing, length 7.2–9.0mm. *Genitalia* (Fig. 11). Internal process of oviscapt truncate, slightly concave apically, oviscapt lobes bearing 6–7 dark spines sub-apically.

Pupa (25 specimens). Length 6.0–8.0mm. Outer lamellae of pupal gills tapering, broadly rounded apically, basal width length ratio 1:2.7; inner lamellae shorter than outer lamellae.

Larva

Fourth Instar (Fig. 14 and Plate 1a). (133 specimens). Length 5.9–14.0mm. Sucker width 0.60–0.89mm. Colour of the cephalic sclerites varying from moderate

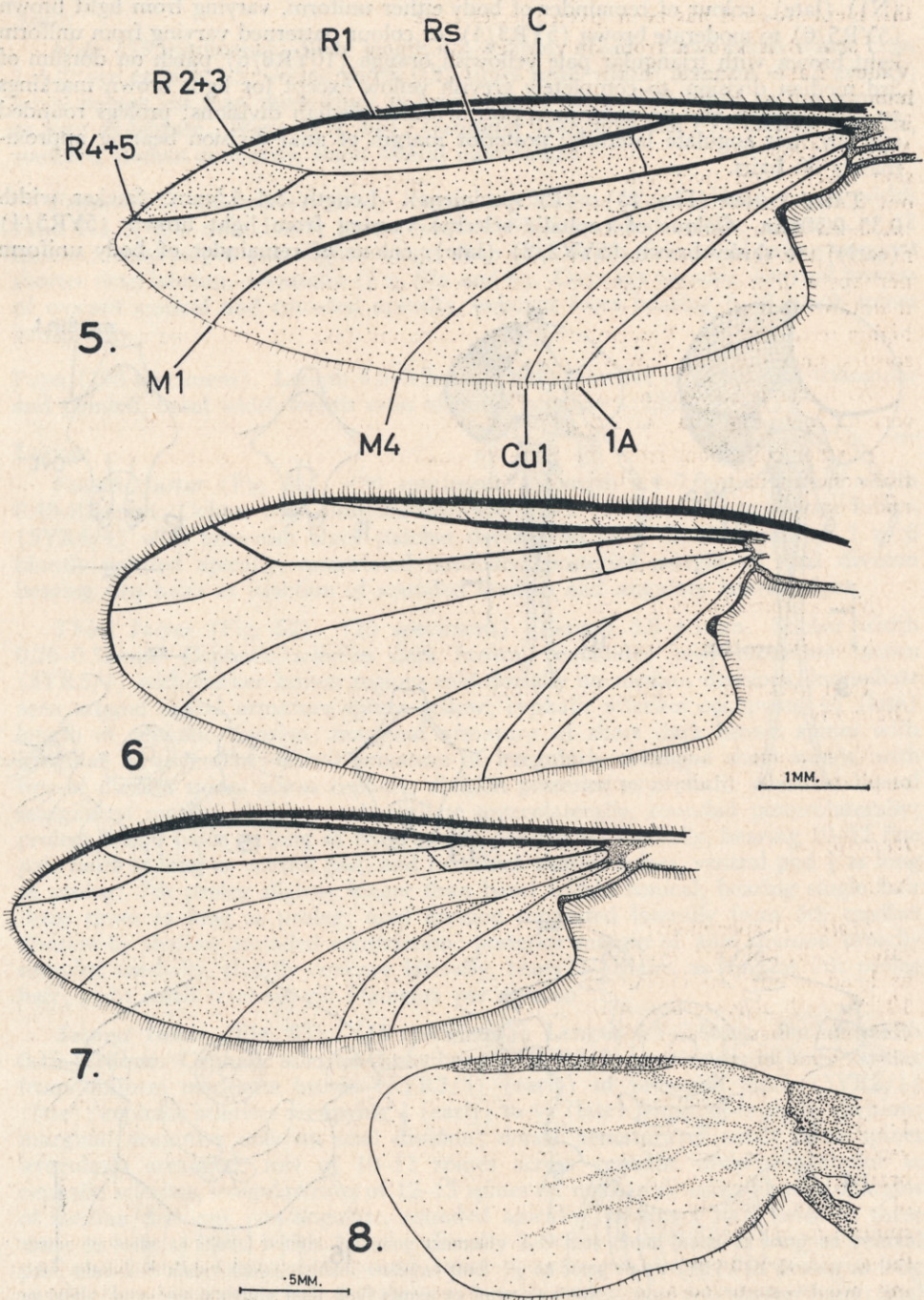


FIG. 5.—Macropterous wing of *N. hudsoni* male. FIG. 6.—Wing of *N. rotalapisculus* male.
 FIG. 7.—Wing of Form C male. FIG. 8.—Brachypterous wing of *N. hudsoni* male.

yellowish orange (10YR7/6) mottled with dusky brown (5YR2/2) (early) to black (N1) (late), colour of remainder of body either uniform, varying from light brown (5YR5/6) to moderate brown (5YR3/4), or colour patterned varying from uniform light brown with triangular pale yellowish orange (10YR8/6) patch on dorsum of 3rd median division, to completely greyish yellow except for light brown markings on 2nd division and on anterior region of other median divisions; prolegs rounded apically, not angulate laterally; posterior margin of anal division bearing approximately 30 hairs.

Third Instar (Fig. 15). (15 specimens). Length 3.4–4.5mm. Sucker width 0.35–0.50mm. Colour of cephalic sclerites varying from light brown (5YR5/4) (early), to dusky brown (5YR2/2) (late), colour of remainder of body uniform

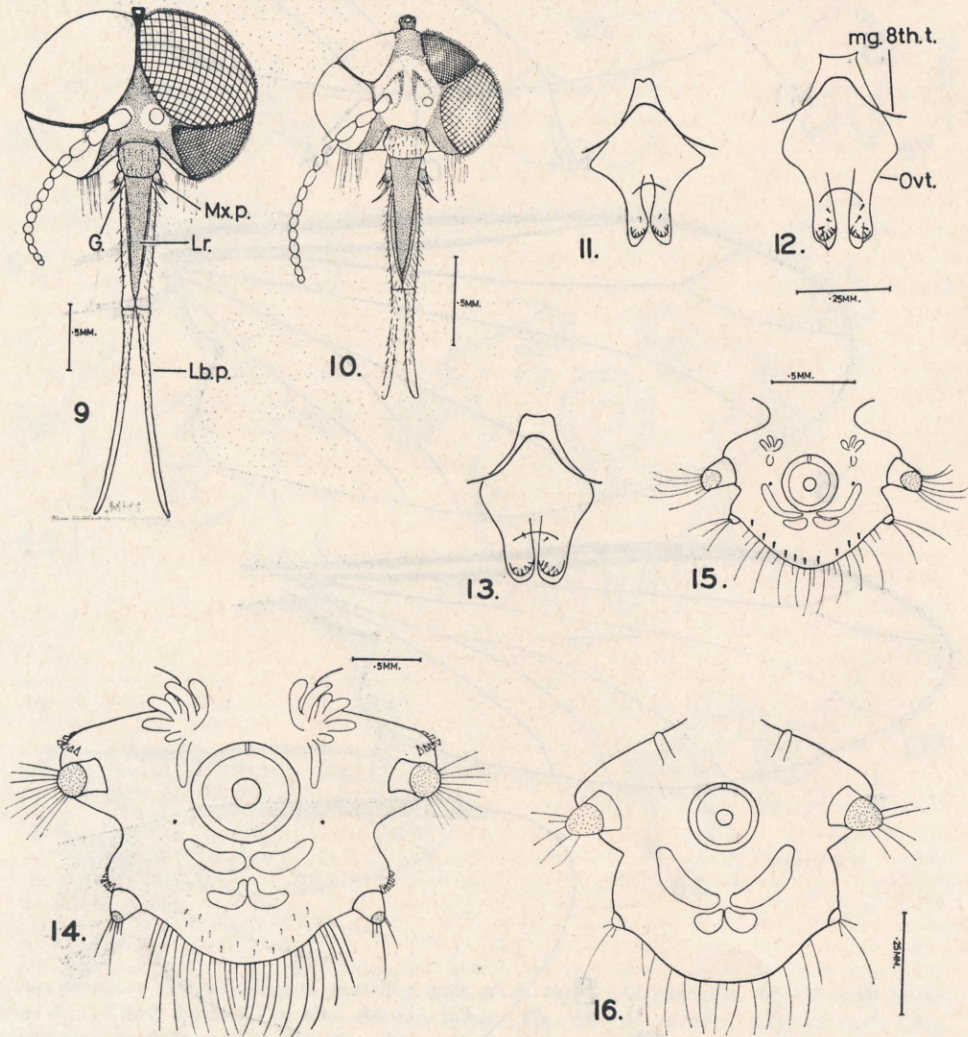


FIG. 9.—Frontal view of head of *N. hudsoni* male. FIG. 10.—Frontal view of head of Form B female. FIG. 11.—Oviscapit of *N. hudsoni* female. FIG. 12.—Oviscapit of *N. rotalapisculus* female. FIG. 13.—Oviscapit of Form C female. FIGS. 14–16.—*N. hudsoni*, ventral views of posterior ends of larvae. FIG. 14.—Fourth instar larva. FIG. 15.—Third instar larva. FIG. 16.—Second instar larva.

but varying from moderate brown (5YR3/4) to light brown; cephalic sclerites occupying 2/3 (early) to 1/3 (late) length of the cephalic division; marginal armature of scales; dorsal armature of short setae irregularly arranged at approximately two seta lengths apart; dorsal cuticle microsculptured into ridges and grooves; lateral edges of median divisions subangulate; prolegs 1–6, 1/5 longer than basal width, subangulate apically, very slightly constricted medially, bearing dorsally short hairs plus seven fine hairs as long as proleg, ventral pad 1/2 as long as proleg; 7th proleg slightly shorter than basal width, bearing 2–3 hairs three times as long as proleg; anal division separated laterally from 5th median division by subangulate constriction; posterior margin of anal division broadly rounded bearing 7–9 irregularly arranged hairs, each as long as hairs on 7th proleg, as well as 12–14 shorter hairs and 10–12 setae ventral to posterior margin; eight tracheal gill filaments per division; anterior anal gill filaments large, partly encircling 6th sucker.

Second Instar (Fig. 16). (10 specimens). Length 2.8–3.4mm. Sucker width 0.19–0.24mm. Colour of cephalic sclerites dusky brown (5YR2/2), remainder of body uniformly light brown 5YR5/4; cephalic sclerites occupying 1/3 (early) to 1/5 (late) length of cephalic division; marginal armature, anteriorly 11 scales per division, posteriorly four scales per division; dorsal armature not apparent; lateral margins of median divisions subangulate anterolaterally, slightly rounded posterolaterally; prolegs 1–6 as long as basal width, rounded apically, slightly constricted medially, bearing dorsally five hairs each as long as proleg, ventral pad 1/3–1/2 as long as proleg; 7th proleg wider than long, bearing one hair 4–5 times as long as proleg plus two smaller hairs, no apparent ventral pad; anal division separated laterally from 5th median division by broadly angulate constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally bearing 12–13 short hairs as long as 7th proleg hair; two tracheal gill filaments per division; posterior anal gill filaments 1/3–1/2 size of anterior filaments.

Distribution (Fig. 26A)

N. hudsoni has the widest distribution of any New Zealand blepharocerid and occurs mainly in open, stable streams and rivers which have a good flow of water, with an altitudinal distribution from just above sea level to 5,000ft. *Neocurupira hudsoni* is microsympatric with *N. tonnoiri*, *N. campbelli*, *Nothohoria micrognathia* and *Peritheates turifer* when the areas of distribution coincide.

Material was examined from the following localities: Red Pine (Pouawhariki) Gully, Moncrieff Scenic Reserve, Croiselles Bay, Marlborough Sounds, (S15/995483), LP, V.M.S., 30; D.A.C., ?-xii-65, CM. Wangamoa River, Nelson, (S14/798367), LA, W. P. Thomas, 22-xii-63; D.A.C., 21-xii-62, 31-xii-62, 1-i-65, CM; anon., 3-ii-64, UA. Maitai River, Nelson, LP, L.J.D., 23-i-50, 23-i-54, EDL; (S20/683262), D.A.C., 27-xii-62, CM. Brook Stream Reservoir, Nelson, (S20/638236), L, D.A.C., 30-xii-64, CM. Marsden Valley, Stoke, (S20/617217), LP, D.A.C., 24-xii-62, 1-i-64, CM. Lee River, Brightwater, (S20/516114), L, D.A.C., 25-xii-62, CM. Buller River Bridge, Lake Rotoiti, (S33/193680), L, L.J.D., 10-i-60, EDL. Travers Valley, Lake Rotoiti, L, B. M. Fitzgerald, 1964, CM. Hopeless Creek, Travers Valley, 2,400ft., LP, J.Flux, 10-ii-65, CM. Sabine River, Lake Rotoroa, L, L.J.D., ?-x-50, EDL. Puhī Puhī, Kaikoura, L.J.D., 6-i-60, EDL. Mount Fyffe, Kaikoura, L.J.D., 14-v-62, EDL. Boyds Creeks, Kaikoura, (S49/890988), LPA, D.A.C., 29-viii-62, 31-xii-62, CM. Kowhai River, Kaikoura, LP, (S49/909936), V.M.S., 2-ix-64, (142); D.A.C., 19-ix-64, CM; (S49/868019), D.A.C., ?-i-66, CM. Jack's Pass, Hanmer, L, L.J.D., 12-v-54, EDL. Waterfall Stream, Lake Taylor, L, F. R. Allison, 14-i-64, CM. Rough Creek, Lewis Pass, LP, D.A.C., 12-ii-62, CM. Mount Arthur, Nelson, A, A. Philpott, 22-xii-21, EDN. Cobb River, Takaka, 2,500ft., L, S. G. Moore, 4-iv-65, CM. Fossil Creek and Brown River, Heaphy Track, LP, J. Grieve and M. Cross, 10-i-65, CM. Barrytown Beach, Barrytown, Greymouth, 10ft., LP, A. G. McFarlane, 17-xii-63, CM. Thirteen Mile Creek, Greymouth, L, L.J.D., 11-i-60, EDL; anon., 28-i-66, UA. Wanganui River, West Coast, LP, V.M.S., 12-x-61, 206. Waikukupa River, West Coast, L.J.D., EDL. Clearwater River, Fox, P, D.A.C., 9-ii-66, CM. Otira, A, A. L. Tonnoir, 16-ii-22, EDN; T. Harris, CM. Warnocks Nob, Otira, A, G. V. Hudson, 13-xii-08, DM. Otira Valley, (S59/050337), D.A.C., 19-i-63, 23-ii-63, CM. Pegleg Creek, Arthur's Pass, (S59/055340), LPA, L.J.D., 30-i-60, EDL; D.A.C., 15-xii-62, CM. Temple Basin, 5,000ft., L, L.J.D., 31-i-58, EDL. Twin Creek, (S59/053322), L, D.A.C., 29-vii-62, CM. Bealey Glacier, Mount Rolleston, (S59/-

027318), LP, Sykes, 9-ii-63, EDL; D.A.C., 3-ix-63, CM. Bealey Chasm, Bealey River, (S59/050313), LPA, D.A.C., 1962-1966, UC. McGraths Creek, (S59/053300), LP, D.A.C., 29-vii-62, CM; A. G. McFarlane, 31-i-65, CM. Punch Bowl, (S59/055295), L, D.A.C., 20-i-62, 20-i-63, CM. Bealey River, A, G. V. Hudson, 10-ii-20, BM, DM. Arthur's Pass, A, A. L. Tonnoir, 18-i-20, EDN; anon., ?-xii-22, DM. Snow Creek, (S59/065264), LP, D.A.C., 28-iv-63, CM. Halpin Creek, (S59/070244), L, L.J.D., 13-iv-62, EDL. Mingha River, (S59/114297), LP, D.A.C., 16-xii-63, CM. Andrews Stream, Hallelujah Flats, (S59/280167), LA, D.A.C., 14-xi-64, CM. Linwood Creek, Minchin River, (S59/278446), LPA, D.A.C., 18-iv-65, CM. Sudden Valley, Hawdon River, (S59/195244), L, D.A.C., 19-iv-64, CM. Betwixt Stream, Cass, (S66/201172), L, D.A.C., 18-iv-64, CM. Ribbon Wood Creek, Cass, L, E. Percival, 20-x-33, (Misc.). West Cass River, (S66/193124), L, D.A.C., 13-xi-64, CM. Cass River, (S66/211161), LP, D.A.C., 24-iii-62, CM. Cass, A, A. L. Tonnoir, ?-ii-25, CM. Masons Creek, Flock Hill, Craigieburn Mountain Range, 3,800ft., A, P. M. Johns, 21-i-65, CM. Ryton River, Lake Coleridge, (S74/053898), L, D.A.C., 10-ii-63, CM. Mount Hutt, 2,500ft., PA, G. Tunncliffe and W. P. Thomas, 29-i-64, CM. Taylor Stream, Ashburton River, LP, D.A.C. and V.M.S., 27-i-64, (123). Moa River, Wilberforce River, L, D.A.C., 19-x-63, (1). Kiwi River, Wilberforce, 2,000ft., LP, D.A.C., 19-x-63, CM. East Kiwi River, L, D.A.C., 19-x-63, (2). Kakapo River, Wilberforce, L, D.A.C., 19-x-63, (4). East Kakapo River, 3,000ft., L, D.A.C., 18-x-63, CM. Lower Kakapo River, 2,000ft., LPA, D.A.C., 18-x-63, CM. Godley Hut, Godley Glacier, L.J.D., 11-xii-58, EDL. Jacks Stream, Mount Cook, L, D. R. Cowley, 24-i-65, UA. Bush Stream, Mount Cook, (S89/773155), L, L.J.D., 14-x-58, EDL; D.A.C. and V.M.S., 11-i-64, (61). Black Birch Stream, Mount Cook, (S89/760300), LP, D.A.C. and V.M.S., 9-i-64, (59 and 59a). Lake Ohau, 1,720ft., L, P. M. Johns, 13-x-63, CM. Parson's Rock Stream, Otematata, LP, D.A.C. and V.M.S., 24-i-64, (108); D.A.C., 29-ii-64, CM. Shingle Creek, Roxburgh, LPA, D.A.C. and V.M.S., 21-i-64, (97). Neck Creek, Lake Hawea, 1,325ft., LPA, D.A.C., 13-i-65, CM. Sawyer's Burn, Lake Hawea, 1,325ft., L, D.A.C., 26-x-64, CM. Camp Stream, Lake Wanaka, 930ft., LP, D.A.C. and V.M.S., 12-i-64, (68). Boundary Creek, Lake Wanaka, 1,000ft., D.A.C. and V.M.S., 12-i-64, (69). Camerons Creek, Makarora River, LP, D.A.C., and V.M.S., 12-i-64, (71); D.A.C., 27-x-64, (197). Brady Creek, Makarora River, L, D.A.C. and V.M.S., 12-i-64, (70). Roaring Swine River, Haast River, 160ft., L, D.A.C. and V.M.S., 14-i-64, (78). Harris Creek, Haast River, L, D.A.C. and V.M.S., 14-i-64, (77). McPherson's Creek, Haast River, LA, D.A.C. and V.M.S., 14-i-64, (79). Gates of Haast, Haast River, LPA, D.A.C. and V.M.S., 14-i-64, (80); D.A.C., 27-x-64, (195). Pyke Creek, Haast River, L, D.A.C. and V.M.S., 14-i-64, (81). Haast River, 1,550ft., LP, D.A.C., 27-x-64, (196). Camp Creek, Haast River, 980ft., D.A.C., 27-x-64, (199). Phoebe Creek, Matukituki River, Lake Wanaka, P, D.A.C., 8-ii-66, CM. Old Homestead Creek, Matukituki River, 1,400ft., LP, D.A.C., 26-x-64, (190); 8-ii-66, CM. Bridal Veil Falls, Matukituki River, 1,400ft., D.A.C., 12-i-65, CM. Raspberry Hut Stream, Matukituki River, PA, D.A.C., 8-ii-66, CM. Lumberbox Creek, Lake Wakatipu, 1,100ft., LP, D.A.C. and V.M.S., 15-i-64, (83); D. R. Cowley, 29-i-65, UA. Nevis River Gorge, Nevis Valley, Lake Wakatipu, LP, D.A.C., 7-ii-66, CM. Piano Flat, Whakaea River, Southland, LP, L.J.D., EDL.

Remarks

Neocurupira hudsoni is the only New Zealand species of blepharocerid which possesses holoptic male adults with the upper eye larger than the lower. In this regard it is similar to the adult male of the Australian *Neocurupira nicholsoni*. The wing venation of these two species is also very similar (Tillyard, 1922b). The wings of *N. hudsoni* adults, in particular those from south of Mount Cook and occasionally from elsewhere, show a reduction in the thickness of vein R2+3 and an increase in the thickness of vein R4+5 (Fig. 5). Specimens have been collected on which the vein R2+3 is considerably reduced and not immediately obvious as is normal. The only known example of brachypterism in male blepharocerids has been found in this species (Fig. 8).

Collections of *N. hudsoni* 4th instar larvae for this work show a range in colour from a uniform colour to a pattern of colour (Plate 1a). Though there is usually a range of colour in any larval population, patterned larvae predominate in populations sampled from regions in Nelson, West Coast and south of Mount Cook. Uniformly coloured larvae predominate in populations from the region between Nelson and Mount Cook.

The commensal chironomid *Dactylocladius commensalis* Tonnoir, 1923b, is microsypatric with *N. hudsoni*.

Neocurupira rotalapisculus n.sp.

TYPE MATERIAL: CM. TYPE LOCALITY: Shepards Stream, Waipouri Falls, Dunedin.

Diagnosis

Male eyes dichoptic, divided subequally, upper facets slightly larger than lower facets. Female frons very wide. Wing of both sexes rounded apically with vein Rs arising basally, not from vein R1.

Description

Adult

Male (four pharate specimens). Body length 6.6–7.3mm. *Head* (Fig. 17). Globular; colour moderate yellowish brown (10YR5/4); depth width ratio 1:1.5; eyes dichoptic, eye ratio 1:0.9, upper facets slightly larger than lower facets, eye margins continuous; vertex area 0.06 times as wide as head width; ocellar turret prominent, anterior ocellus prominent; antenna of 14 articles, five proximal articles longer than wide, remainder moniliform; clypeus as long as wide, colour pale yellowish orange (10YR8/6), darker on proximal border, bearing 20–24 short, black hairs; labrum darker than clypeus, with heavily pigmented proximal border, shorter than head depth, slightly longer than proximal segment of labial palpus; maxillary palpus two segmented, proximal segment small, distal segment black, truncated, bearing anterolaterally 17–19 black hairs; galea prominent, 0.66 times as long as maxillary palpus; labial palpus twice as long as head depth, distal segments diverging; 15–17 lateral facial hairs. *Thorax*. As for *N. hudsoni*. *Wing* (Fig. 6). Length 7.5–8.1mm. Vein Rs arising from wing base, vein 1A not reaching wing margin, wing apex rounded. *Genitalia* (Fig. 22). Posterior lateral margin of cercus rounded, median concavity notched basally, sides straight to slightly concave; dististyles as for *N. hudsoni*.

Female (one pharate specimen). Body length 8.4mm. *Head* (Fig. 18). Colour as for male; depth width ratio 1:1.2; eyes dichoptic, eye ratio 1:1.8, upper facets slightly smaller than lower facets; vertex area 0.33 times as wide as head width, only slightly protruding anteriorly from eye level; ocellar turret raised, base diverging, anterior ocellus prominent; antenna of 14 articles, moniliform, proximal three articles larger than rest; clypeus wider than long, colour pale yellowish orange (10YR8/6), bearing 23–25 short, black hairs; labrum darker than clypeus, with lighter colour proximal border, longer than proximal segment of labial palpus, finely tapering; maxillary palpus two segmented, distal segment larger, constricted basally, angulate distolaterally, bearing 11–13 black hairs; galea prominent, twice as long as maxillary palpus; labial palpus 1.5 times as long as head depth, distal segment short; 4–5 lateral facial hairs. *Thorax*. As for *N. hudsoni*. *Wing*. Venation and shape similar to male, length 8.1mm. *Genitalia* (Fig. 12). Internal process of oviscapt tapering, apex shallowly concave, oviscapt lobes bearing 7–8 short, clear spines subapically.

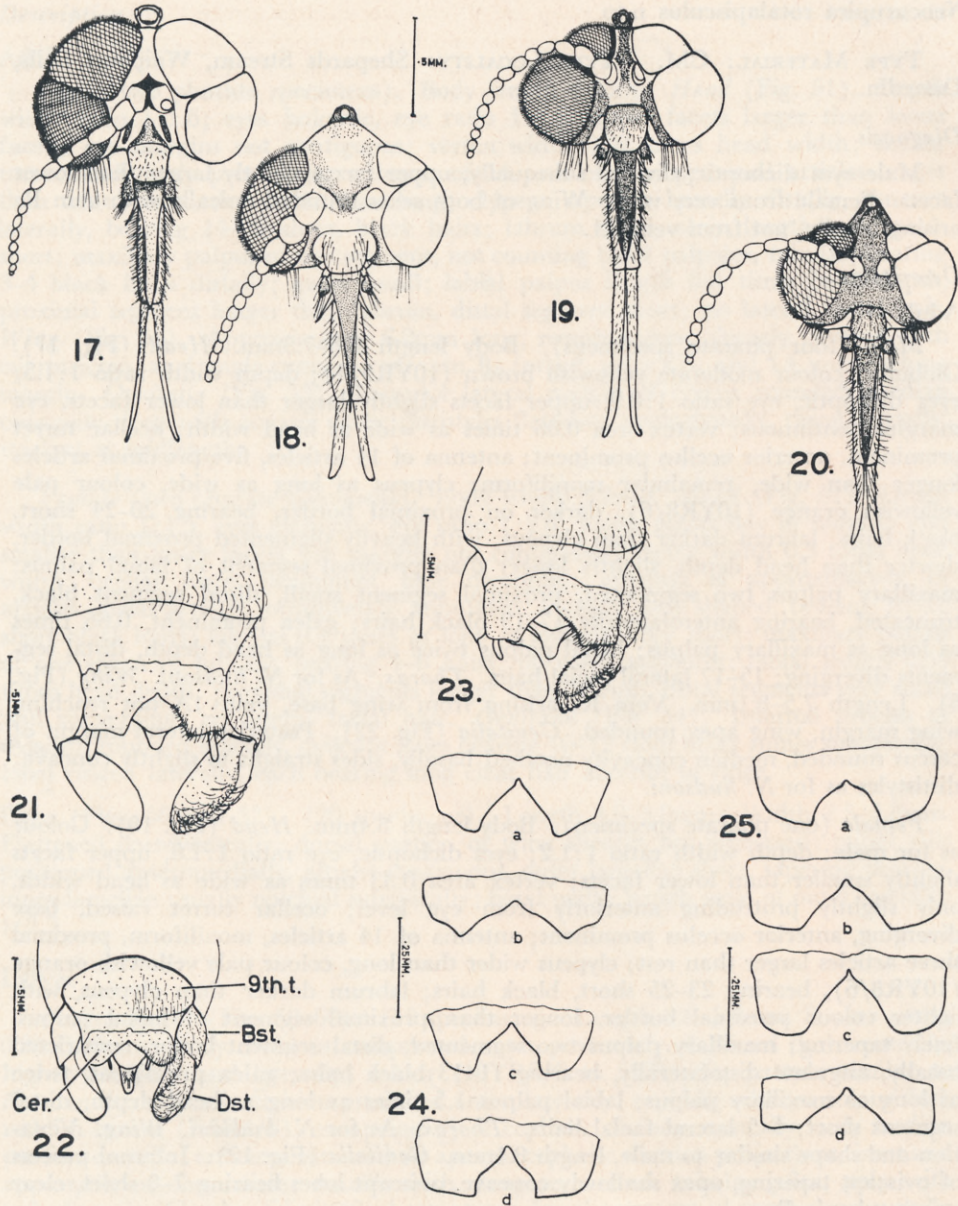
Pupa (five specimens). Length 7.0–8.7mm. Width 3.1–3.8mm. Similar to *N. hudsoni*. Basal width length ratio of outer lamellae 1:2.5.

Larvae. Similar in all stages to *N. hudsoni*.

Distribution (Fig. 26A).

N. rotalapisculus is to date known only from a restricted area near Dunedin.

Material was examined from the following localities: Shepards Stream, Waipouri Falls, Dunedin, (S163/708666), approx. 800ft., LP, D.A.C., 18-x-64, (167); C. Devine, 8-xi-64, CM. Post Office Stream, Mount Maungatua, Dunedin, (S163/767750), approx. 100ft., LP, D.A.C., 18-x-64, (164); 5-ii-66, CM.



Figs. 17-18.—Frontal views of head of *N. rotalapisculus*. Fig. 17.—male. Fig. 18.—female. Figs. 19-20.—Frontal views of head of Form C. Fig. 19.—Male. Fig. 20.—Female. Fig. 21.—Dorsal view of *N. hudsoni* male genitalia. Fig. 22.—Dorsal view of *N. rotalapisculus* male genitalia. Fig. 23.—Dorsal view of Form C male genitalia. Fig. 24.—Variation in shape of the cercus of *N. hudsoni* males. Fig. 25.—Variation in shape of the cercus of Form C males.

Remarks

The adult male exhibits an interesting eye structure (Fig. 17), which is intermediate between the holoptic condition of *N. hudsoni* and the dichoptic condition of Form C. The wing (Fig. 6) is different from that of *N. hudsoni* for the vein Rs arises from the wing base and not from vein R1, and the vein 1A does not reach

the wing margin. Apically the wing of *N. rotalapisculus* is more blunt than that of *N. hudsoni*. The specific name refers to the rounded apex of the wing. Genitalia and body of *N. rotalapisculus* male adults are very similar to those of *N. hudsoni*. Females of *N. rotalapisculus* show considerable differences in head structure from females of *N. hudsoni* and those of Form C. The vertex area is wider, more rounded dorsally and does not protrude greatly above the level of the eye as it does in *N. hudsoni* females. The galea and the distal segments of the maxillary palpus are more prominent than in *N. hudsoni*.

The oviscapt (Fig. 12) shows a mixture of characters similar to those shown by the oviscapt of *N. hudsoni* and of Form C. The distal lobes are more like those of *N. hudsoni* (Fig. 11) but the internal process is more like that of Form C (Fig. 13). The subapical spines are clear, in contrast to those of both *N. hudsoni* and Form C which are black.

The larvae associated with the pupae of *N. rotalapisculus* are highly patterned in a manner similar to other larvae of the *hudsoni*-complex, and are morphologically indistinct from *N. hudsoni* larvae.

The commensal chironomid *Dactylocladius commensalis* Tonnoir has not as yet been found associated with the larvae of *N. rotalapisculus*.

FORM A

Adult

Male (three pharate specimens). Body length 7.9–9.0mm. *Head*. As for *N. hudsoni*; labial palpus from 1.2–1.7 times as long as head depth; 4–5 lateral facial hairs. *Genitalia*. As for *N. hudsoni*.

Female (two pharate specimens). Similar to *N. hudsoni* females.

Larvae. Not known.

Distribution

Otago, P, anon., CM.

Remarks

Apart from the shorter labial palpi and fewer lateral facial hairs of the male, Form A is very similar to and probably conspecific with *N. hudsoni*. Form A is placed in the same series as the "southern" forms because the exact location is unknown and its members possess relatively short labial palpi similar to Form B.

FORM B

Adult

Male (three pharate specimens). *Head* (Fig. 10). Depth width ratio 1:0.77; eyes dichoptic, eye ratio 1:1.2, upper and lower eye not contiguous; vertex slightly raised, 0.17 times as wide as head width; maxillary palpus as long as labrum; galea as long as maxillary palpus; labial palpus 1.7 times as long as head depth; 10–11 lateral facial hairs. *Body*. Similar to *N. hudsoni*.

Female. Not known.

Distribution (Fig. 26A).

Form B has, so far, been found only in populations containing both *N. hudsoni* and Form C.

Material was available from two localities: Raspberry Hut Stream, Matukituki Valley, Lake Wanaka, 1,500ft., D.A.C., 8-ii-66, CM. Motatapu Gorge, Lake Wanaka, approx. 950ft., D.A.C., 9-ii-66, CM.

Remarks

The shape of the head and ocellus, and the non-contiguous eye margins of Form B are more similar to those of *N. hudsoni* than to Form C, while the eye ratio

and the proportions of the mouth parts are more similar to those of Form C than to *N. hudsoni*. Because Form B is known only to occur with *N. hudsoni* and Form C, and shows a mixture of head characteristics of these associates, it is considered here to be a hybrid between *N. hudsoni* and Form C.

FORM C

Adult

Male (15 specimens). Body length 6.8–8.0mm. *Head* (Fig. 19). Trapezoidal; colour varying from dusky yellowish brown (10YR2/2) to brownish black (5YR2/1); depth width ratio 1:1.5; eyes dichoptic, eye ratio 1:1.5, upper and lower facets equal in size, eye margins contiguous, black unfaceted peripheral band around upper eye; vertex area 0.1 times as wide as head width; ocellar turret raised, constricted basally; antenna of 14 articles, moniliform; clypeal margin of frons light in colour, lateral areas darker; clypeus as long as wide, distal edge lighter in colour, bearing 16–20 short black hairs; labrum black, slightly shorter than proximal segment of labial palpus; maxillary palpus 2 segmented, distal segment larger and black in colour, bearing anterolaterally 18–20 black hairs; galea twice as long as distal segment of maxillary palpus; labial palpus 2.2 times as long as head depth, distal segment slightly longer than clypeus plus labrum, diverging; 10–12 lateral facial hairs. *Thorax*. As for *N. hudsoni*. *Wing* (Fig. 7). Similar in shape and venation to *N. hudsoni* but not in length, 6.2–7.3mm. *Genitalia* (Figs. 23 and 25). Posterior lateral margin of cercus variable, median concavity always notched basally (as in *N. hudsoni*); dististyles as for *N. hudsoni*.

Female (three specimens). Body length 7.0–7.9mm. *Head* (Fig. 20). Globular; colour brownish black (5YR2/1); depth width ratio 1:1.3; eyes dichoptic, eye ratio 1:2.8, upper facets smaller than lower facets; vertex area 0.17 times as wide as head width, protruding above eye level to form keel-like structure; ocellar turret raised, prominent, base diverging; antenna of 14 articles; clypeus as long as wide, dark with distal dusky yellow (5Y6/4) edge, bearing 16–20 short black hairs; labrum black, slightly longer than proximal segment of labial palpus; maxillary palpus 2 segmented, segments of equal size, distal segment black, bearing antero-laterally 8–10 black hairs; galea twice as long as maxillary palpus; labial palpus 1.5 times as long as head-depth, distal segments short; 10–14 lateral facial hairs. *Thorax*. As for male. *Wing*. Length 8.0–9.1mm. As for male but more membranous and junction of vein A1 to margin very weak. *Genitalia* (Fig. 13). Internal process of oviscapt constricted laterally, shallowly concave apically, oviscapt lobes bearing 6–8 short black spines subapically.

Pupa (30 specimens). Length 5.8–6.4mm. Width 2.5–2.9mm. Similar to *N. hudsoni*. Basal width length ratio of outer gill lamellae 1:3.0, sides of posterior outer lamellae gradually tapering, apex rounded; middle lamellae longer and wider than outer lamellae, lateral margins curved, constricted basally (Fig. 3).

Larvae. Similar in all stages to *N. hudsoni*.

Distribution (Fig. 26a).

Form C occurs in habitats similar to those occupied by *N. hudsoni* and has a similar altitudinal distribution. The known area of distribution of Form C extends from Lake Wanaka to Milford Sound and Lake Te Anau. No known collections of blepharocerids have been made in the area south of Lake Te Anau, but it is expected that Form C and perhaps other blepharocerid forms will eventually be discovered in that area.

Material was examined from the following localities: Motatapu Gorge, Lake Wanaka, 1,300ft., P, D.A.C., 8-ii-66, CM. Phoebe Creek, Matukituki Valley, Lake Wanaka, 1,300ft., P, D.A.C., 8-ii-66, CM. Raspberry Hut, Matukituki Valley, 1,400ft., P, D.A.C., 8-ii-66, CM. Cadronna River, 3,200ft., LP, D.A.C., 25-x-64, 11-i-65, CM. 12 Mile Creek, Queenstown,

1,030ft., L?, D.A.C., 25-x-64, (188). Dooleys Creek, Queenstown, 1,100ft., LPA, D.A.C., 9-i-65, CM. Ballarat Creek, Mount Aukum, L?, C. Devine, 23-iv-65, CM. Invincible Creek, Rees Valley, 1,500ft., L?, D.A.C., 23-x-64, (182). 25 Mile Creek, Rees Valley, 1,550ft., L?, D.A.C., 23-x-64, (183). Little Devil Creek, Rees Valley, 3,150ft., L?, D.A.C., 24-x-64, (184). Lennox Falls, Rees Valley, 1,550ft., L?, D.A.C., 24-x-64, (186). Eglington River, L?, V.M.S., 20-x-61, 223. Walker Creek, Eglington River, LP, V.M.S., 2-x-61, 225; D.A.C. and V.M.S., 17-i-64 (89a). Worsley River, Lake Te Anau, A, anon., 30-xii-27, AM. Wesley Creek, Eglington River, 1,200ft., LPA, D.A.C. and V.M.S., 17-i-64, (90); anon., 31-i-65, UA. 45 Mile Creek, Eglington River, 1,400ft., LP, D.A.C. and V.M.S., 17-i-64, (91). Hollyford River, LA, D.A.C. and V.M.S., 18-i-64, (93). Jamestown River, Hollyford River, L?, S. C. Woods, ?-ix-64, CM. Donne River, Milford Sound, 200ft., LA, D.A.C. and V.M.S., 19-i-64, (94). Cleddau River, Milford Sound, 1,050ft., L?, D.A.C. and V.M.S., 19-i-64, (95). Bowen Falls, Milford Sound, 50ft., L?, D.A.C., 18-i-64, CM.

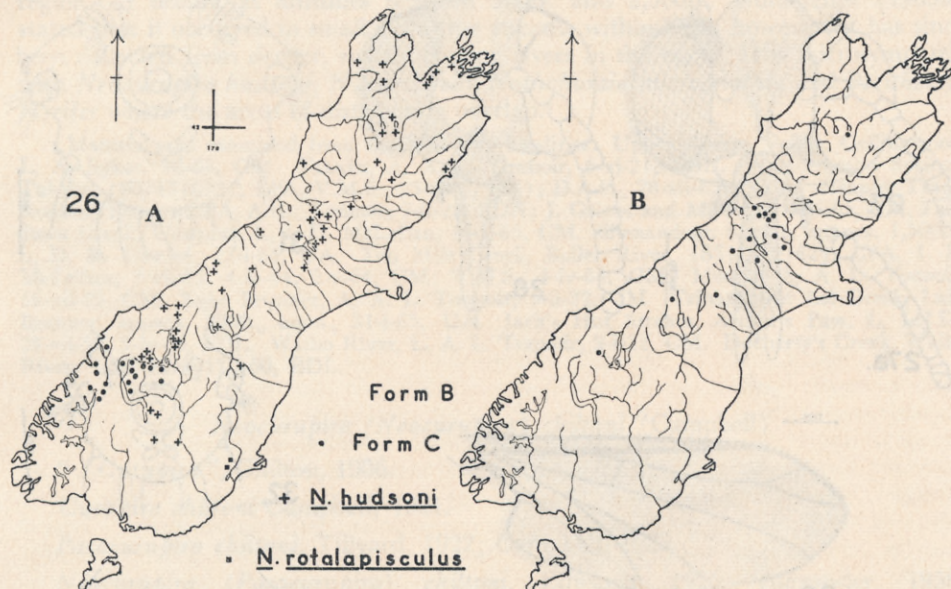


FIG. 26.—A. Map of South Island showing localities of *N. hudsoni*, *N. rotalapisculus* and Form B (shown on map A thus ---) and Form C. B. Map of South Island showing localities of *N. campbelli*.

Remarks

Both sexes of Form C have wings very similar to those of *N. hudsoni* adults. The Form C females are very similar in head structure and genitalia to the females of *N. hudsoni*. The Form C males have similar genitalia to those of *N. hudsoni* males, but are dichoptic, a fact first reported by Campbell (1923) and apparently overlooked by Dumbleton (1963a).

Apart from the differences in the eye structure of the male and a slight difference in the shape of the pupal gill lamellae, Form C is very similar morphologically in all stages to *N. hudsoni*.

Neocurupira (Neocurupira) campbelli Dumbleton

Neocurupira (Paracurupira) campbelli Dumbleton, 1963.

TYPE MATERIAL: EDL. TYPE LOCALITY: Pegleg Creek, Arthur's Pass, Westland.

Diagnosis

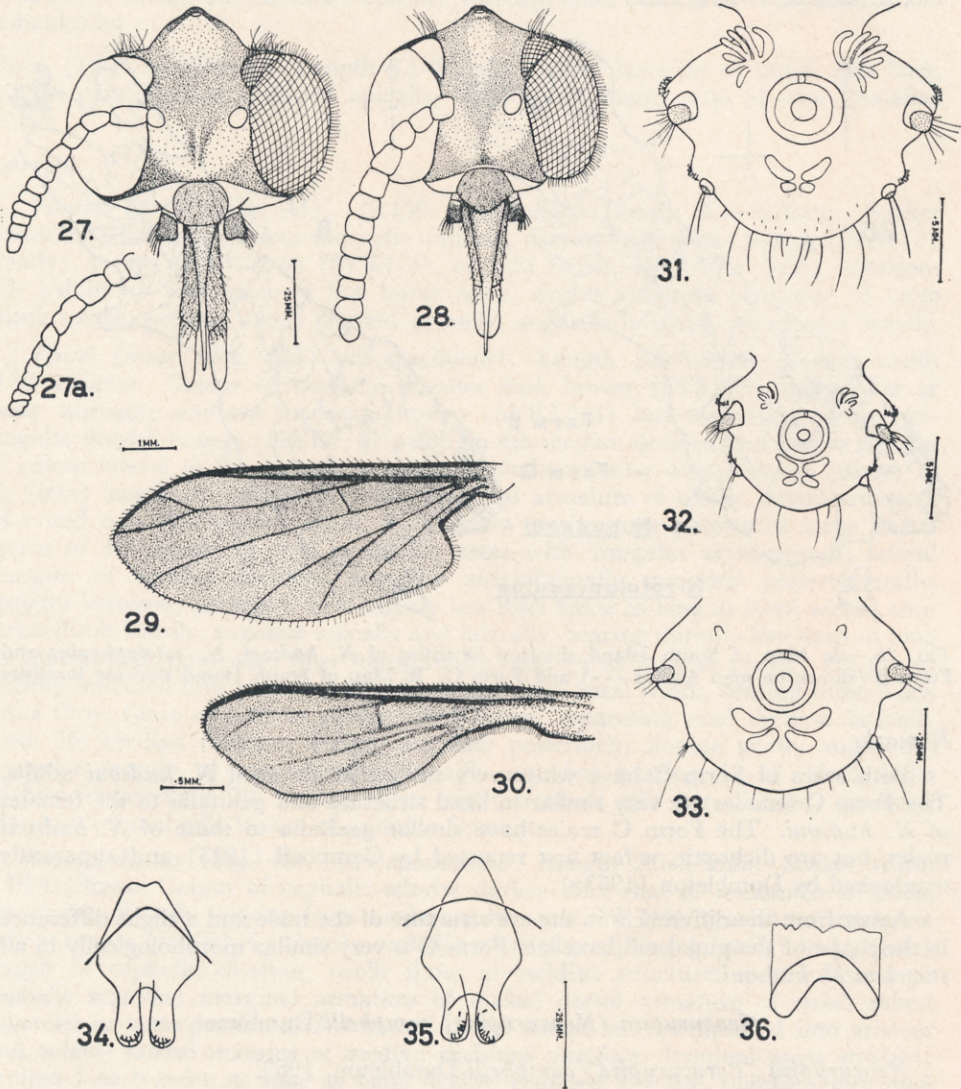
Smaller than other species, wings greyish, mouthparts subequal in length to head depth, antenna articles wider than long, female often brachypterous.

Description

Adult

Male (81 specimens). Body length 4.5–6.8mm. *Head*. Head depth width ratio 1:1.2; eye ratio 1:2.0; vertex width 0.28 times head width; antenna of 11 articles; labrum shorter than labial palpus; labial palpus subequal in length to head depth. *Genitalia* (Fig. 36). Posterior margin of cercus broadly concave, lateral margins rounded.

Female (Macropterous). (22 specimens). Body length 5.6–9.0mm; wing length 3.5–4.0mm. *Head* (Fig. 27). Head depth width ratio 1:1.4; eye ratio 1:4.2;



FIGS. 27–36.—*N. campbelli*. Fig. 27.—Frontal view of head of macropterous female. Fig. 27a.—Aberrant antenna of macropterous female. Fig. 28.—Frontal view of head of brachypterous female. Fig. 29.—Macropterous wing of female. Fig. 30.—Brachypterous wing of female. Figs. 31–33.—Ventral views of posterior ends of larvae: Fig. 31—Fourth instar. Fig. 32.—Third instar. Fig. 33.—Second instar. Fig. 34.—Oviscapt of brachypterous female. Fig. 35.—Oviscapt of macropterous female. Fig. 36.—Cercus of male.

vertex width 0.31 times head width; antenna of 12 articles; clypeus rounded; labrum shorter than labial palpus; labial palpus subequal in length to head depth, first segment of labial palpus shorter than labrum. *Genitalia* (Fig. 35). Internal process of oviscapt conical, oviscapt lobes bearing 7–9 clear short spines subapically.

(Brachypterous). (Six specimens). Body length 5.0–6.0mm. Wing length 0.6–2.5mm. *Head* (Fig. 28). Head depth width ratio 1:1.2; eye ratio 1:3.5; vertex width 0.28 times as wide as head width; antenna of 12 articles; clypeus subangulate laterally and distally; labial palpus variable in length. *Genitalia* (Fig. 34). Internal process of oviscapt concave apically, oviscapt lobes bearing 7–9 black short spines subapically.

Pupa (522 specimens). Length 4.0–6.2mm. Outer lamellae of pupal gills tapering to narrow rounded apex; basal width length ratio of outer lamellae 1:3.4.

Larvae

Fourth Instar (Fig. 31). (567 specimens). Length 4.4–8.0mm. Sucker width 0.48–0.59mm. Colour uniform dusky yellowish brown (10YR2/2); prolegs rounded apically, not angulate laterally; posterior margin of anal division bearing 6–12 irregularly arranged black hairs.

Third Instar (Fig. 32). (25 specimens). Length 2.8–4.7mm. Sucker width 0.30–0.36mm. Colour of cephalic sclerites black; remainder of body uniformly dark brown (5YR2/4) to brownish black (5YR2/1); cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) of length of cephalic division; marginal armature of setae; no apparent dorsal armature; lateral margins of median divisions rounded; prolegs 1 to 6 slightly longer than basal width, cone shaped, sharply rounded apically, bearing dorsally 10–12 fine hairs as long as ventral pad, ventral pad occupies $\frac{1}{3}$ – $\frac{1}{2}$ of length of proleg; 7th proleg as long as wide, bearing apically two black hairs, one five times as long as proleg; anal division separated laterally from 5th median division by very shallow angulate constriction; posterior margin of anal division broadly rounded bearing 4–5 black hairs irregularly arranged, as long as 7th proleg hairs; eight tracheal gill filaments per division.

Second Instar (Fig. 33). (Eight specimens). Length 1.9–2.6mm. Sucker width 0.17–0.18mm. Colour of cephalic sclerites black; remainder of body uniformly dark brown (5YR2/4); cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) length of cephalic division; no marginal armature; dorsal armature consisting of lanceolate setae, pattern similar to spines on third instar of *N. chiltoni*; dorsal cuticle microsculptured into grooves and ridges; lateral margin of median divisions same as for third instar; prolegs 1 to 6 as long as basal width, cone shaped, sharply rounded apically, bears dorsally fine pale hairs as long as pad, ventral pad occupies $\frac{1}{2}$ of proleg length; 7th proleg small, as long as basal width, bearing apically one black hair 5–7 times as long as proleg, plus 2–3 shorter hairs; anal division not separated laterally from 5th median division by constriction; posterior margin anal division broadly rounded and continuing beyond the 7th proleg to the 5th division, bearing 7–9 short black hairs; two small tracheal gills per division.

Distribution (Fig. 26b)

Dumbleton (1963a) considered that *N. campbelli* was of restricted distribution occurring only in the Arthur's Pass region. However, collections since then show the area of distribution to extend from Lake Rototoiti, Nelson, to Lake Wanaka, Otago. *N. campbelli* is microsympatric with *N. hudsoni* and *P. turriifer* when the areas of distribution coincide. The altitudinal distribution is from 1,400ft. to 4,500ft.

Material has been examined from the following localities: Hakano Stream, Travers River, Lake Rototoiti, Nelson, 3,500ft., L, J. Flux, 25-xi-64, CM. Townsend Creek, Minchin Pass, Arthur's Pass, (S59/282485), 3,800ft., LP, D.A.C., 18-iv-65, CM. Linwood Creek, Minchin River, (S59/278455), LPA, D.A.C., 18-iv-65, CM. Temple Basin, Arthur's Pass, (S59/-067324), L, D.A.C., 20-xi-63, 22-xi-64, CM. Lower Otira River Gorge, LP, V.M.S., 12-iii-65,

CM. Pegleg Creek, Arthur's Pass, (S59/055340), LPA, L.J.D., 13-iv-62, EDL; D.A.C., 15-xii-62, CM. Bealey Chasm, Arthur's Pass, (S59/050313), LPA, D.A.C., 1962-1966, UC. Bealey River, (S59/054296), L, D.A.C., 7-ii-62, CM. McGrath's Creek, Arthur's Pass, (S59/053300), L, D.A.C., 29-vii-62, CM. Punch Bowl, Arthur's Pass, (S59/055295), LPA, D.A.C., 20-i-62, 20-i-63, CM. Avalanche Creek, Arthur's Pass, (S59/054285), L, D.A.C., 4-i-62, CM. Rough Creek, Arthur's Pass, (S59/045275), LP, D.A.C., 16-xii-62, CM. Snow Creek, Arthur's Pass, (S59/065264), LP, D.A.C., 28-ix-63, CM. Halpin's Creek, Arthur's Pass, (S59/070244), A, L.J.D., 13-iv-62, EDL. Mingha River, (S59/114297), LP, D.A.C., 16-xii-63, CM. Masons Stream, Flock Hill, Craigieburn Mountain Range, 3,800ft., A, P. M. Johns, 21-i-65, CM. Lyndon Stream, Fog Peak, Porter's Pass, (S74/218864), LP, R. S. Bigelow, 13-ii-62; A. G. McFarlane, 25-xi-64, CM. Mount Hutt, 2,500ft., LPA. G. Tunnicliffe and W. P. Thomas, 29-i-64, CM. Kakapo River, Wilberforce River, 2,000-3,800ft., LP, D.A.C., 18-x-63, CM. Kiwi River, Wilberforce River, 2,100ft., L, D.A.C., 19-x-63, CM. Lyell Glacier, Rakaia River, A, P. M. Johns, 25-xi-64, CM. Fox Peak, Two Thumb Mountain Range, 3,000ft., 4,500ft., L, D.A.C., 20-x-63, (6), (7), (9). Black Birch Stream, Mount Cook, 2,500ft., 2,750ft., LP, D.A.C. and V.M.S., 9-i-64, (59 and 59c). Old Homestead Creek, Matukituki River, Lake Wanaka, 1,400ft., LP, D.A.C., 26-x-64, (190); 8-ii-66, CM.

Remarks

Although Dumbleton (1963a) did not collect macropterous *N. campbelli* females, he suspected their existence. Craig (1966) has shown that the percentage of brachypterous pharate female adults has an inverse relationship to water temperature. The female macropterous wing and the male wing are very similar (Fig. 29). The female brachypterous wing (Fig. 30) varies in length from 0.6-2.5mm. The longest brachypterous wing could possibly be used for flight, but in all cases dissection showed that the flight muscles were atrophied. The trichation and development of the veins C and R1 are similar in the macropterous and brachypterous wings but the veins R2+3, R4+5, M1, M4, Cu1 and A1 of the brachypterous wing are poorly developed (Fig. 30).

The head depth width ratio of the macropterous female is greater than that of the brachypterous female; the ocellar turret is rounder, protrudes further and the clypeus is more rounded than those of the brachypterous female. Labial palpi of brachypterous females are variable in length, ranging from just longer than the labrum to shorter than the labrum. The antennal articles of both forms of female are normally distinct but some adults have the distal antennal articles partially or completely fused in an irregular manner (Fig. 27a).

Craig (1963) first reported the occurrence of the nematode *Agamomermis* sp. in *N. campbelli* adults and pupae. Parasitised males exhibit the female number of 12 antennal articles and it is possible that the nematodes castrate the males, though this has not been verified by dissection. Parasitised females show no obvious external morphological effects. Similar effects are produced by individuals of *Agamomermis* sp. parasitising the males of *Culicoides* (Ceratopogonidae) (Callot, 1959).

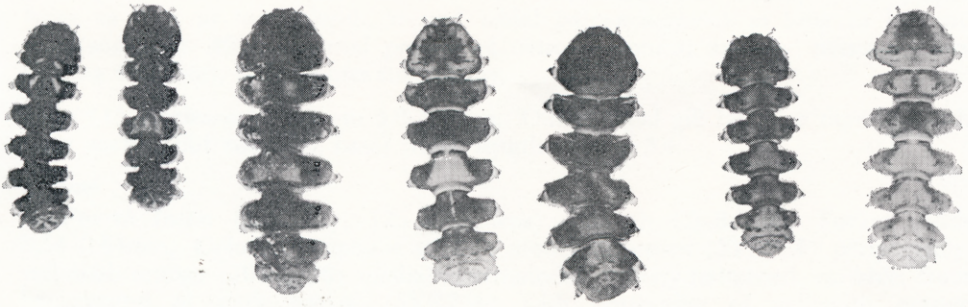
A small sample of larvae similar to the 4th instar larvae of *N. campbelli* was collected from the Matukituki Valley, Lake Wanaka, (26-x-64), in association with *N. hudsoni* larvae. These larvae were completely jet black instead of the normal dusky yellowish brown, with clear scales. The sucker width was larger, 0.59-0.68mm. One 3rd instar larva was in this sample, colour jet black, sucker size, 0.40-0.45mm. A single pharate male adult of *N. campbelli* has since (8-ii-66) been collected from the same location. (Unfortunately the sample of larvae has since been misplaced.)

THE *tonnoiri*-COMPLEX

Though geographically allopatric, *Neocurupira chiltoni* and *N. tonnoiri* are morphologically similar in all stages. All larval instars of *N. tonnoiri* and *N. chiltoni* show similarities in the shape of the angulate prolegs, shape of the posterior margin of the anal division, size of the marginal armature (larger than other species) and colour pattern. However, *N. tonnoiri* does not possess large black spines on the dorsal surface of the 4th instar larva. The adults of both species vary in detail but are similar, particularly in the venation and shape of the anal angle of the wing



a



b

(a) A series of *N. hudsoni* fourth instar larvae showing range in colour pattern. (b) A series of *N. tonnoiri* fourth instar larvae showing range in colour pattern.

(Figs. 41 and 53). The anal angle of members of both species is less pronounced than that of other species of New Zealand blepharocerids. The eggs of both *N. tonnoiri* and *N. chiltoni* are, apart from size, very similar in shape and colouration (Craig, 1967b).

Because the similarities between *N. chiltoni* and *N. tonnoiri* are greater than the similarities between them and the other *Neocurupira* species, it is considered that *N. chiltoni* and *N. tonnoiri* are closely related and form a species complex.

Neocurupira (Neocurupira) tonnoiri Dumbleton

Neocurupira (Paracurupira) tonnoiri Dumbleton, 1963a.

TYPE MATERIAL: EDL and CM. TYPE LOCALITY: Waiho, Westland.

Diagnosis

Male eye ratio 1:2.1, concavity of cercus deep and rounded, no black dorsal spines on 4th instar larva.

Description

Adult

Male (20 specimens). Body length 5.0–7.2mm. *Head*. Head depth width ratio 1:1.3; eye ratio 1:2.1; vertex width 0.25 times head width; antenna of 15 articles; labial palpus twice as long as head depth. *Wing* (Fig. 40). Anal angle of wing approximately 110°, all veins reaching wing margin. *Genitalia* (Fig. 48). Cercus variable, deep rounded median concavity.

Female (four specimens). Body length 4.0–6.0mm. *Head*. Head depth width ratio 1:1.4; eye ratio 1:2.3; vertex width 0.35 times head width; labial palpus twice as long as head depth, second labial palpus segment as long as labrum. *Genitalia* (Fig. 49). Internal process of oviscapt conical apically, oviscapt lobes bearing 4–6 short, black spines subapically.

Pupa (15 specimens). Length 5.0–5.5mm. Outer pupal gill lamellae tapering with apex narrow but rounded, basal width length ratio 1:3.4.

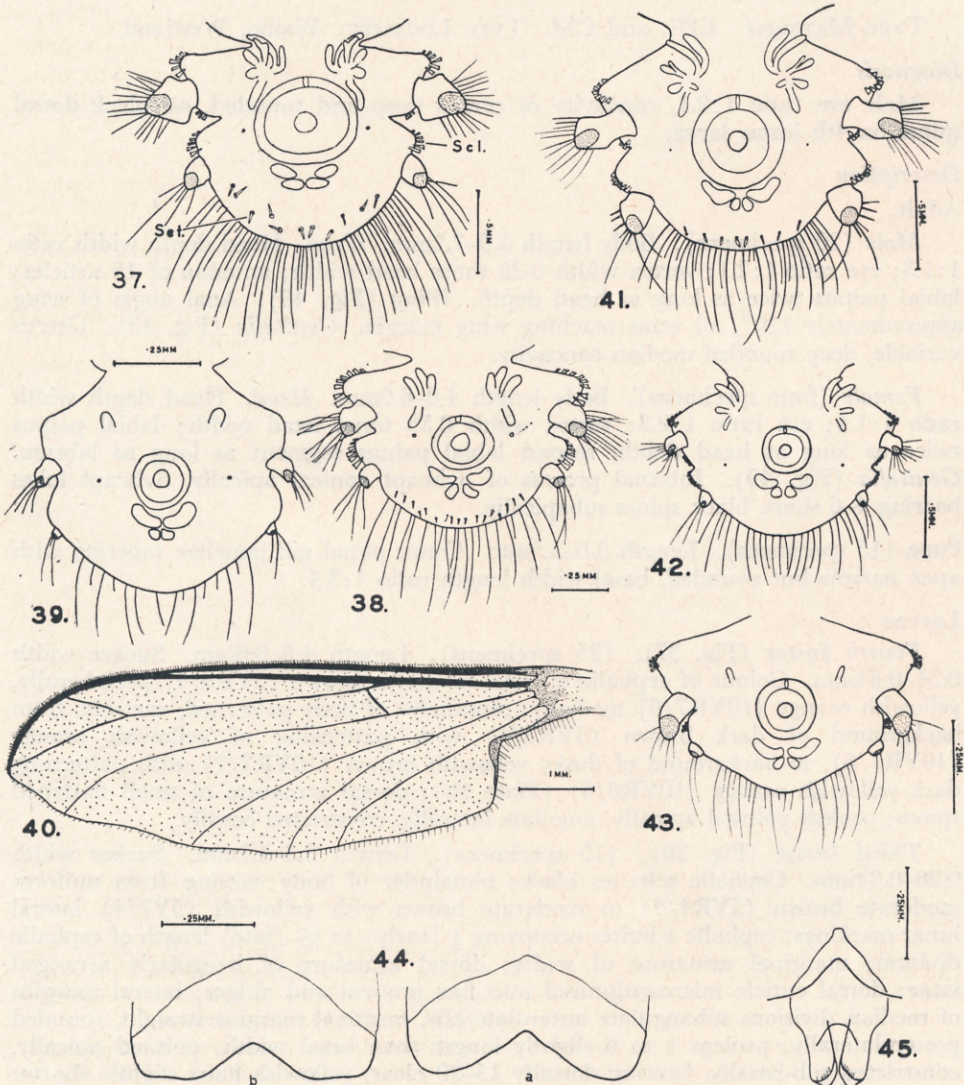
Larvae

Fourth Instar (Fig. 37). (25 specimens). Length 4.5–8.6mm. Sucker width 0.54–0.64mm. Colour of cephalic sclerites moderate brown (5YR3/4) peripherally, yellowish orange (10YR7/6) medially; remainder of body patterned, variable, from background of dark brown (5YR2/4) with patterning of yellowish orange (10YR7/6), to background of dusky yellowish brown (10YR2/2) with patterning dark yellowish orange (10YR6/6) (Plate 1b); dorsal armature of small flattened spines; prolegs pointed apically, angulate laterally, constricted basally.

Third Instar (Fig. 38). (15 specimens). Length 3.3–4.7mm. Sucker width 0.26–0.32mm. Cephalic sclerites black; remainder of body varying from uniform moderate brown (5YR4/4) to moderate brown with yellowish (5Y7/4) lateral lunar markings; cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) length of cephalic division; marginal armature of scales; dorsal armature of irregularly arranged setae; dorsal cuticle microsculptured into fine grooves and ridges; lateral margins of median divisions subangulate anterolaterally, terminal margins straight, rounded posterolaterally; prolegs 1 to 6 slightly longer than basal width, pointed apically, constricted sub-basally, bearing dorsally 15–20 clear, yellowish hairs slightly shorter than the proleg, ventral pad occupying $\frac{1}{3}$ length of proleg; 7th proleg relatively large, slightly longer than basal width, bearing apically 3–5 hairs, two to three times as long as proleg; anal division separated laterally from 5th median division by deep acutely angulate constriction; posterior margin of anal division rounded with 7th proleg indented, bearing 10–14 clear hairs as long as 7th proleg plus hair,

shorter hairs alternating with longer hairs, row of 17–19 short setae ventral and parallel to the posterior margin; eight tracheal gill filaments per division.

Second Instar (Fig. 39). (10 specimens). Length 2.0–2.8mm. Sucker width 0.14–0.18mm. Cephalic sclerites dark brown (5YR2/4); remainder of body varying from uniform moderate brown (5YR3.5/4) to moderate brown with yellowish (5Y7/4) lateral lunar markings; cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) length of cephalic division; marginal armature of 10–12 scales anterolaterally on each median division and 4–5 posterolaterally; dorsal armature of scattered setae; lateral margins of median divisions sharply angular anterolaterally, broadly angular posterolaterally, terminal margin straight; prolegs 1 to 6, $\frac{1}{3}$ longer than basal width,



FIGS. 37–40.—*N. tonnoiri*. Figs. 37–39.—Ventral views of posterior ends of larvae. Fig. 37.—Fourth instar. Fig. 38.—Third instar. Fig. 39.—Second instar. Fig. 40.—Male wing. Figs. 41–45.—*N. chiltoni*. Figs. 41–43.—Ventral views of posterior ends of larvae. Fig. 41.—Fourth instar. Fig. 42.—Third instar. Fig. 43.—Second instar. Fig. 44.—Variation in male cerci. Fig. 45.—Oviscapt of female.

slightly constricted sub-basally, bearing dorsally 4–5 clear hairs slightly shorter than proleg, ventral pad occupies $\frac{1}{4}$ length of proleg; 7th proleg as long as basal width, bearing apically 3–4 hairs, three to four times as long as proleg; anal division separated laterally from 5th median division by shallow subangulate constriction; posterior margin of anal division broadly rounded bearing 7–9 hairs as long as 7th proleg hair, smaller hairs between larger hairs; two tracheal gill filaments per division; posterior anal gill filaments $\frac{1}{3}$ size of anterior gill filaments.

Distribution¹

N. tonnoiri appears to be restricted to the West Coast of the South Island, extending from Takaka, south to the Waiho River and east to the Arthur's Pass region. It occurs at altitudes between 500ft. and 2,500ft. Dumbleton (1963a) stated that it occurred in small cascading streams within bush, however, it has since been collected from deeper, swiftly flowing rivers in the open. It is microsympatric with *Neocurupira hudsoni*, *N. campbelli*, *Nothohoraia micrognathia* and *Peritheates turifer* where the areas of distribution overlap.

Material was examined from the following localities: Upper Aorere Valley, Collingwood, L. A. Baker, ?-i-66, CM. Takaka, A. A. L. Tonnoir, 6-xi-21, EDN. Waikoropupu Springs, Takaka, (S8/171822), LPA, V.M.S., 25-x-63, (10); D.A.C., 28-xii-63, (130). Heaphy Track, Goulund Downs, LPA, A. L. Tonnoir, 7-ii-22, EDN; J. Grieve and M. Cross, 10-i-65, CM. Fair-down Creek, Westport, L. I. D. McLellan, 16-v-65, CM. Shenandoah Saddle, approx. 1,500ft., L. D. R. Cowley, 22-i-64, UA. Ten Mile Creek, Buller River, (S31/627162), LPA, I. D. McLellan, ?-vii-63, 4-iv-64, 2-v-64, CM; V.M.S., 4-iv-64, CM. Moana, A. A. L. Tonnoir, 16-xii-25, CM. Lake Brunner, A. A. L. Tonnoir, 5-ii-22, CM. Tributary of Eel Creek, Lake Brunner, approx. 500ft., anon., 31-i-65, UA. Jack's Hut Stream, Arthur's Pass, L. L.J.D., 28-vii-58, 3-iv-64, EDL. Waiho River, L. A. L. Tonnoir, 9-i-22, CM. Docherty's Creek, Waiho River, L. L.J.D., 11-i-60, EDL.

Neocurupira (Neocurupira) chiltoni (Campbell)

"? *Curupira*", Chilton, 1906.

Curupira chiltoni Campbell, 1921.

Paracurupira chiltoni, Tillyard, 1922; Campbell, 1923.

Neocurupira (Paracurupira) chiltoni, Edwards, 1929; Alexander, 1958; Dumbleton, 1963a.

Institute housing type material unknown. TYPE LOCALITY: Purau Stream, Banks Peninsula, Canterbury.

Diagnosis

Male eye ratio 1:1.0, concavity of cercus wide and shallow, 4th instar larva with black dorsal spines.

¹ Since this paper went to press, L. J. Dumbleton has kindly supplied me with *Neocurupira tonnoiri* pharate male and female pupae and a fourth instar larva, collected from Stoney Creek, Rakiapura Valley, Stewart Island, ?-11-68.

The larva, while definitely *N. tonnoiri*, show similarities to that of *N. chiltoni*. The adult characteristics are also obviously of *N. tonnoiri*, with the exception of the male cercus which is distinctly *chiltoni*-like, and the female oviscapt which has a pair of supernumerary lobes and is therefore unlike any other New Zealand blepharocerid oviscapt.

The presence of *N. tonnoiri* on Stewart Island tends to confirm the Fiordland-Stewart Island refugium postulated by P. M. Johns (pers. comm.) (Fig. 71) as *N. tonnoiri* is found to the north of this refugium at Waiho River, Westland. Although *N. tonnoiri* has not yet been found in Fiordland it is probable that it will eventually be collected from this area.

The *chiltoni*-like characteristics shown by this population of *N. tonnoiri* are very interesting and may after detailed study give further insights into the phylogeny of the *tonnoiri*-complex.

Description

Adult

Male (818 specimens). Body length 5.4–8.8mm. *Head*. Head depth width ratio 1:1.2; eye ratio 1:1.0; vertex width 0.12 times head width; labial palpus twice as long as head depth. *Wing* (Fig. 50). *Genitalia* (Fig. 44). Cercus wide, shallowly concave medianly, rounded laterally, variable.

Female (90 specimens). Body length 4.4–8.4mm. *Head*. Head depth width ratio 1:1.4; eye ratio 1:2.0; vertex width 0.25 times head width; labial palpus less than twice as long as head depth. *Genitalia* (Fig. 45). Internal process of oviscapt constricted subapically, rounded apically; oviscapt lobes bearing 7–9 fine, clear spines subapically.

Pupa (1,011 specimens). Length 4.1–8.2mm. Outer lamellae of pupal gills long, almost parallel-sided, rounded apically, basal width length ratio of outer lamellae 1:3.6.

Larvae

Fourth Instar (Fig. 41). (2,150 specimens). Length 5.1–10.5mm. Sucker width 0.60–0.65mm. Colour normally uniform, varying from dusky brown (5YR2/2) (early), to moderate brown (5YR4/4), or light brown (5YR5/6) (late), occasionally exhibiting patterning of 3rd instar larva; dorsal armature consisting of large black spines; prolegs 1 to 6 pointed apically, angulate laterally, constricted basally.

Third Instar (Fig. 42). (25 specimens). Length 2.6–5.6mm. Sucker width 0.30–0.36mm. Colour of cephalic sclerites dark brown (5YR2/4), remainder of body normally uniform moderate brown (5YR3.5/4) but often with dorsal triangular greyish-orange (10YR7/4) patch on 4th median division and lighter patches of colour lateral to the cephalic sclerites; cephalic sclerites occupying $\frac{3}{5}$ (early) to $\frac{3}{10}$ (late) length of cephalic division; marginal armature of scales; dorsal armature of raised tubercles bearing short, thick spines in the same pattern as large dorsal spines of 4th instar, as well as smaller setae with irregular arrangement; lateral margins of median divisions angulate anterolaterally, rounded posterolaterally, straight between; prolegs 1 to 6 slightly less than twice as long as basal width, constricted sub-basally, angulate apically and laterally, bearing dorsally five hairs as long as ventral pad, plus other finer hairs, ventral pad $\frac{1}{3}$ as long as proleg; 7th proleg slightly indented into posterior margin, longer than basal width, bearing three black hairs three times as long as proleg; constriction separating anal division laterally from 5th median division, sharply angulate posteriorly, sloping gently anteriorly; posterior margin of anal division broadly rounded bearing 18–22 black hairs slightly longer than 7th proleg hairs; eight tracheal gills per division; posterior filaments of anal gills $\frac{1}{3}$ size of anterior filaments.

Second Instar (Fig. 43). (25 specimens). Length 2.0–2.9mm. Sucker width 0.18–0.19mm. Colour of cephalic sclerite darker than that of remainder of body, remainder of body varying from moderate brown (5YR3/4) (early) to moderate yellow brown (10YR5/4) (late); cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) length of cephalic division; ocelli show as reddish structures posterolateral to cephalic sclerites; marginal armature of scales; dorsal armature of small raised tubercles in same pattern as 3rd instar; dorsal cuticle microsculptured into grooves and ridges; lateral margins of median divisions angulate, terminal areas straight; prolegs 1 to 6 twice as long as basal width, rounded apically, slightly constricted laterally, dorsally bearing 2–3 brown hairs as long as ventral pad as well as other finer hairs, ventral pad $\frac{1}{3}$ as long as proleg; 7th proleg as long as basal width, bearing two black hairs three times as long as proleg; anal division separated laterally from 5th median division by deep acutely angulate constriction; posterior margin of anal division very broadly subangulate, bearing 6–10 hairs four times as

long as 7th proleg, plus 12–14 shorter hairs; two tracheal gill filaments per division; posterior filaments of anal gills $\frac{1}{3}$ size of anterior filaments.

First Instar (Figs. 46 and 47). (16 specimens from laboratory hatched eggs). Length 0.8–1.6mm. Sucker width 0.057–0.067mm. Colour uniform, light brownish grey (5YR6/1) (early), to light brown (5YR6/4) (late); cephalic sclerites of body colour, occupying $\frac{1}{2}$ (early) to $\frac{1}{4}$ (late) length of cephalic division; antenna of one article, bearing sensory spines distally; no marginal armature; dorsal armature as

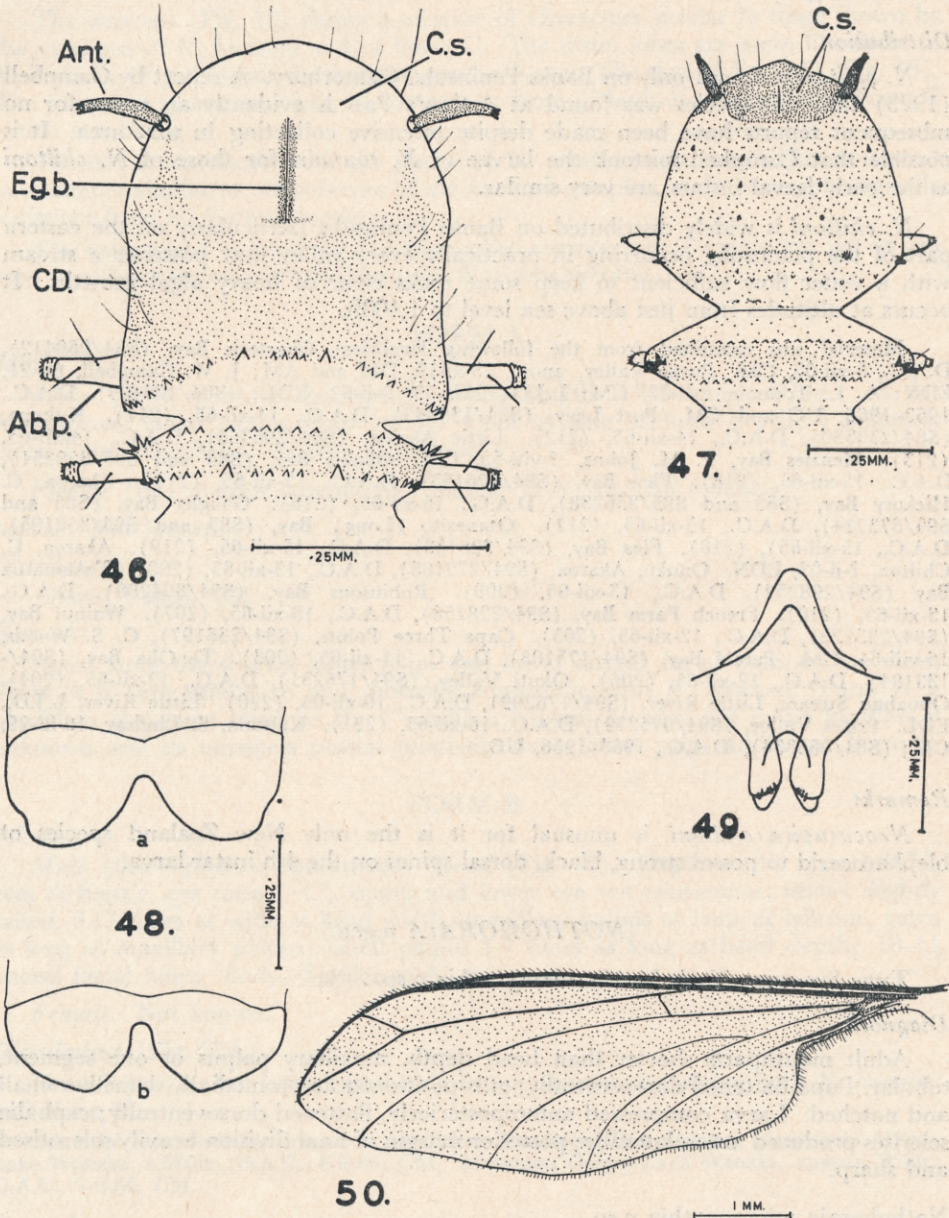


FIG. 46.—Dorsal view of cephalic region of newly hatched *N. chiltoni* first instar larva. FIG. 47.—Ditto of late first instar larva. FIG. 48.—*N. tonnoiri*, variation in male cercus. FIG. 49.—*N. tonnoiri* oviscapt. FIG. 50.—*N. chiltoni* wing of male.

rows of stout, black spines across anterior and posterior surfaces of divisions, larger spines on lateral edges of divisions; lateral margins of median divisions of early larva (Fig. 46) acutely angulate anterolaterally, obtusely angulate posterolaterally, of late larva (Fig. 47) acutely rounded apically; prolegs 1 to 6 conical with extensile tip, bearing dorsally two black hairs; 7th proleg small conical structure, bearing single black hair; anal division separated laterally from 5th median division by subangulate constriction; posterior margin of anal division bare, highly rounded; no tracheal gills.

Distribution

N. chiltoni is found only on Banks Peninsula, Canterbury. A report by Campbell (1923) that this species was found at Arthur's Pass is evidently an error, for no subsequent reports have been made despite intensive collecting in that area. It is possible that Campbell mistook the larvae of *N. tonnoiri* for those of *N. chiltoni* as the early larval instars are very similar.

N. chiltoni is widely distributed on Banks Peninsula, particularly on the eastern part of the peninsula, occurring in practically every valley that possesses a stream with a water flow sufficient to keep some rocks clear of heavy algal growths. It occurs at altitudes from just above sea level to 1,100ft.

Material was examined from the following localities: Charteris Bay, (S84/060412), D.A.C., 5-vii-65, CM. Purau Valley, anon., 23-xi-19, DM and AM; J. W. Campbell, 6-i-21, EDN; A. L. Tonnoir, 2-ii-22, CM; L.J.D., 22-x-59, 9-ii-62, EDL; (S84/105409), D.A.C., 1962-1966, UC and CM. Port Levy, (S84/139365), D.A.C., 14-xii-65, (211). Kukupa, (S84/233330), D.A.C., 14-xii-65, (212). Little Akaloa, (S84/296365), D.A.C., 14-xii-65, (213). Menzies Bay, P. M. Johns, ?-viii-55, CM. Okains Bay, (S85 and S95/329351), D.A.C., 15-xii-65, (218). Flea Bay, (S94/326153), D.A.C., 15-xii-65, (219). Akaroa, C. Hickory Bay, (S85 and S95/356238), D.A.C., 15-xii-65, (216). Goughs Bay, (S85 and S95/373224), D.A.C., 15-xii-65, (217). Otanerito (Long) Bay, (S85 and S95/358195), D.A.C., 15-xii-65, (218). Flea Bay, (S94/326153), D.A.C., 15-xii-65, (219). Akaroa, C. Chilton, ?-ii-03, EDN. Onuku, Akaroa, (S94/272188), D.A.C., 13-xii-65, (208). Takamatua Bay (S94/298252), D.A.C., 13-xii-65, (209). Robinsons Bay, (S94/304280), D.A.C., 13-xii-65, (210). French Farm Bay, (S94/228258), D.A.C., 13-xii-65, (207). Wainui Bay, (S94/225222), D.A.C., 12-xii-65, (205). Cape Three Points, (S94/236197), C. S. Woods, 16-viii-64, CM. Peraki Bay, (S94/175188), D.A.C., 11-xii-65, (203). Te Oka Bay, (S94/133184), D.A.C., 12-xii-65, (206). Okuti Valley, (S94/176251), D.A.C., 12-xii-65, (204). Opuahau Stream, Little River, (S94/176299), D.A.C., 16-xii-65, (220). Little River, L.J.D., EDL. Prices Valley, (S94/075279), D.A.C., 16-xii-65, (221). Kaituna, S. Lindsay, 16-iii-29, CM; (S84/068334), D.A.C., 1963-1966, UC.

Remarks

Neocurupira chiltoni is unusual for it is the only New Zealand species of blepharocerid to possess strong, black, dorsal spines on the 4th instar larva.

NOTHOHORAIA n.gen.

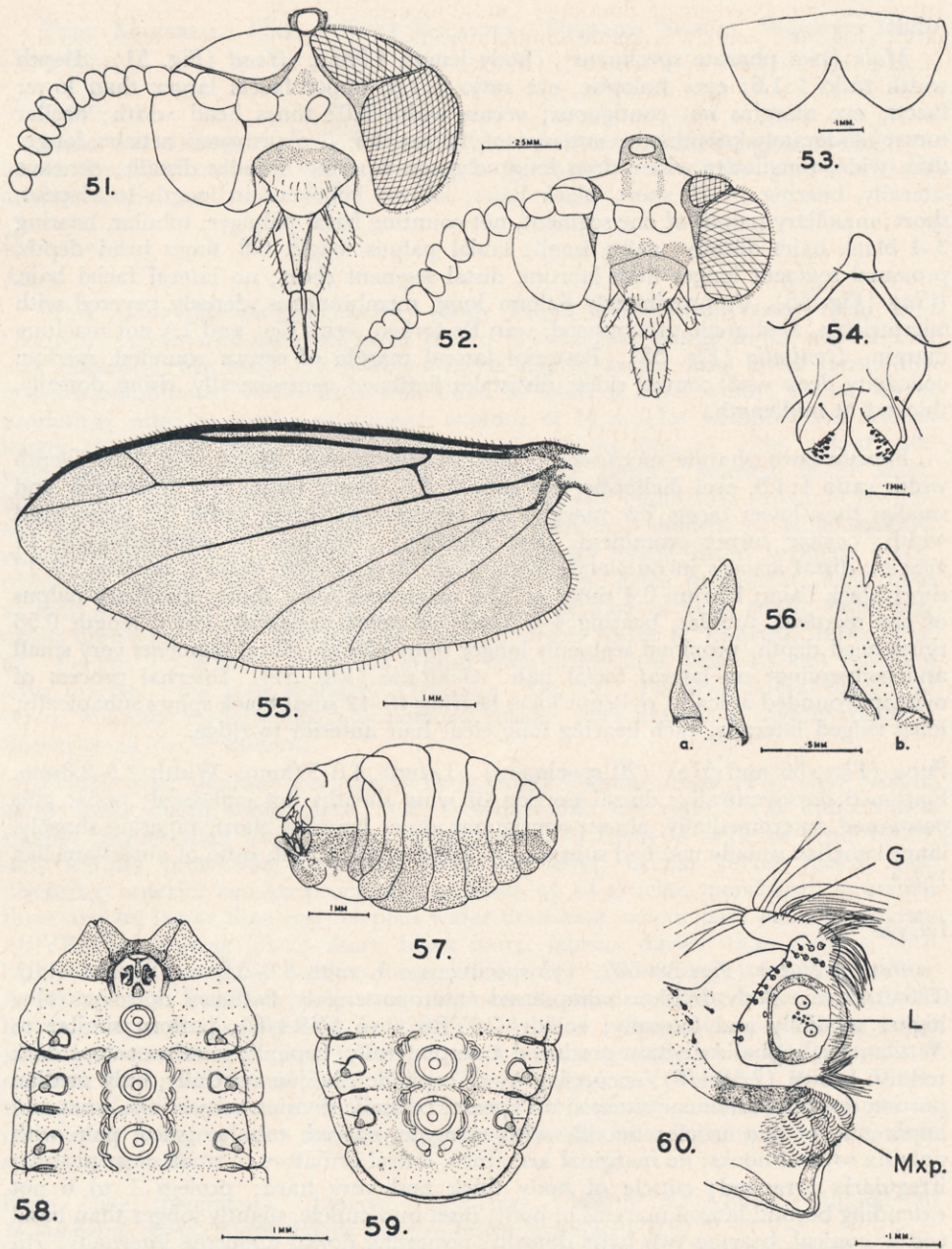
TYPE SPECIES: *Nothohoraia micrognathia* n.sp.

Diagnosis

Adult mouthparts shorter than head depth, maxillary palpus of one segment, tubular. Pupa flattened dorsoventrally; gills positioned anteromedially, lamellae small and notched. Larva compressed anteroposteriorly, flattened dorsoventrally; cephalic sclerites produced anterolaterally; posterior margin of anal division heavily sclerotised and sharp.

Nothohoraia micrognathia n.sp.

TYPE MATERIAL: CM. TYPE LOCALITY: Fuchsia Creek, Lower Buller Gorge, Westport.



FIGS. 51-60.—*Nothohoraia micrognathia* n.sp. Fig. 51.—Frontal view of male head. Fig. 52.—Ditto female. Fig. 53.—Cercus of male. Fig. 54.—Oviscapt of female. Fig. 55.—Male wing. Fig. 56.—Pupal gills; a. anterior lamellae, b. posterior lamellae. Fig. 57.—Dorsal view of pupa. Fig. 58.—Ventral view of anterior and Fig. 59 of posterior end of fourth instar larva. Fig. 60.—Left larval maxilla.

*Description**Adult*

Male (two pharate specimens). Body length 4.9mm. *Head* (Fig. 51). Depth width ratio 1:1.6; eyes holoptic, eye ratio 1:1.6, upper facets larger than lower facets, eye margins not contiguous; vertex width 0.02 times head width; ocellar turret moderately prominent; antenna of 14 articles, two proximal articles longer than wide, remainder wider than long; clypeus tapering broadly distally, concave laterally, bearing 14–20 short, black hairs; labrum subequal in length to clypeus, short; maxillary palpus of one segment, not counting basal palpiger, tubular, bearing 3–4 black hairs distally; galea small; labial palpus length 0.8 times head depth, proximal segment longer than labrum, distal segment short; no lateral facial hair. *Wing* (Fig. 55). Approximately 6.0mm long, membranous, densely covered with microtrichia, anal angle pronounced, vein Rs forked, veins Cu₁ and 1A not reaching margin. *Genitalia* (Fig. 53). Posterior lateral margin of cercus rounded, median concavity deep with convex sides; dististyles flattened ventrobasally, rising dorsally, thickest at midlength.

Female (two pharate specimens). Body length 5.2mm. *Head* (Fig. 52). Depth width ratio 1:1.5, eyes dichoptic, eye ratio 1:2.6, upper facets few in number and smaller than lower facets, eye margins not contiguous; vertex width 0.3 times head width; ocellar turret prominent, base diverging; antenna of approximately 14 articles, distal articles incompletely annulated; clypeus cone shaped, bearing 10–12 short black hairs; labrum 0.4 times as long as clypeus, very short; maxillary palpus of one segment, tubular, bearing 4–6 hairs; no galea apparent; labial length 0.56 times head depth, proximal segments longer than labrum, distal segments very small and converging; no lateral facial hair. *Genitalia* (Fig. 54). Internal process of oviscapt rounded apically, oviscapt lobes bearing 10–12 stout black spines subapically, lobes ridged laterally, each bearing long clear hair anterior to ridge.

Pupa (Figs. 56 and 57). (20 specimens). Length 4.0–5.0mm. Width 2.5–2.8mm. Flattened dorsoventrally; dorsal portion of wing sheaths not embossed; pupal gills positioned anteromedially, almost contiguous, outer lamellæ short, tapering sharply, inner lamellæ usually notched subapically; basal width length ratio of outer lamellæ 1:2.2.

Larvae

Fourth Instar (Figs 58–60). (15 specimens). Length 3.0–5.0mm. Sucker width 0.36–0.45mm. Body divisions compressed anteroposteriorly, flattened dorsoventrally, higher medially and laterally; colour (10YR8/6 to 5YR4/6), pattern similar to *N. tonnoiri*; cephalic division produced anterolaterally; cephalic sclerites colour dark reddish brown (7.5R4/6), occupying $\frac{1}{3}$ of cephalic division ventrally, only median portion dorsally; antennae situated on apex of cephalic division projections, inset and apparently of one article; maxilla with elongate, curved, tubular galea, palp with only six rows of hooks; no marginal armature; dorsal armature of small clear pustules irregularly arranged; cuticle of body thick and very hard; prolegs 1 to 6 not extending beyond lateral margins of body, inset into cuticle, slightly longer than basal width, conical, bearing two hairs dorsally, possessing dorsal apodeme internally; 7th proleg represented by two small hairs; posterior margin of anal division heavily sclerotised, sharply defined, not bearing hairs; 10 tracheal gill filaments per body division, curved at midlength; anal gills small.

Third Instar (four specimens). Length 2.0–2.7mm. Sucker width 0.20–0.25mm. Colour dark yellowish red (2.5YR3/8), cephalic sclerites reddish brown (10R2/1); six tracheal gills per body division; body shape and other characters similar to 4th instar larva.

Second Instar (one specimen). Length 1.9mm. Sucker width 0.15mm. Body very flattened; colour dark reddish brown (10R3/4), cephalic sclerites (10R2/1); median divisions sloping laterally, margins sharply defined and crenulate; anterior projections of cephalic division not pronounced; two long curved tracheal gill filaments per body division; otherwise similar to the 3rd and 4th instar larvae.

Egg. Length 0.58mm, bluntly rounded.

Distribution

Nothohoraia micrognathia is known only from a single locality on the West Coast, where it is microsypatric with *Neocurupira hudsoni* and *N. tonnoiri*.

Type locality: Fuchsia Creek, Lower Buller Gorge, Westport, (S31/167628), approx. 800ft., LP, I. D. McLellan, 18-vi-65, 23-xii-65, 11-vi-66, 2-vii-66, CM.

Remarks

The taxonomic position of *Nothohoraia* is difficult to determine. The pharate adults are similar to *Neocurupira campbelli* in wing shape, venation and trichation, and in short labial palpi with long pupal sheaths. However, the peculiar tubular maxillary palpi are more similar to those of *Horaia* Tonnoir, a Himalayan genus, and to those of *Apistomyia*. How much importance can be attached to the similarities of the wings and mouthparts of *Nothohoraia micrognathia* and *Neocurupira campbelli* is not known, for similar wing structure and mouthparts have arisen independently within the subfamilies of the Blepharoceridae. Indeed wings and mouthparts of *N. micrognathia* appear similar to those of Chilean *Paltostoma* species (Edwards, 1929).

Male and female genitalia of *Nothohoraia* do not indicate a close relationship with *Neocurupira campbelli* or with any other New Zealand blepharocerid. The flattened pupa of *Nothohoraia* with its notched inner gill lamellae is also unlike that of any known New Zealand blepharocerid. However, similar pupae have arisen a number of times within the Blepharoceridae (e.g., *Apistomyia*, *Blepharocera* and *Elporia*—personal material) and therefore this type of pupa cannot be used to indicate relationships.

The remarkably specialised larvae of *Nothohoraia* are unlike those of any other known blepharocerid genus with the exception of *Horaia*. The cephalic projections present on third and fourth instar larvae of *Nothohoraia* are probably unique in the Blepharoceridae but may be homologous with the erect, black horn-like spines just behind the cephalic sclerites of *Horaia* larva R1 (Tonnoir, 1930b). The number of maxillary palp hooks (Fig. 60) is very much reduced when compared with those of other blepharocerid larvae (Craig, 1967a)¹. Both *Nothohoraia* and *Horaia* larvae are compressed anteroposteriorly and show little division of the body. In addition they both possess much thicker and harder cuticle than normal, prolegs inserted into the body via a socket and manipulated by a well-developed apodeme, 7th prolegs represented by two small hairs, a heavily sclerotised posterior margin of the anal division which is sharp ventrally and tracheal gills which tend to curve posteriorly. The similarities although well defined between later instars are very striking between the second instar larva of *Nothohoraia* and later larval instars of *Horaia*. The fourth and third instars of *Nothohoraia* are more specialised than *Horaia* as the abdominal prolegs do not project laterally and the normal convex dorsal shape has become more angular. It is considered that the similarities that exist between these two genera indicate a close relationship. The similarities then between adults of *Nothohoraia* and *N. campbelli* are the result of convergent evolution. Like-wise the similarities between the pupae of *Nothohoraia*, *Apistomyia*, *Blepharocera* and *Elporia* are due to convergence. Although larval morphology

¹ Anthon and Lyneborg have presented a more reasonable interpretation of the blepharocerid larval maxilla in *Spolia. zool. Mus. haun.* 27: 1-57, 1968.

indicates a close relationship to *Horaia*, the current classification of Blepharoceridae is based on adult characters and this would place *Nothohoraia* in *Neocurupira*.

The larvae of *Nothohoraia* show relationships to *Horaia*, the pupae to a number of blepharocerid genera and the adults to those of *Neocurupira*, therefore a new genus was required. As the larval characters of this new genus give a better indication of relationships to other genera than do adult characters, the generic name *Nothohoraia*, is based on the larva. The specific name *micrognathia* refers to the main diagnostic character of the adult, the short mouth parts.

PERITHEATES Lamb, 1912

Peritheates Lamb, 1912.

TYPE SPECIES: *P. turriifer* Lamb.

Diagnosis

Wing vein Rs unforked, ending on wing apex; larva with marginal armature of stout spines.

Description

Adult

Eye divided, male dichoptic; antenna of 12 articles; maxillary palpus short, one-segmented; wing vein Rs unforked, ending on wing apex; male dististyle long and slender. *Pupa*. Gills positioned anterolaterally, lamellae three times as long as wide.

Larvae. Marginal armature of short spines; prolegs bearing spines and hairs.

Remarks

Tillyard (1922a) and Dumbleton (1963a) recognised three species of *Peritheates*; *P. turriifer*, *P. intermedius* and *P. harrisi*. *P. harrisi* is distinctly larger than the first two. Tillyard separated *P. turriifer* and *P. intermedius* on the basis of the ocellar turret shape, the male genitalia and the colour of the abdominal segments, but Tillyard's figures of the male genitalia show differences that are dependent on the angle of observation, a fact also mentioned by Dumbleton (1963a).

The larvae are practically indistinguishable, though Dumbleton (1963a) did attempt to show specific differences. Adults of *P. intermedius* collected from the type locality (Brooks Stream Reservoir, Nelson), are not identifiable with any certainty, as the basal constriction of the ocellar turret is not as pronounced as indicated by Tillyard (1922a). Adult *Peritheates* collected from the Whangamoia River, Nelson, are equally referable to either *P. intermedius* or *P. turriifer* if Tillyard's keys are used.

The very close similarity of *P. intermedius* to *P. turriifer* in all stages has been mentioned by Dumbleton (1963a), who suggested that these two species may be identical. He has since (pers. comm.) indicated that he now considers the forms to be conspecific. I agree, and *P. intermedius* is placed in synonymy with *P. turriifer*.

Peritheates turriifer Lamb

Peritheates turriifer Lamb, 1912; Campbell, 1921; Tillyard, 1922; Dumbleton, 1963a.

Peritheates intermedius Tillyard, 1922; Tonnoir, 1930b; Dumbleton, 1963a.
New Synonymy.

TYPE MATERIAL: CMB. TYPE LOCALITY: Warnock's Creek, Otira, Westland.

Diagnosis

Smaller in size than *P. harrisi*, wing length approximately 6mm; ocellar turret prominent; larval posterior margin of anal division angular and bearing only two long hairs.

Description

Adult

Male (57 specimens). Body length 4.2–4.7mm. *Head*. Head depth width ratio 1:1.2; eye ratio 1:1.5; vertex width 0.23 times head width; antenna of 12 articles; labial palpus less than three times as long as head depth, first labial palpus segment as long as labrum. *Wing* (Fig. 64). *Genitalia* (Fig. 65b and c). Cercus variable, rounded median concavity, slight lateral indentation.

Female (37 specimens). Body length 4.0–5.2mm. *Head*. Head depth width ratio 1:1.2; eye ratio 1:1.9; vertex width 0.33 times head width; antenna of 12 articles; labial palpus only slightly longer than head depth, first labial palpus segment shorter than labrum. *Genitalia* (Fig. 67a and b). Oviscapt variable, internal process of oviscapt conical and rounded apically, oviscapt lobes bearing 8–12 black spines subapically.

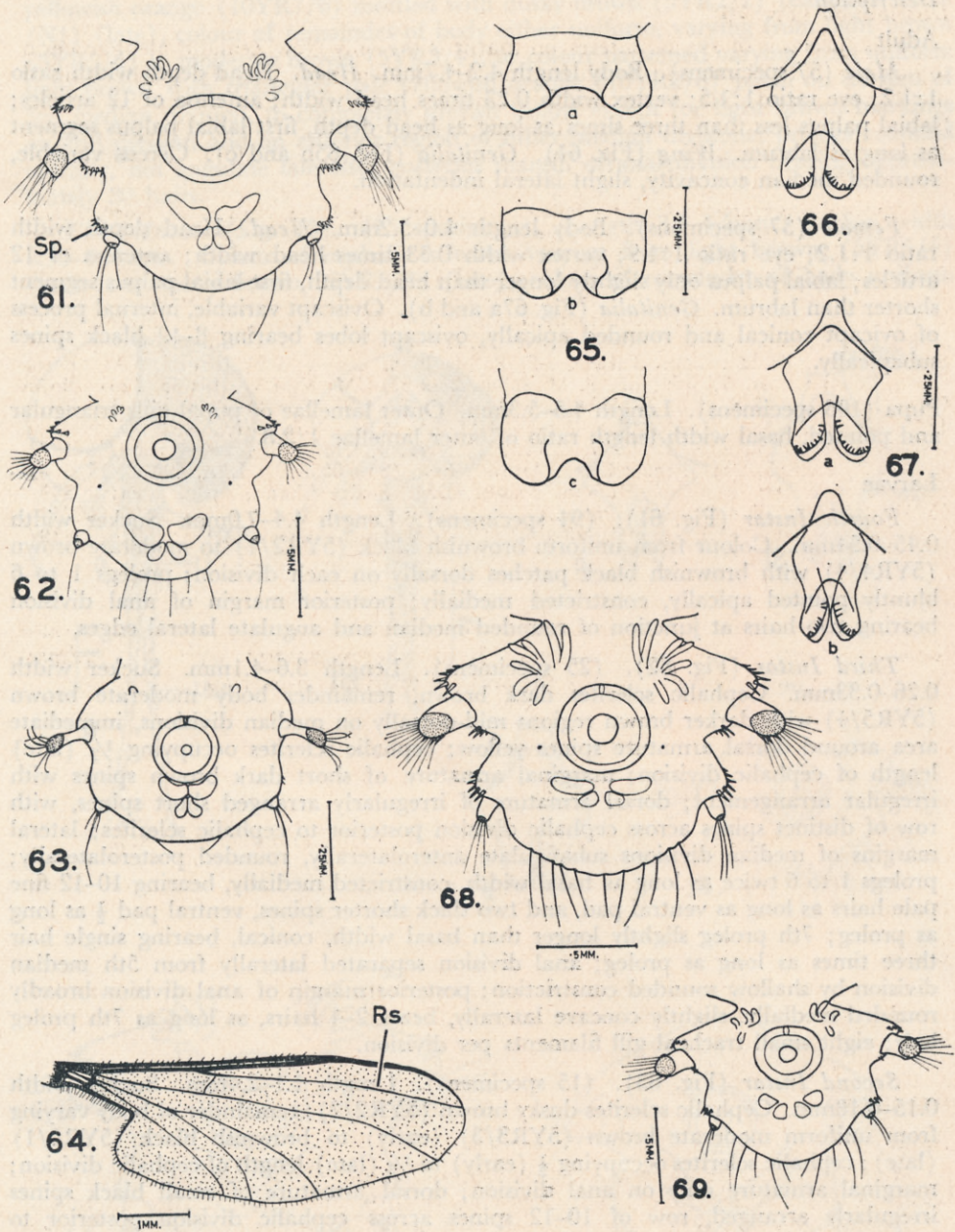
Pupa (103 specimens). Length 4.5–5.3mm. Outer lamellae of pupal gills triangular and pointed, basal width length ratio of outer lamellae 1:2.8.

Larvae

Fourth Instar (Fig. 61). (94 specimens). Length 4.4–7.0mm. Sucker width 0.45–0.54mm. Colour from uniform brownish black (5YR2/1) to moderate brown (5YR4/4) with brownish black patches dorsally on each division; prolegs 1 to 6 bluntly pointed apically, constricted medially; posterior margin of anal division bearing two hairs at junction of rounded median and angulate lateral edges.

Third Instar (Fig. 62). (25 specimens). Length 3.6–4.1mm. Sucker width 0.26–0.33mm. Cephalic sclerites dark brown, remainder body moderate brown (5YR5/4) with darker brown regions mid-dorsally on median divisions, immediate area around dorsal armature spines yellow; cephalic sclerites occupying $\frac{1}{3}$ (late) length of cephalic division; marginal armature of short dark brown spines with irregular arrangement; dorsal armature of irregularly arranged short spines, with row of distinct spines across cephalic division posterior to cephalic sclerites; lateral margins of median divisions subangulate anterolaterally, rounded posterolaterally; prolegs 1 to 6 twice as long as basal width, constricted medially, bearing 10–12 fine pale hairs as long as ventral pad, and two thick shorter spines, ventral pad $\frac{1}{2}$ as long as proleg; 7th proleg slightly longer than basal width, conical, bearing single hair three times as long as proleg; anal division separated laterally from 5th median division by shallow rounded constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally, bears 2–4 hairs, as long as 7th proleg hair; eight small tracheal gill filaments per division.

Second Instar (Fig. 63). (15 specimens). Length 1.1–2.4mm. Sucker width 0.15–0.18mm. Cephalic sclerites dusky brown (5YR2/2); remainder of body varying from uniform moderate brown (5YR3/3) (early) to brownish black (5YR2/1) (late); cephalic sclerites occupying $\frac{1}{2}$ (early) to $\frac{1}{3}$ (late) length of cephalic division; marginal armature only on anal division; dorsal armature of small black spines irregularly arranged, row of 10–12 spines across cephalic division posterior to cephalic sclerites, irregular rows of 12–13 spines on median divisions; lateral margins of median divisions non-angulate, rounded apically; prolegs 1 to 6 twice to three times as long as basal width, bearing dorsally 7–9 fine clear hairs as long as ventral pad, also 1–3 short stout spines, ventral pad $\frac{1}{3}$ as long as proleg; 7th proleg as long as wide, bearing a single hair 6–8 times as long as proleg, plus two shorter hairs; anal division separated laterally from 5th median division by very shallow rounded constriction; posterior margin of anal division slightly rounded medially, flat to very slightly rounded laterally, bearing two short hairs at junction of lateral and medial edges; two tracheal gill filaments per division.



Figs. 61-63.—Ventral views of posterior ends of *P. turriker* larvae. Fig. 61.—Fourth instar. Fig. 62.—Third instar. Fig. 63.—Second instar. Fig. 64.—*P. turriker*, wing of male. Fig. 65a.—Cercus of *P. harrisi* male. Figs. 65b and c.—Variation in the cercus of *P. turriker* males. Fig. 66.—Oviscapt of *P. harrisi* female. Fig. 67.—Variation in the oviscapt of *P. turriker* females. Fig. 68.—Ventral view of posterior end of *P. harrisi* fourth instar larva. Fig. 69.—Ditto of *P. harrisi* third instar larva.

Distribution (Fig. 70)

This species is of special interest in that it is the only New Zealand blepharocerid to occur in both North and South Islands. It is known from only the southern tip of the North Island, but in the South Island has been collected extensively in the Nelson and Arthur's Pass regions. The distribution of *P. turriker* in the area between Nelson and Arthur's Pass is poorly known. It has an altitudinal distribution of between 200ft. and 3,500ft.

Material was examined from the following localities: The Forks, Hutt River, North Island, A. A. Philpott, ?-i-21, EDN; J. Muggeridge, 16-ii-21, EDN. Whangamoia River, Nelson, (S14/798367), A, D.A.C., 31-xii-62, 1-i-65, CM. Nelson, A, A. Philpott, 10-xii-20, EDN. Coads Creek, Dun Mountain, (S20/687205), LPA, A. Philpott, 21-i-22, 28-x-22, 22-xi-22, 28-xii-22, EDN; D.A.C., 2-xii-61, 29-i-62, 29-xii-62, CM. Maitai River, Nelson, L, L.J.D., 23-i-50, EDL. Brook's Stream Reservoir, Nelson, (S20/638237), LPA, R. J. Tillyard, 2-i-22, EDN; D.A.C., 30-xii-64, CM. Cobb River, Takaka, 2,500ft., L, S. G. Moore, 4-iv-65, CM. Suicide Creek, Boulder Lake, Takaka, LP, P. M. Johns and V.M.S., 28-x-63, CM. Portia Creek, Boulder Lake, 3,500ft., LP, P. M. Johns, 28-x-63, CM; V.M.S., 28-x-63, (28). Boyds Creek, Kaikoura, (S49/890988), LPA, D.A.C., 29-viii-62, CM. Ten Mile Creek, Buller River, (S31/162628), LA, I. D. McLellan, 2-iv-64, CM. Warnock's Nob, Otira, A, G. V. Hudson, 5-xii-08, DM. Otira, A, A. L. Tonnoir, 9-ii-22; T. Harris, DM. Otira Valley (S59/050377), A, D.A.C., 23-ii-63, CM. Pegleg Creek, Arthur's Pass, (S59/055340), LPA, D.A.C., 15-xii-62, CM. Arthur's Pass, A, G. V. Hudson, ?-xii-22, DM. Bealey Chasm, Arthur's Pass, (S59/050313), 2,750ft., D.A.C., 1962-1965, UC. Jack's Hut Stream, Arthur's Pass, (S59/053311), L, L.J.D., 13-iv-62, EDL; D.A.C., 20-xi-63, CM. Avalanche Creek, Arthur's Pass, (S59/054285), L, D.A.C., 4-i-62, CM.

Remarks

P. turriker occurs mainly in small torrential bush-covered streams but is also found in larger, open, stable rivers. It is microsympatric with *N. hudsoni*, *N. campbelli* and *N. tonnoiri* where the areas of distribution overlap.

Peritheates harrisi (Campbell)

Apistomyia harrisi Campbell, 1921.

Peritheates harrisi, Tillyard, 1922; Campbell, 1923; Dumbleton, 1963a.

Institute housing type material unknown. TYPE LOCALITY: Ohakune, North Island.

Diagnosis

Larger than *P. turriker*, wing approximately 8mm long; ocellar turret rounded; larval posterior margin of anal division crenulate and bearing more than two long hairs.

Description

Adult

Male (two pharate specimens). Body length 4.8 and 5.5mm. *Head*. Head depth width ratio 1:2.0; eye ratio 1:1.7; vertex width 0.19 times head width; antenna of 12 articles; labrum longer than first segment of labial palpus; labial palpus three times as long as head depth. *Genitalia* (Fig. 65a). Cercus wide, very shallow median concavity.

Female (five pharate specimens). Body length 5.5-6.0mm. *Head*. Head depth width ratio 1:2.2; eye ratio 1:2.0; antenna of 12 articles; labial palpus twice as long as head depth, second segment shorter than labrum. *Genitalia* (Fig. 66). Internal process of oviscapt concave apically, oviscapt lobes bearing 8-10 clear spines subapically.

Pupa (seven specimens). Length 4.9-6.0mm. Outer lamellae of gill longer than *P. turriker*, more rounded apically, basal width length ratio 1:3.1.

Larvae

Fourth Instar (Fig. 68). (12 specimens). Length 4.3–8.1mm. Sucker width 0.47–0.54mm. Cephalic sclerites black, remainder of body uniformly yellowish brown (10YR3/2); posterior margin of anal division bearing 9–10 hairs, inset at bases.

Third Instar (Fig. 69). (One specimen only). Length 4.0mm. Sucker width 0.35mm. Cephalic sclerites black, remainder of body moderate brown (5YR4/4) with dorsal median moderate brown (5YR3/4) patches; cephalic sclerites occupying $\frac{1}{3}$ length of cephalic division; marginal armature of short sharp clear spines; dorsal armature of short sharp black spines irregularly arranged laterally, also as irregular rows across anterior and posterior of median divisions; lateral margins of median divisions subangulate anterolaterally, less angulate posterolaterally; prolegs 1 to 6 longer than basal width, rounded apically, constricted medially, bearing dorsally 2–3 spines plus numerous fine pale hairs longer than ventral pad, ventral pad $\frac{1}{2}$ as long as proleg; 7th proleg as long as basal width, bearing 3–5 hairs $1\frac{1}{2}$ times as long as proleg; anal division separated laterally from 5th median division by shallow subangulate constriction; posterior margin of anal division broadly rounded medially, slightly concave laterally, bearing 4–5 irregularly placed larger hairs and 5–6 smaller hairs medially; eight tracheal gill filaments per division; anal gill filaments small.

Second Instar. No material available.

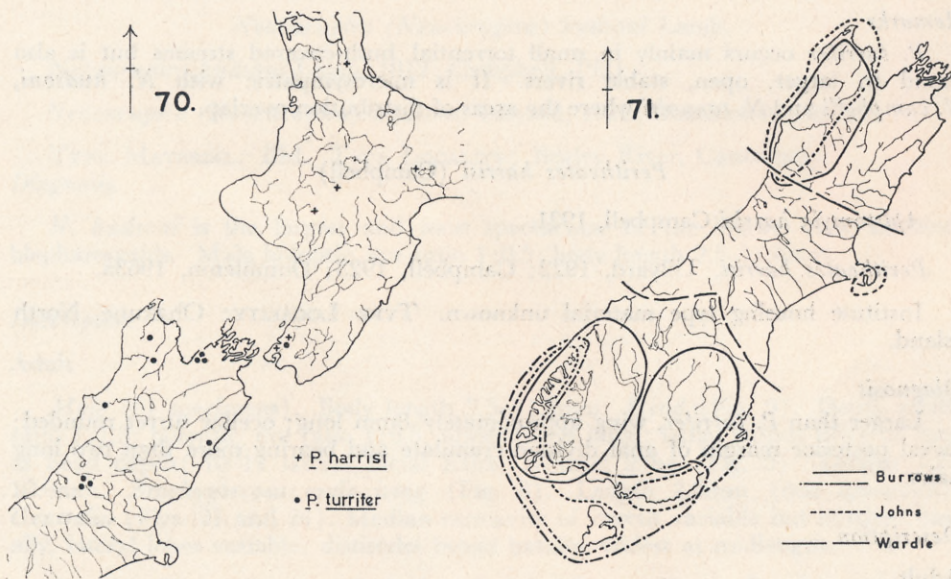


FIG. 70.—Map of portion of New Zealand showing localities of *P. harrisi* and *P. turriifer*.
FIG. 71.—Refugia as suggested by Wardle (1963), Burrows (1965) and P. M. Johns (pers. comm.) which may be applicable to the distribution of New Zealand blepharocerids.

Distribution (Fig. 70)

This species is known at present only from the North Island and collections indicate that it could be widely spread throughout the mountainous areas. Little is known about the habitat of this species; Dumbleton (1963a) stated that it occurs in bush-covered streams. It has an altitudinal distribution of between 500ft. and 2,250ft.

Material was examined from the following localities: Te Aroha, A, anon., 1-iii-23, CM. Waiorongomai Stream, Te Aroha, L, P. M. Johns, 14-i-64, CM. Makau Stream, Lake Waikare Moana, 2,220ft., LP, M. Winterbourne, 28-iii-64, CM; J. McLean, 31-iii-64, UA. Whaka-

puparui Stream, Chateau Tongariro, L, M. Winterbourne, ?-v-64CM. Waipuna Stream, National Park, L, D. R. Cowley, 23-ii-65, UA. Ohakune, LA, A. L. Tonnoir, 8-iii-23, CM; L.J.D., 13-x-60, EDL. Akatarawa River, L, L.J.D., 11-x-60, EDL. Mathew Stream, Wellington, LP, S. G. Moore, ?-vi-65, CM.

LARVAL TERATOLOGY

Larvae of New Zealand species of blepharocerids are very uniform in their morphology throughout their area ranges. This may be the result of serious defects or mutations being removed from the population by the rigorous habitat occupied by the larvae.

Larvae collected from frequently flooded streams often show scar-marks on the dorsal surface. These are probably the result of stone damage. The scars are quite distinct from the following abnormalities:

Neocurupira campbelli

Fourth Instars

- (a) Loss of $\frac{2}{3}$ of right side of both 5th median and anal divisions (two examples).
- (b) Posterior margin of anal division shallowly concave medially; black posterior hairs absent (one example).

Neocurupira chiltoni

Fourth Instars

- (a) Posterior margin of anal division notched medially; strong posterior hairs absent from notched area (one example).
- (b) Loss of $\frac{2}{3}$ of right side of both 5th median and anal divisions (one example).

Neocurupira hudsoni

Fourth Instar

- (a) Complete loss of right 7th proleg; only one posterior anal gill filament, the latter being placed medially (three examples).

Second Instar

- (a) Complete loss of left 7th proleg (three examples).

Peritheates turriifer

Third Instar

- (a) Left 7th proleg displaced anteriorly to constriction between 5th median and anal divisions, proleg protruding at right angles to body axis, similar in shape to first instar proleg (one example).

These abnormalities could be predator damage but because of their similarities it is considered that they are of a genetic nature and that they may indicate how the Edwardsiniinae and *Apistomyia* larvae evolved reduced anal divisions.

PHYLOGENY OF THE INDO-AUSTRALASIAN APISTOMYIINAE

From a study of the morphology of the family, Tillyard (1922b) considered that the Blepharoceridae arose in Jurassic times. Alexander (1958 and 1963), despite a lack of fossil evidence, on the basis of the virtual world-wide distribution of the Blepharoceridae, suggested that the family originated during the mid-Mesozoic or even earlier during the Permian.

Tillyard (1922b), Tonnoir (1923c), Kitakami (1950) and Alexander (1958 and 1963) considered that the primitive Edwardsiniinae were ancestral to the

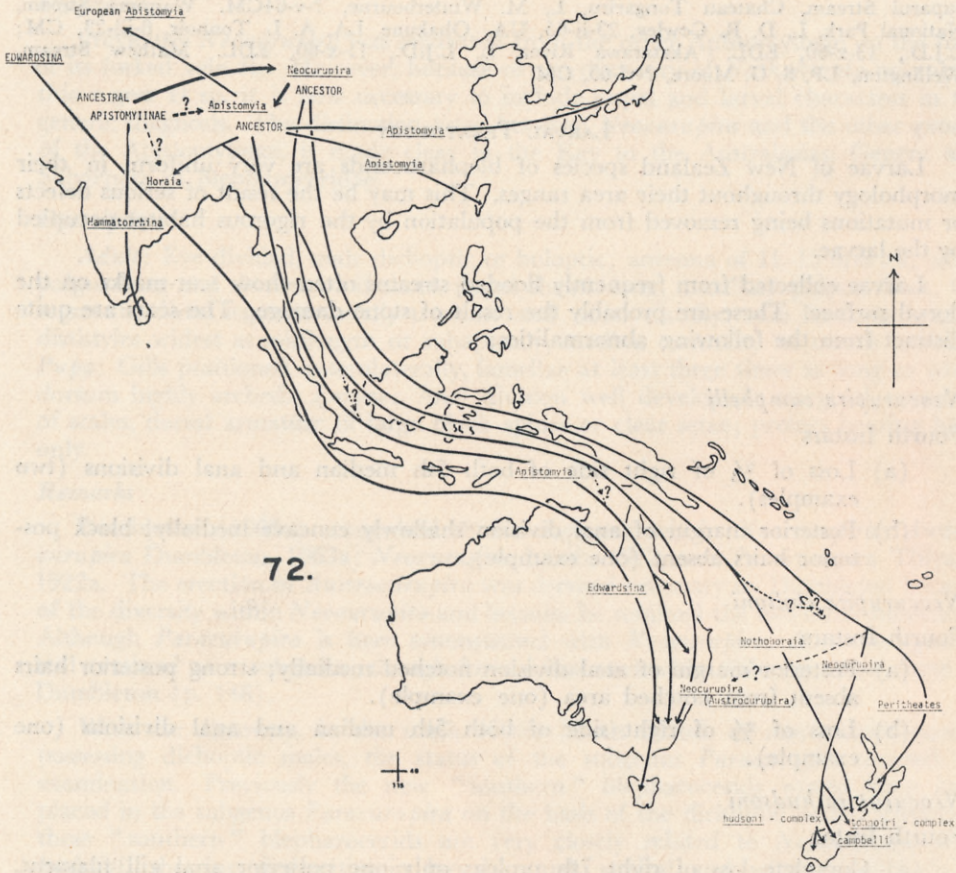


FIG. 72.—The probable phylogenies and dispersal routes of the Apistomyiinae. Broken lines and query marks indicate uncertain relationships.

remainder of the Blepharoceridae. However, Edwards (1929) believed that it was unwarranted to assume an ancestral nature for *Edwardsina* and more recently Stuckenberg (1958) after examining the affinities of *Edwardsina* and *Paulianina* with other Blepharoceridae came to the same conclusion. However, even if the Edwardsiniinae were not ancestral, phylogenies of Blepharoceridae are usually based on *Edwardsina*-like ancestors.

The major evolutionary trends in the blepharocerid adults appear to have been reduction of venation, development of divided eyes, loss of mandibles and reduction of the other mouthparts. These trends have taken place independently within the subfamilies of blepharocerids, resulting at times in considerable convergence. Within the Apistomyiinae the extent of reduction in venation is one of the main characteristics separating the genera. The most primitive venation is in *Neocurupira hudsoni* and *Neocurupira tonnoiri* where vein Rs is forked and all veins reach the wing margin (Figs. 5 and 40). Other *Neocurupira* species show some reduction in venation. *Neocurupira chiltoni*, and *N. rotalapisculus* of the *hudsoni*-complex do not have vein 1A reaching the margin and *N. campbelli* has neither vein 1A nor Cu1 reaching the margin. The simple vein Rs of *Peritheates* probably came from a neocurupirid vein Rs by loss of vein R2+3. That this was the pathway of reduction is suggested by the very weak vein R2+3 found now on some specimens of *Neocurupira hudsoni*. The presence of a spur vein R2+3 on vein Rs in some specimens of

Horaia montana (Tonnoir, 1930b) suggests a similar pathway of reduction for this genus. *Horaia* as well shows great reduction in vein 1A. The simple but curved vein Rs of *Apistomyia* probably came from the forked vein Rs by loss of vein R4+5. However, there is no direct evidence to indicate that this in fact was the pathway of reduction. Greatest reduction in venation has occurred in *Hammatorrhina* where vein Rs is not present. Unfortunately little is known about *Hammatorrhina* and there is no evidence to indicate the pathway of reduction.

As the Edwardsiniinae possess large undivided eyes, other blepharocerids with divided eyes are considered to be more recently evolved. Stuckenberg (1955) showed that modification of the eyes in *Elporia* may have taken a number of pathways to result in convergence. As the majority of male apistomyid blepharocerids are holoptic, it is believed here that this represents the primitive apistomyid eye condition. Only *Peritheates*, *Nothohoraia* and the *Neocurupira* species (with one exception, *N. hudsoni*), have dichoptic males. The evolution of dichoptic males in *Neocurupira* (*Neocurupira*) appears to have taken place three times; *N. campbelli*, the *tonnoiri*-complex, and *N. rotalapisculus* and Form C of the *hudsoni*-complex; a situation comparable to that in *Elporia*. Downes (1969) has suggested a sexual role for the divided eye in Simuliidae. This may have some influence on eye evolution, but insufficient is known about the sexual habits of blepharocerids to suggest a similar reason for the evolution of divided eyes or why holoptery appears to have given rise to dichoptery.

The Apistomyiinae are separated from the other blepharocerid subfamilies mainly on the basis of the long diverging labial palpi and form a relatively distinct group. However, in 1963(a) Dumbleton described *Neocurupira campbelli* which has short labial palpi (a subfamilial characteristic of the Paltostominae), and in this work *Nothohoraia micrognathia*, also with short labial palpi, is described. Both these blepharocerids have, however, long pupal sheaths on the short labial palpi as well as having other apistomyid characteristics. Dumbleton considered that the short labial palpi of *Neocurupira campbelli* were the result of a recent single mutation, and until the pupal labial sheaths of the Paltostominae are examined in detail, Dumbleton's explanation remains the best both for *Neocurupira campbelli* and for *Nothohoraia micrognathia*.

Stuckenberg (*in litt.* 1967) has mentioned that in New Caledonia, there is in addition to neocurupirid blepharocerids, a blepharocerid with vestigial mouth parts and a straight vein Rs. He states that this form with vestigial mouth parts is obviously related to the neocurupirids. It would be interesting, when all stages have finally been described, to speculate on the relationships of this new blepharocerid with *Nothohoraia micrognathia* and *Neocurupira campbelli*.

Although blepharocerid pupal shape is very conservative, the gills show considerable variation. Surprisingly, the gills of Edwardsiniinae pupae are the most complex (Tonnoir, 1924, and Stuckenberg, 1958); the more primitive gills of four lamellae are found on the pupae of the other subfamilies. Within the Apistomyiinae the pupal gills are of two forms. Those of *Horaia*, *Neocurupira* and *Peritheates* with the lamellae long and placed anterolaterally, and those of *Apistomyia* and *Nothohoraia* with the lamellae short, notched and placed anteromedially. Unfortunately both types of gills have arisen independently within other subfamilies so that it is not possible to say which is the derived form. However, within the Apistomyiinae it is suggested that the *Neocurupira*-type is the more primitive.

There are a number of distinct larval forms within the Apistomyiinae. Generally, there has been a reduction of the anal division and the 7th proleg, and an anterior-posterior compression of the body division. The *Neocurupira* (*Neocurupira*)-*Peritheates* larvae show the least amount of reduction of the anal division and still retain obvious 7th prolegs. The *Apistomyia*-*Neocurupira* (*Austrocurupira*) larvae have a reduced anal division and the 7th prolegs are either very reduced or absent.

Horaia larvae are compressed anteroposteriorly and have heavily sclerotised cuticle particularly on the edges of the cephalic and anal divisions. *Nothohoraia* larvae are similar in many respects to *Horaia* but are flattened dorsoventrally and have a specialised cephalic division. The larvae of *Nothohoraia* are the most highly evolved of any known blepharocerid.

All apistomyid genera can be derived from a neocurupirid ancestor similar in all stages to *Neocurupira hudsoni*. *Horaia* retained the holoptic male, reduced the vein R2+3 to an occasionally occurring spur vein on vein Rs, retained the long pupal gill lamellae but evolved a highly specialised larval form. *Apistomyia* retained the holoptic male, lost vein R4+5 to give a simple though curved vein Rs, evolved shorter pupal gill lamellae and larvae with reduced anal divisions. *Neocurupira* (*Austrocurupira*) retained the holoptic male, forked vein Rs and long pupal gill lamellae but the larvae with reduced anal divisions are distinctly *Apistomyia*-like. The combination of characteristics shown by *Neocurupira* (*Austrocurupira*) could represent a pre-*Apistomyia* condition. *Peritheates* evolved dichoptic males, lost vein R2+3 but retained the long pupal gills and neocurupirid larvae. The larvae have subsequently evolved some apistomyid characteristics. *Nothohoraia* evolved dichoptic males very similar to *Neocurupira campbelli* but the pupa is apistomyid in every respect. The larvae of *Nothohoraia* probably segregated from a common stock with *Horaia* and then specialised even further than *Horaia*.

With the discovery of blepharocerid forms with taxonomic characters that cut across presently accepted generic and subfamilial limits, it may be necessary in the near future to reconsider the present classification of the Blepharoceridae.

ZOOGEOGRAPHY OF THE AUSTRALASIAN BLEPHAROCERIDAE

Because the Blepharoceridae are, in almost all stages of their life cycle, dependent on fast flowing water, Tillyard (1922b) believed that the dispersal of this family took place along definite land bridges, not by sea or air carriage, and for this reason Edwards (1929) also believed the family to be of special value in zoogeography. However, Edwards pointed out that blepharocerids are known from an isolated volcanic island and suggested that migration by sea routes may occur. The distribution and affinities of the New Zealand *Neocurupira chiltoni* suggests that aerial colonisation is also possible. Nevertheless it is agreed here that the main dispersal routes of the Blepharoceridae were along land. Because of their specialised habitats and low vagility, blepharocerids are probably of equal importance with Chironomidae (Brundin, 1966 and 1967) and the Trichoptera (Ross, 1956 and 1967) in zoogeography.

Edwardsininae: The distribution of the Edwardsininae (South Africa, South Australia, Tasmania and South America) may be taken to suggest a southern origin for this subfamily. Tillyard (1922b) believed that the then known distribution of Australian blepharocerids could best be explained by the evolution of the Blepharoceridae in a temperate Antarctica. Tonnoir (1930a) also believed that the Australian species of *Edwardsina* were of southern origin. Hennig (1960) considered that the affinities of the present subgenera of *Edwardsina* also suggests a southern origin in the Antarctic but he reserved his judgement until there was further detailed systematic research. With recent geological evidence concerning antarctic land connection (Adie, 1963), continental drift (Wilson, 1963 and Cox *et al.*, 1967) and the existence of Gondwanaland (King, 1967), the possibility that the Edwardsininae evolved and dispersed in the south cannot be discounted.

However, Darlington (1965), after reviewing the probable climatic history and present distribution of significant plants and animals on the lands surrounding the Antarctic Continent now, concludes that it was not an important centre of evolution. Stuckenberg (1958) from his considerations of the affinities of the Edwardsininae to other Blepharoceridae, believed that the centre of origin of the

Edwardsiniinae was not southern but more likely in the Northern Hemisphere. Dumbleton (1963b) indicated in a figure that the Australian *Edwardsina* arrived from the north.

No matter which way *Edwardsina* arrived in Australia, the present distribution of Australian blepharocerids¹ can best be explained by *Edwardsina* arriving in Australia when Tasmania was still connected to the mainland, with more specialised blepharocerids arriving after the Oligocene when Tasmania had become an island (Darlington, 1965). If *Edwardsina* and the other blepharocerids came from the north as is more generally believed at present (Fig. 72), then the suggested origin of Australian blepharocerids is similar to Ross's (1956) suggested origin for Australian caddisflies. Ross believed that there were two invasions of mountain caddisflies into Australia. The first, of primitive genera, arrived during the late Mesozoic when the Malay Archipelago was probably an extensive land mass connected intermittently with New Guinea and Australia. The second invasion, consisting of more specialised genera, entered Australia during the Miocene through island chains between south-eastern Asia, New Guinea and Australia. It is possible that, as well as the primitive caddisflies, *Edwardsina* arrived in Australia during the Cretaceous, with the Apistomyiinae and the more specialised caddisflies arriving during the Miocene.

According to Fleming (1962), Suggate (1963), Ross (1965) and King (1967) New Zealand was probably connected to Asia by way of New Caledonia during the late Cretaceous. As *Edwardsina* is considered to have colonised Australia during this era why it failed to reach New Zealand is difficult to explain. However, it is possible that the timing and placing of New Zealand's Cretaceous northern connection occurred after *Edwardsina* was already in Australia and when the more specialised blepharocerids were moving southwards.

The origin of the Blepharoceridae in the Northern Hemisphere, with the most primitive form (Edwardsiniinae) existing now in the southern-most land extensions of the Southern Hemisphere is in general agreement with Darlington (1965) who believed that evolution and dispersal run generally from large to small land masses. The presence of Edwardsiniinae in the Southern Hemisphere could be regarded as the result of southerly migration from the northern centre of origin with the northern stock now extinct. In principle this is similar to the hypothetical scheme proposed by Darlington for carabid beetles.

Apistomyiinae: This subfamily includes all the remaining Australasian blepharocerids.

Because he believed the Edwardsiniinae were ancestral, Tillyard (1922b) considered that the Australasian Apistomyiinae were of a southern origin. Tonnoir (1930a), however, because of the comparatively specialised *Apistomyia* species occurring in Australia and the absence of *Edwardsina* from New Zealand believed that the Australasian Apistomyiinae were from the north. Both Hennig (1960) and Dumbleton (1963a and b) believed that the various genera of the Apistomyiinae were derived independently from the Paltostominae; Dumbleton indicated that they came from the north. Dumbleton (1963a) suggests as an alternative that *Apistomyia* may have arisen within Australia from *Neocurupira* and then migrated north. It is believed here, however, that the present distribution² of *Apistomyia* is the result of an Asian origin rather than an Australian origin, and that relationships shown between the Apistomyiinae genera indicate a monophyletic origin (Fig. 72).

The relationship between the Australian and New Zealand species of *Neocurupira* is not clear. Tonnoir (1930a) was not at all satisfied that the Australian *N. nicholsoni* Tillyard was congeneric with the New Zealand *N. hudsoni*, as the

¹ *Edwardsina* found in Tasmania and Australia, *Apistomyia* and *Neocurupira* (*Austrocurupira*) found only in Australia.

² Corsica, Cyprus, Northern India, Eastern Australia, Formosa and Japan.

N. nicholsoni larvae are more similar to those of *Apistomyia* (with reduced anal divisions, dorsal and marginal armature of spines) than to those of *N. hudsoni* (with well-developed anal divisions, marginal armature of scales). Dumbleton (1963a) subsequently placed *N. nicholsoni* in the subgenus *Austrocurupira*. These larval similarities may be interpreted to mean that *Austrocurupira* is more closely related to *Apistomyia* than to *Neocurupira* (sensu stricto). It is then more likely that *Austrocurupira* gave rise to *Apistomyia* by loss of the vein R4+5 as Dumbleton (1963a) has suggested, though not necessarily in Australia (Fig. 72). It is suggested here that *Austrocurupira* probably arrived in Australia during the Miocene with *Apistomyia*, rather than during the Cretaceous with *Edwardsina*, for *Austrocurupira* is not found on Tasmania. If this was so, *Austrocurupira* then has no direct link with New Zealand *Neocurupira* which are considered to have arrived during the late Cretaceous when New Zealand was probably connected to the north (Fleming, 1962, and others). However, until further studies are undertaken on the affinities of the Australasian *Neocurupira* the status of the subgenus *Austrocurupira* remains unchanged.

According to Dumbleton (1963a) Tillyard regarded *Neocurupira* as giving rise to *Apistomyia* and *Peritheates*. Morphologically this view is logical if it is accepted that *Peritheates* has lost vein R2+3 and *Apistomyia* vein R4+5, though as Dumbleton has pointed out the curved vein Rs in *Apistomyia* is difficult to explain. Dumbleton also agreed with this origin of *Peritheates* and suggested that *Peritheates* segregated from the *Neocurupira* stock within New Zealand. The present distribution of *Peritheates* interpreted in the light of past geological and climatic changes in New Zealand, coupled with the fact that loss of vein R2+3 appears to be taking place in some members of the *hudsoni*-complex now makes Dumbleton's suggestion highly acceptable.

After the northern connection was broken in the late Cretaceous and during the mid-Eocene New Zealand was a single land mass. By the Oligocene this land mass was transgressed by the sea to such an extent that two islands resulted, one situated over the north-east of the present North Island, the other reaching from the middle of the present South Island to the south of Stewart Island. According to Fleming (1962) there is evidence that much of New Zealand at this time was peneplained and very low lying with some mountains present in the south. How blepharocerids managed to survive this period with its probably sluggish streams and rivers is difficult to suggest but it may be significant that *Neocurupira chiltoni* can at present survive in water very much slower than that normally tolerated by other species (Craig, 1966). It is considered that during this period, when New Zealand first consisted of two islands, *Peritheates* separated from the ancestral stock by evolution of dichoptic males and the loss of vein R2+3. The present distribution of the genus *Peritheates* (Fig. 70) suggests that it arose in the northern island, *Neocurupira* retaining the more primitive characters in the southern island.

New Zealand again became a single land mass during the Lower Miocene, lying approximately over the present position of New Zealand. Fleming (1962 and 1963) believed that the Miocene in New Zealand was warmer than any previous age and that the alpine zone (between tree-line and permanent snow) did not exist in New Zealand at that time. The effect of higher temperatures on blepharocerids of that time is not known but it is significant that blepharocerids exist now in the tropics. It is possible that some blepharocerids took refuge in the then southern-most land extension along with the alpine flora (Wardle, 1963). It is assumed that during this period *Peritheates* migrated south to at least the limits of the present South Island and that *Neocurupira*, having evolved in the cooler south, was prevented from migrating north to any extent. During the Upper Miocene there is evidence (Fleming, 1962) that temperatures were cooler and that considerable faulting of the

land mass in the Marlborough area took place. Why *Neocurupira* did not manage to migrate north at this time is difficult to explain but it is not found in the present North Island and would appear to have reached the Marlborough Sounds after the present Cook Strait was formed during the Pliocene–Pleistocene. It is possible that *Neocurupira* did in fact reach the “North” Island but subsequently became extinct. However, the fact that *Neocurupira* species are at present found in a wide-spread range of habitats in the South Island makes the suggestion of extinction in the North Island unlikely.

During the early Pliocene New Zealand again consisted of two islands. The South Island was of approximately the present configuration but extended across the present Cook Strait on to the south-western tip of the present North Island. A shallow sea separated this peninsula from the northern part of the North Island (Fleming, 1962). It is considered that during this period *Peritheates harrisi* evolved in the then North Island and *P. turriifer* in the then South Island. It is further postulated that when the present Cook Strait was rapidly formed during the Pliocene–Pleistocene a small population of *Peritheates turriifer* was isolated from the South Island; and that, when the shallow sea regressed off the centre of the North Island, *Peritheates harrisi* migrated south until now it is found in the small southern area of the North Island inhabited by *Peritheates turriifer* (Fig. 70).

The presence on Banks Peninsula of *Neocurupira chiltoni*, the only New Zealand blepharocerid with large black spines on the fourth instar larva, is extremely interesting. This peninsula is a remnant of two extinct volcanoes which were probably initially active during the Cretaceous (Liggett and Gregg, 1965). They were again active during the Pliocene–Pleistocene and very slightly during the Pleistocene–Holocene. The volcanoes were separated from the main South Island until approximately the last volcanic activity when they were connected to the mainland by low aggraded plains. As the last volcanic activity was very limited, Banks “Peninsula” was probably available for colonisation by blepharocerids during the Pleistocene. Dumbleton (1963a) considered that *Neocurupira chiltoni* evolved from aerial colonists as the aggraded Canterbury Plains do not provide suitable ecological conditions for invasion by water. Except for large spines on the fourth instar larva, *Neocurupira chiltoni* is very similar in egg shape, larval morphology and general adult morphology to *Neocurupira tonnoiri*. Therefore it is considered that the aerial colonists of Banks Peninsula were of the *tonnoiri*-type. The nearest that *Neocurupira tonnoiri* is known to approach Banks Peninsula is Arthur’s Pass, a direct distance of 70 miles. If, as at present, the prevailing winds were westerly during the Pleistocene, as suggested by Gage (1964), it is quite probable that the original colonists could have been blown the intervening distance. However, if blepharocerid adults can become aerial colonists it is surprising that other species of blepharocerids occurring at Arthur’s Pass have not found their way to Banks Peninsula.

Mount Egmont, Taranaki, North Island, is very similar to Banks Peninsula for it is a recently extinct volcanic dome separated from the main mountain chain and known blepharocerid localities by ecologically unsuitable terrain. Despite intensive searching by a number of collectors, no blepharocerids have yet been discovered, though both L. J. Dumbleton and A. G. McFarlane (pers. comm.) indicate that other freshwater fauna is abundant on the mountain. Located west of blepharocerid localities Mount Egmont has little chance of aerial colonisation from the predominantly westerly winds. During the Last Pleistocene Glaciation, Mount Egmont was connected to the north-west of the South Island by a flat aggraded plain, probably similar to the present Canterbury Plains. This ecologically unsuitable terrain was no doubt the main reason that no South Island blepharocerids reached the North Island and vice versa during this period.

The present distribution of the remaining *Neocurupira* species makes it difficult to form a hypothesis concerning their pattern of evolution. It seems likely that the

original *hudsoni*-complex stock became separated into two or possibly three populations some time after the Oligocene or perhaps during the Pliocene–Pleistocene periods. The separation, which has given rise to *Neocurupira hudsoni* and the “southern” blepharocerids, appear to have taken place after the evolution of the commensal chironomid association, as it is unlikely that such an association would evolve twice. The known distribution of *Neocurupira hudsoni* and Form C strongly suggests that the populations of these two blepharocerids have only very recently regained contact, probably since the retreat of the ice at the end of the last Pleistocene Glaciation. The evolutionary stages between the holoptic males of *Neocurupira hudsoni* and the dichoptic males of Form C are suggested by the series: *Neocurupira hudsoni* → Form A → *N. rotalapisculus* → Form C. The distribution of *Neocurupira campbelli* suggests that this species has been associated with *Neocurupira hudsoni* for a considerable time, for apart from an altitudinal restriction its geographic range practically coincides with that of *Neocurupira hudsoni* (Fig. 26). *Neocurupira campbelli* is the only other species of New Zealand blepharocerid which tolerates the commensal chironomid *Dactylocladius commensalis* and this suggests two possible origins for *Neocurupira campbelli*. Firstly, that *Neocurupira campbelli* separated early from the *hudsoni*-complex stock just as the chironomid association was developing and no further development took place, or secondly, that there is no close relationship and the rare examples of chironomid on *N. campbelli* are brought about by local conditions either forcing the chironomid to associate with the blepharocerid or the blepharocerid into accepting the chironomid. Dumbleton (1963a) suggested that the parent species of *N. campbelli* might be *N. tonnoiri*. However, as the larvae of *N. campbelli* are more similar to *N. hudsoni* larvae than to any other New Zealand blepharocerid and the only known examples of brachypterous wings in the Blepharoceridae occur in these two species, it is more probable that the parent species was *N. hudsoni* and not *N. tonnoiri*.

As *Nothohoraia* is believed to be closely related to *Horaia*, the ancestral stock of *Nothohoraia* probably constituted a separate invasion to that of the *Neocurupira* stock, however, these both occurred at the same time during the Cretaceous. There is only one species of *Nothohoraia* known at present and that from a single locality. It is possible that the New Caledonian blepharocerid with vestigial mouthparts represents a remnant of the southward migration of the ancestral *Nothohoraia* into New Zealand.

Refugia (Fig. 71): The present distribution of certain groups of plants suggested to Wardle (1963) and to Burrows (1965) that there were refugia for plants in the Nelson and Otago-Southland regions during the Last Pleistocene Glaciation. The distribution of New Zealand terrestrial invertebrates also indicates that refugia were present, though not necessarily during the Last Glaciation. According to R. S. Bigelow (pers. comm.) the relationships and distribution of the South Island grasshoppers agree generally with the limits of the refugia as set by Wardle and Burrows. From the relationships and distributions of certain members of the Carabidae (Coleoptera) and Sphaerotrictoptidae (Diplopoda), P. M. Johns (pers. comm. and 1964) believes that refugia were located as in Figure 71.

The climatic factors, which are likely to affect the distribution of flora and terrestrial fauna during periods of glaciation, with the exception of lack of water, would probably not greatly effect the distribution of blepharocerids. Gage (1964) considered that the Last Glaciation was not as severe as has generally been believed and that there were considerable amounts of running water present. These conditions would no doubt favour the survival and distribution of blepharocerids.

It is strange therefore that the present distribution of some of the South Island blepharocerids agrees very closely with the refugia suggested by Wardle (1963), by Burrows (1965) and by P. M. Johns (pers. comm.). The distribution of *P. turrifer* (Fig. 70) within the South Island is, with the exception of the single location at

Kaikoura, very similar to the refugium suggested by Burrows and by P. M. Johns in north-west Nelson. The overall distribution of *P. turrifer* in the South Island agrees with the refugium suggested by Wardle. The distribution of *N. tonnoiri* though extending well down the West Coast, agrees well with the north-western Nelson refugium suggested by Burrows and by P. M. Johns. Both *P. turrifer* and *N. tonnoiri*, while occurring in open streams, are mainly found in bush-covered streams, suggesting that their present distribution is in some way connected with vegetation.

The presence of *Nothohoraia* within the limits of the north-west Nelson refugium, along with *Neocurupira hudsoni*, *Neocurupira tonnoiri* and *Peritheates turrifer*, indicates that this area is important for New Zealand blepharocerids and that it should be investigated thoroughly.

The known distribution of *N. campbelli* and *N. hudsoni* fit generally the distribution of certain alpine plants which Burrows (1965) suggests survived the Last Glaciation. It is of interest that *N. campbelli* is restricted to higher altitudes.

It is considered that *N. rotalapisculus* and Form C of the *hudsoni*-complex evolved in the two southern refugia suggested by Burrows and P. M. Johns.

The distribution of *N. chiltoni* agrees in general with a refugium suggested by P. M. Johns (pers. comm.) on the eastern part of Banks Peninsula (Fig. 71). However, the distribution of *N. chiltoni* is probably influenced more by a lack of suitable streams on the western part of the peninsula than by the existence of any refugium.

To explain more fully the present distribution and relationships of New Zealand blepharocerids and in particular those of the interesting *hudsoni*-complex and *Nothohoraia*, a more detailed study of the affinities and distribution of New Zealand blepharocerids and associated freshwater fauna is required.

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