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Revision of the genus *Caenota* Mosely (Trichoptera: Calocidae), with descriptions of 2 new species and the larva of *C. nemorosa* Neboiss

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Abstract

The caddisfly genus *Caenota* Mosely 1953 (in Mosely & Kimmins 1953) currently contains 5 species known from eastern Australia. *Caenota* is distinguished from other Calocidae genera by having adult males with greatly expanded maxillary palpi and a large membranous process associated with the antennal scape. Of the 5 described species, the larvae of only 1 is known. Here, we describe 2 new species, *Caenota cudonis* **sp. nov.** and *C. equustagna* **sp. nov.**, from adult, larval, and pupal material. Also, we describe for the first time the larva of *C. nemorosa* Neboiss. These descriptions increase the number of *Caenota* species to 7 and the number of associated and described larvae to 4. This paper also provides descriptions of features associated with the adult head capsule of all described species of *Caenota*. Each of the known species is considered, with illustrations and re-descriptions of these features given.

Key words: caddisfly, pupa, taxonomy, Australia, cytochrome oxidase sub unit I (COI), elongation factor-1 alpha (EF1α), Cadherin (CAD), RNA polymerase sub unit 2 (POL2)

Introduction

Species of *Caenota* Mosely 1953 (in Mosely & Kimmins 1953) are medium-sized caddisflies and the largest members of the family Calocidae Ross 1967. Their range extends throughout eastern Australia from Tasmania to North Queensland (Neboiss 1984). The males of *Caenota* are conspicuous, with greatly expanded maxillary palpi and membranous expansions associated with each antennal scape, rising above the head in a cap-like fashion.

The genus *Caenota* was originally established in the family Sericostomatidae Stephens 1836 to accommodate 2 species: *C. plicata* Mosely 1953 (in Mosely & Kimmins 1953) and *C. simulans* Mosely 1953 (in Mosely & Kimmins 1953). These species were later transferred to Calocidae, based on having a spur count of 2:2:4. Subsequently, *C. galeata* Neboiss 1984, *C. nemorosa* Neboiss 1984, and *C. monteithi* Neboiss 1984, were added from North Queensland.

Of the 5 known species, the only associated larva belongs to *C. plicata*. From the literature it is evident that this association was known within taxonomic circles before the larva was officially described, highlighting one of the facets of what has become known as the taxonomic impediment. Drecktrah (1984) reared a number of caddisfly species from larvae to adults, including *C. plicata*. In his paper he described the immature stages of *Alloecella grisea* Banks 1939, and mentioned his intent to provide descriptions of the immature stages of the other species in later publications. Dean and Cartwright (1987) reported collecting the larva of *C. plicata* in a Victorian stream. Jackson (1991) provided descriptions and illustrations of the larva in her dissertation, but it was not until 7 years later (Jackson 1998) that a description was supplied in a professional journal; even then, the details of how the association of larva and male was accomplished were lacking.

Many taxonomic descriptions of Trichoptera rely heavily on characteristics of the genitalia and wings for

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diagnoses and pay little attention to other features. In most cases this occurs to the extent that only the wings and genitalia are illustrated, leaving knowledge gaps for future researchers. Males of *Caenota* species exhibit highly modified maxillary palpi and antennae that are useful as diagnostic characters. Mosely and Kimmins (1953) provided brief descriptions and illustrations of the antennae and maxillary palpi of *C. plicata* and *C. simulans*. However, these are lacking in detail and are denuded of setae, despite the fact that setae can be used to distinguish species. No illustrations and only brief descriptions of the antennae and maxillary palpi were provided by Neboiss (1984) for the 3 Queensland species. This paper presents illustrations and re-descriptions of the structures associated with the adult head capsule for all the known species of *Caenota*.

Descriptions of males, females, larvae, and pupae of *C. cudonis* **sp. nov.** and *C. equustagna* **sp. nov.** are provided in this paper. Associations of the larvae with the diagnosable males of each species were inferred through genetic analyses and examination of pharate pupae. These techniques are also used to associate larval and adult specimens of *C. nemorosa*, facilitating for the first time a description of the larva of this species. Thus, this paper increases the number of associated and publicly described larvae from 1 to 4 and the total number of species recognised in this genus to 7.

Material and methods

Adult, larval, and pupal specimens of *C. cudonis*, *C. equustagna*, *C. nemorosa*, and *C. plicata* were collected between 2007 and 2009 either directly into 100% ethanol or first into 70% ethanol and then later transferred into 100% ethanol. No material of *C. galeata*, *C. monteithi* or *C. simulans* was available for genetic analysis. However, specimens of *C. galeata*, *C. monteithi*, and *C. nemorosa* were borrowed for morphological study from the Museum of Victoria, Melbourne, Victoria, Australia (MV). A single specimen of *C. nemorosa* and 2 specimens of *C. plicata* were accessed through the Australian National Insect Collection, Canberra, Australian Capital Territory, Australia (ANIC). The only known specimen of *C. simulans* is housed at the British Museum of Natural History, London, United Kingdom (BMNH). Illustrations and descriptions for this species are based on photographs provided by the BMNH. Specimens of *C. cudonis* and *C. equustagna*, collected for this study, are deposited in the Australian Museum, Sydney, New South Wales, Australia (AM). Specimens of *C. nemorosa,* collected for this study, are deposited in the Queensland Museum, South Brisbane, Queensland, Australia (QM), and specimens of *C. plicata* are deposited either in the Tasmanian Museum and Art Gallery, Hobart, Tasmania, Australia (TMAG) or the Museum of Victoria, depending on the state in which they were collected.

The genitalia of *C. nemorosa*, C. *cudonis* and *C. equustagna* were cleared in potassium hydroxide (KOH). Larval sclerites were extracted from pupal cases and used to associate pharate male pupae with larvae. Keys used to identify specimens were those of Jackson (1998) and Neboiss (1986, 1992). Terminology of wing venation follows Holzenthal *et al.* (2007). The extreme modification of wing venation of these species makes identification of individual veins difficult. Labels on the illustrations of the wings indicate our interpretation of the main veins. Terminology of larval characters, other than for the positions of gills, follows Jackson (1998) and Williams and Wiggins (1981). Placement of gills on the abdominal segments varies among specimens. Therefore, we provide a schematic of the possible positions of the gills (Fig. 6). Terminology of adult characters follows Holzenthal *et al.* (2007), Neboiss (1991), and Neboiss (1992). Where references to the planes of the maxillary palpi are given, inner and outer surfaces refer to these surfaces as they would apply to *C. galeata*, *C. monteithi*, *C. nemorosa*, and *C. cudonis*, where the maxillary palpi are capable of being held close together, forming an enclosure in front of the head. In *C. plicata* the maxillary palpi are rotated approximately 45 degrees so that the inner surfaces face more dorsally and the palpi do not come together to form an enclosure.

Specimens were examined using a Nikon SMZ1500 microscope. Photographs were taken using a Nikon DS-Fi1 camera mounted on a Nikon SMZ1500 microscope. Helicon Focus 5.3.7 was used to create photographs with a greater than usual depth of field. Photographs were edited using GIMP 2.6.11. Line drawings of the wing venation were obtained from tracings of the colour photos.

Specimens used in genetic analyses are listed in Table 1. Two methods were employed for the extraction, amplification, and sequencing of DNA. The method employed for each specimen is indicated in Table 1 where it is represented by the institute where genetic material was extracted. For the first method, extractions and Polymerase Chain Reaction (PCR) amplifications were performed at La Trobe University following the methods of Webb and Suter (2010) and sequencing was performed at Macrogen, Inc. (Seoul, Korea).

TABLE 1. Details for sequenced voucher specimens, including GenBank, and La Trobe University (LTU) accession numbers and processing institutions. AM = Australian Museum, ANIC = Australian National Insect Collection, CCDB = Canadian Centre for DNA Barcoding, MV = Museum Victoria, QM = Queensland Museum, TMAG = Tasmanian Museum and Art Gallery.

Species	Specimen	LTU Accession number	Deposited	Institute where extracted	COI GenBank Accession number	EF1α GenBank Accession number	POL2 GenBank Accession number	CAD GenBank Accession number
C. plicata	Female	ANIC300000_02	ANIC	CCDB	KF026882			
C. plicata	Female	ANIC300000_03	ANIC	CCDB	KF026896			
C. plicata	Male	MS130	MV	CCDB	KF026878	KF027026	KF040528	
C. plicata	Male	MS131	MV	CCDB	KF026826	KF026991	KF040513	
C. plicata	Female	MS132	MV	CCDB	KF026843	KF027003	KF040520	KF027093
C. plicata	Female	MS133	MV	CCDB	KF026801	KF026976	KF040504	
C. plicata	Larva	MS656	MV	CCDB	KF026822			
C. plicata	Larva	MS657	MV	CCDB	KF026828	KF026993	KF040515	
C. plicata	Larva	MS658	MV	CCDB	KF026922	KF027054	KF040537	
C. plicata	Larva	MS659	MV	CCDB	KF026841	KF027001		
C. plicata	Larva	MS660	MV	CCDB	KF026808			
C. plicata	Larva	MS688	MV	CCDB	KF026940			
C. plicata	Female	MS857	MV	CCDB	KF026888			
C. plicata	Larva	MS875	MV	CCDB	KF026936	KF027064		
C. plicata	Larva	MS876	MV	CCDB	KF026815			
C. plicata	Male	MS1586	TMAG	LTU		KF147239		KF147249
C. plicata	Male	MS1587	TMAG	CCDB	KF026934	KF027063		KF027104
C. plicata	Larva	MS1600	TMAG	CCDB	KF026827	KF026992	KF040514	
C. plicata	Larva	MS1601	TMAG	CCDB	KF026871	KF027021		
C. plicata	Larva	MS1603	TMAG	LTU		KF147243		
C. plicata	Larva	MS1604	TMAG	LTU		KF147245		
C. plicata	Larva	MS1608	TMAG	LTU		KF147236		
C. plicata	Larva	MS1611	TMAG	CCDB	KF026898			

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TABLE 1. (Continued)

Species	Specimen	LTU Accession number	Deposited	Institute where extracted	COI GenBank Accession number	EF1α GenBank Accession number	POL2 GenBank Accession number	CAD GenBank Accession number
C. plicata	Larva	MS1617	TMAG	CCDB	KF026812	KF026983	KF040508	
C. plicata	Larva	MS1618	TMAG	CCDB	KF026844	KF027004		
C. plicata	Larva	MS1623	TMAG	CCDB	KF026944	KF027069		
C. plicata	Larva	MS1624	TMAG	LTU		KF147228		
C. plicata	Larva	MS1633	TMAG	CCDB	KF026817			
C. plicata	Larva	MS1638	TMAG	CCDB	KF026950	KF027075		
C. plicata	Larva	MS1639	TMAG	CCDB	KF026837	KF026999		
C. plicata	Larva	MS1640	TMAG	CCDB	KF026842	KF027002		
C. plicata	Larva	MS1641	TMAG	CCDB	KF026919	KF027050		
C. plicata	Male	MS1646	TMAG	CCDB	KF026877	KF027025	KF040527	
C. plicata	Male	MS1647	TMAG	CCDB	KF026851	KF027007		
C. plicata	Larva	MS1656	TMAG	CCDB		KF147227		
C. plicata	Male	MS1662	TMAG	CCDB		KF147235		
C. plicata	Male	MS1663	TMAG	CCDB	KF026873	KF027022		
C. plicata	Larva	MS1666	TMAG	CCDB	KF026845	KF027005		
C. plicata	Larva	MS1667	TMAG	CCDB	KF026884	KF027027		
C. nemorosa	Male	MS331	QM	CCDB	KF026807	KF026980	KF040505	KF027086
C. nemorosa	Male	MS332	QM	CCDB	KF026816	KF026985	KF040509	KF027089
C. nemorosa	Male	MS333	QM	CCDB	KF026930	KF027059		KF027103
C. nemorosa	Larva	MS334	QM	CCDB	KF026796	KF026972		KF027082
C. nemorosa	Larva	MS336	QM	CCDB	KF026803	KF026978		KF027084
C. nemorosa	Larva	MS338	QM	CCDB	KF026858	KF027013		
C. nemorosa	Larva	MS348	QM	CCDB	KF026802	KF026977		
C. nemorosa	Larva	MS349	QM	CCDB	KF026860	KF027015		

……*continued on the next page*

TABLE 1. (Continued)

Species	Specimen	LTU Accession number	Deposited	Institute where extracted	COI GenBank Accession number	EF1α GenBank Accession number	POL2 GenBank Accession number	CAD GenBank Accession number
C. nemorosa	Female	MS377	QM	LTU	KF026792	KF026970	KF040502	
C. nemorosa	Female	MS379	QM	CCDB	KF026913			
C. nemorosa	Female	MS394	QM	CCDB	KF026911	KF027045		KF027101
C. nemorosa	Female	MS397	QM	CCDB	KF026867	KF027019		KF027098
C. nemorosa	Larva	MS404	QM	CCDB	KF026921	KF027053		
C. nemorosa	Male	ANIC300000_07	ANIC	CCDB	KF026777			
C. cudonis	Female	MS74	AM	CCDB	KF026854	KF027010		KF027095
C. cudonis	Male	MS75	AM	CCDB	KF026908	KF027043		
C. cudonis	Larva	MS701	AM	CCDB	KF026949	KF027074		
C. cudonis	Larva	MS702	AM	CCDB	KF026774	KF026959		
C. cudonis	Larva	MS740	AM	CCDB	KF026952	KF027077		KF027109
C. cudonis	Female	MS741	AM	CCDB	KF026856	KF027012		KF027096
C. cudonis	Male	MS759	AM	CCDB	KF026770	KF026956		
C. cudonis	Male	MS760	AM	CCDB	KF026931	KF027060		
C. cudonis	Female	MS761	AM	CCDB	KF026821	KF026989		
C. cudonis	Larva	MS846	AM	CCDB	KF026855	KF027011		
C. cudonis	Larva	MS847	AM	CCDB	KF026782	KF026965		
C. cudonis	Larva	MS848	AM	CCDB	KF026791			
C. cudonis	Male	MS1013	AM	CCDB	KF026824			
C. equustagna	Larva	MS90	AM	CCDB	KF026804	KF026979		KF027085
C. equustagna	Male	MS772	AM	CCDB	KF026863	KF027017	KF040524	
C. equustagna	Female	MS773	AM	CCDB	KF026947	KF027072	KF040541	
C. equustagna	Female	MS774	AM	CCDB	KF026820	KF026988	KF040512	
C. equustagna	Larva	MS784	AM	CCDB	KF026948	KF027073	KF040542	KF027108

……*continued on the next page*

TABLE 1. (Continued)

Species	Specimen	LTU Accession number	Deposited	Institute where extracted	COI GenBank Accession number	EF1α GenBank Accession number	POL2 GenBank Accession number	CAD GenBank Accession number
C. equustagna	Larva	MS785	AM	CCDB	KF026823	KF026990		KF027090
C. equustagna	Larva	MS786	AM	CCDB	KF026831	KF026995	KF040517	
C. equustagna	Larva	MS981	AM	CCDB	KF026918	KF027049		
C. equustagna	Larva	MS982	AM	CCDB	KF026893	KF027033	KF040531	
C. equustagna	Male	MS988	AM	CCDB	KF026829	KF026994		
C. equustagna	Female	MS1063	AM	CCDB	KF026941	KF027066		
T. variegata		MS4					KF040539	KF027106
T. variegata		MS45				KF027023	KF040526	
T. variegata		MS77					KF040522	
T. variegata		MS78					KF040506	
T. variegata		MS79					KF040532	
T. variegata		MS80					KF040497	
T. variegata		MS81					KF040519	
T. variegata		MS173				KF027048	KF040535	
T. variegata		MS221					KF181926	
T. variegata		MS222					KF040530	
T. variegata		MS235				KF027046		
T. variegata		MS237				KF026960		
T. variegata		MS238				KF147226		
T. variegata		MS244			KF026875			
T. variegata		MS318			KF026773			
T. variegata		MS1597				KF027047		
T. variegata		MS1598				KF027076	KF040543	
T. variegata		MS1621				KF026986	KF040511	
T. variegata		MS1622				KF027020	KF040525	

A 658-bp fragment of the mitochondrial gene cytochrome oxidase subunit I (COI), a 490-bp fragment of the nuclear gene elongation factor-1 alpha (EF1α), a 790-bp fragment of the nuclear gene RNA polymerase subunit 2 (POL2), and an 850-bp fragment of the nuclear gene Cadherin (CAD) were amplified. Primers used for amplifying gene fragments are detailed in Table 2. Primers were M13-tailed to facilitate sequencing. The PCR cocktail for reactions consisted of 4 µl buffer, 20 µl 10% w/v trehalose, 0.8 µl dNTPs, 2 µl 50 mM $MgCl_2$, 0.8 µl of each primer, 0.1 µl taq polymerase (Invitrogen), 0.01–5 µl of DNA template, and water to 40µl. For COI, PCR conditions consisted of 1 min at 94°C; 5 cycles of 1 min at 94°C, 1.5 min at 45°C, 1.5 min at 72°C; 35 cycles of 1 min at 94°C, 1 min at 50°C, 1 min at 72°C; and 4 min at 72°C. For EF1α, PCR conditions consisted of 4 min at 94°C; 29 cycles of 20 sec at 94°C, 45 sec at 55°C, 45 sec at 72°C; and 5 min at 72°C. The PCR products were purified and sequenced in both directions by Macrogen, Inc. (Seoul, Korea). Contigs were assembled in DNABaser 2.75 (www.DnaBaser.com) and aligned with default settings in Clustal X as implemented in MEGA5.05 (Tamura *et al.* 2011). The sequences were examined for the presence of double peaks, frame shifts, and stop codons.

TABLE 2. Primers used for genetic analysis.

Gene fragment	Primer name	Sequence	Source
COI	HCO2198 (forward)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer *et al*. 1994
	LCO1490 (reverse)	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*. 1994
EF1α	EF1α F (forward)	ATCGAGAAGTTCGAGAARGARGC	Kjer *et al*. 2001
	EF1αIntR (reverse)	CCAYCCCTTGAACCANGGCAT	Kjer *et al*. 2001
CAD	743nF-ino (forward)	GGIGTIACIACIGCITGYTTYGARCC	Johanson & Malm, 2010
	1028r-ino (reverse)	TTRTTIGGIARYTGICCICCCAT	Johanson & Malm, 2010
POLII	polfor2 (forward)	TGGGAYGSYAAAATGCCKCAACC	Johanson & Malm, 2010
	polrev2 (reverse)	TYYACAGCAGTATCRATRAGACCTTC	Johanson & Malm, 2010

The second method was used for sequencing the COI gene only and was performed at the Canadian Centre for DNA Barcoding (CCDB), Guelph, Ontario, Canada. This method is stipulated in the document, Protocols: Glass fiber plate DNA extraction and can be found at http://www.dnabarcoding.ca/CCDB_DOCS/CCDB_DNA_Extraction.pdf. For specimens where DNA was extracted through this method the EF1α gene was amplified at La Trobe University using the extractions provided by CCDB and following the previous method outlined. All gene sequences were submitted to GenBank; accession numbers are given in Table 1.

Evolutionary models were tested using MrModeltest (Nylander 2004) and PAUP (Swofford 1999). Genes were partitioned according to codon position. All evolutionary models were selected from the Akaike Information Criterion given in the MrModeltest outputs (Nylander 2004). More than 1,000,000 generations were run in MrBayes 3.1 (Ronquist & Huelsenbeck 2003), with a sample taken at every 1000 generations, until the average standard deviation of split frequencies fell below 0.01. The first 25% of trees generated were deleted from the statistical summary as 'burn in'. The resultant trees (Figs. 1–4) were rooted using a sequence or sequences of *Tamasia variegata* Mosely 1936 and for the COI tree also a sequence of *Tamasia acuta* Neboiss 1984.

Species boundaries were originally determined based on the morphology of genital structures of the adult males. Gene trees created from COI, EF1α, POL2, and CAD sequences were used to test the morphologically inferred species boundaries. Following the methods of Zhou *et al*. (2007), a clade was considered to be a species if it was monophyletic and if the morphologically based boundaries were represented in each of the gene trees. Associations of morphologically and molecularly identifiable adult males with their conspecific larvae were tested by adding sequence data from larval specimens to the adult data and recreating the COI and EF1α gene trees. An association was considered to be true if a larval sequence was identical to an adult sequence or was nested within adult sequences. Associations were not established if sequences of larvae did not conform to these criteria.

A morphological matrix including 33 characters was used to further investigate the morphological relationships among species and augment the genetic analyses. Character states are provided in Table 3 and the matrix in Table 4. The morphological matrix contained seven taxa, including all species within the family and an outgroup species, *Tamasia variegata*. Information on the characteristics of the larvae of *C. simulans*, *C. galeata*,

TABLE 3. Character states used for the morphological phylogenetic analyses. Characters are numbered 1 to 33.

Character number	Life stage and sex	Body section	Character	Character states			
				0	1	2	3
1	Larva	Frontoclypeus	shape of lateral margins on anterior portion of frontoclypeus	parallel or somewhat rounded out (Fig. 23)	converging (Fig. 13)	diverging	
2			position of seta 6 of frontoclypeus	occurs in posterior distal corner of anterior portion of frontoclypeus (Figs 42 and 64)	occurs half way along lateral margin of anterior portion of frontoclypeus (Fig. 23)		
3		Foretrochantin	number of setae on dorsal margin of foretrochantin	a single seta (Fig. 44)	numerous setae (Fig. 66)		
4		Pronotum	setal patterning on pronotum	scattered throughout anterior half of dorsal surface (Fig. 24)	occurring in a broad, distinct band (Figs 43 and 65)		
5		Metanotum	number of setae on metanotal setal area 1	5 to 6 setae	~ 8 setae	2 setae	
6			number of setae on metanotal setal area 2	1 seta	2 setae		
7			number of setae on metanotal setal area 3	2 to 3 setae	5 to 7 setae		
8		Abdomen	gills present or absent	absent on all segments	present on segment II and III but absent on segment IV	present on segments II-IV	
9	Female	Wings	shape of r1-r2 cross vein of forewing	straight (Fig. 57)	concave (Fig. 36)		
10		Head	size of anterior medial setal warts of head	large	small but distinct	small and indistinct often reduced to punctures only (Fig. 47)	
11			shape of anterior setal warts of head	tear shaped (pointed anteriorly)	rounded		
12		Legs	coloration of hind leg	without markedly darker colourings	with very dark area on tibia	with lightly darkened tibia	

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TABLE 3. (Continued)

Character number	Life stage and sex	Body section	Character	Character states			
				0	1	2	3
13		Abdomen	shape of ventral setal patch of abdominal segment VIII	broad with posterior margin relatively straight (Fig. 32)	slender with posterior margin broadly concave (Fig. 53)	broad with posterior margin setal patch slightlyconcave	slender with posterior margin relatively straight
14	Male	Antennae	length of scape and 1st antennal segments	normal (Figs 7, 8, 11, 16, 17)	elongate and fused (about as long as thorax) (Figs 9 and 10)		
15		Scape	shape and size of anterior projection arising from scape relative to posterior projection	slender, much smaller than posterior projection (Figs 8, 10, and 17)	broad, large but smaller than posterior projection (Fig. 45)	broad, large and larger than posterior projection (Fig. 25)	
16			length of anterior process on posterior projection of scape	absent (Figs 7, 9 and 16)	long (Fig. 12)	short (Fig. 46)	not applicable
17			length of setal tuft anterodorsally on posterior projection of scape	absent (Figs 7, 9, and 16)	long (Fig. 26)	short (Figs 12 and 46)	not applicable
18			setation on posterior projection of scape	absent or very sparse on lateral surface (Figs 25 and 26)	covering lateral surface (Figs 8, 10, 11, 17 and 45)	not applicable	
19		Maxillary Palpi	shape of segment I	broad and rounded, forming a cup-like shape held in front of the head, with setal area facing inward (Figs 8, 10, 17, 25)	more slender with setal area facing more dorsally (Figs 11, 45)		
20			adornments on segment I	without subapicomesal projection	with subapicomesal projection (Figs 14 and 15)		
21			setation on segment I	predominantly on ventral surface (Figs 8 and 25)	scattered throughout lateral surface (Figs 10, and 11)		
22			shape of segment II	broad and rounded, cuplike, held in front of the head, with setal area facing inward (Figs 8, 10, 17, 25)	broad, somewhat trapezoid with divergent dorsal and ventral surfaces (Fig 11)	broad, somewhat quadrilateral with relatively parallel dorsal and ventral margins (Fig 45)	more slender (See Mosely 1936 Fig. 12)

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TABLE 3. (Continued)

Character number	Life stage and sex	Body section	Character	Character states			
				0	1	2	3
23			ventral setation on segment II	absent (Figs 8, 10, and 17)	scattered (Figs 11 and 45)	dense fringe (Fig. 25)	
24			anterior setation on segment II	absent or sparse (Figs 8, 10, 17 and 45)	disk-like fringe (Fig. 11)	dense fringe following ventral fringe (Fig. 25)	
25			setae on lateral surface of segment II	sparse (Figs 25 and 45)	scattered throughout (Figs 10 and 11)		
26			anterior dorsal flange on segment II	absent or small (Figs 25 and 45)	present or large (Figs 8, 10, 11 and 17)		
27			shape of segment III	small globular (Figs 16 and 45)	large (about half size of segment II) (See Mosely 1936 Fig. 12)		
28			shape of segment IV	small globular (Figs 16 and 45)	large (See Mosely 1936 Fig. 12)		
29			length of segment V	longer than length of segs 1 and 2 combined (long) (Figs 7, and 8)	about length of segment II (short) (Figs 10, 17, and 45)	about length of segment III (very short) (Figs 11 and 12)	absent or not applicable
30			setation on segment V	setae absent distally	setae densely covering or extending over distal margin (Figs 9, 16, 45, and 46)	setae only sparsely covering distal surfaces (Fig. 7)	absent or not applicable
31		Genitalia	shape of phallocrypt	indistinct	extended beyond seg X (Figs 27, 28, 48, and 49)	bulbous (See Neboiss 1984 Fig. 23)	
32			shape of each inferior appendage	long, zigzag-shape (Figs 27, 28, 48, and 49)	broad basally with simple curved projection, spine present distally (See Neboiss 1984 Figs 23 and 27)	slender basally with simple curved projection (See Neboiss 1984 Fig. 30)	broad basally with short projection (See Mosely 1936 Figs 13 and 15)
33			length of preanal appendages	almost as long as segment X	about half as long as seg. X (Figs 27, 28, 48, and 49)		

and *C. monteithi* was absent from the matrix. Furthermore, all adult female and some adult male characters were not included for *C. simulans*. A Maximum Parsimony (MP) analysis of the morphiological characters was undertaken using Phylogenetic Analysis Using Parsimony (PAUP) (Swofford, 1999), employing a heuristic search and tree-bisection-reconnection (TBR) branch swapping. All characters were treated as un-ordered and with equal weighting. Bootstrap values were calculated using 1000 iterations.

TABLE 4. Morphological matrix. Characters correspond to those given in Table 2.

	Characters															
Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
C. cudonis	0	0	0	1	0	0	{0/1}	1	1	0	0	0	0	0	2	2
C. equustagna	1	0	1	1	{0/1}	{0/1}	{0/1}	1	{0/1}	2	0	{0/2}	2	0	1	2
C. galeata	?	?	?	?	?	?	?	?	1	1	1	0	1	0	0	0
C. monteithi	?	?	?	?	?	?	?	?	1	2	1	0	1	1	0	0
C. nemerosa	0	1	0	0	{0/1}	0	1	2	1	2	1	1	1	0	0	0
C. plicata	1	0	0	1	{0/1}	0	1	1	1	{1/2}	0	{0/2}	2	0	1	1
C. simulans	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?
T. variegata	2	0	0	0	2	0	1	0	0	0	0	0	3	0	0	3

	Characters																
Species	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
C. cudonis	1	0	0	0	0	0	2	2	0	0	0	0	0	0	1	0	1
C. equustagna	2	1	1	0	{0/1}	2	1	0	0	0	0	0	1	1	1	0	1
C. galeata	0	1	0	0	0	0	0	0	0	1	0	0	0	2	2	1	1
C. monteithi	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0	2	0
C. nemerosa	0	1	0	0	1	0	0	0	1	1	0	0	1	1	0	1	0
C. plicata	2	1	1	0	1	1	1	1	1	1	0	0	2	1	1	0	1
C. simulans	?	?	?	1	?	3	?	?	?	?	0	?	?	?	1	0	0
T. variegata	3	2	1	0	0	1	1	0	0	0	1	1	3	3	0	3	0

Results

Sequences for the 4 genes were obtained from *C. nemorosa*, *C. cudonis*, *C. equustagna*, and *C. plicata* specimens as indicated in Table 1. Delimitation of the 4 *Caenota* species analysed was supported in the COI, EF1α, and CAD gene trees. No specimens of *C. cudonis* yielded POL2 sequences, so for this gene only 3 of the 4 species were analysed and found to form monophyletic clades. Delimitation was supported with 100% posterior probability by the COI and CAD gene trees for each of the species. In the EF1α gene tree, delimitation was supported by 100% posterior probabilities for the *C. plicata*, *C. equustagna*, and *C. nemorosa* clades and by 97% posterior probability for the *C. cudonis* clade. All 3 clades in the POL2 gene tree were supported with 100% posterior probabilities.

Morphological evidence implied the associations of the larvae of *C. nemorosa*, *C. cudonis*, and *C. equustagna* with their adult male. For each species, male pupae exhibiting the diagnostic adult male genital characters and their corresponding larval sclerites were successfully collected. Associations between males and larvae of each species were further supported by the COI and EF1α gene trees. Data were not available to form associations of *C. nemorosa*, or *C. cudonis* for the POL2 gene. For the CAD gene tree, only *C. nemorosa* yielded enough data to form an association.

In the COI gene tree, larvae were nested among adult males in each of the species clades. The *C. equustagna* clade included specimens of larvae which shared identical sequences to a male (MS772) and the *C. cudonis* clade included 2 larvae and 2 males with identical sequences. No larval and adult male *C. nemorosa* specimens shared identical COI sequences. Each of the clades on the COI gene tree supported the association of the females with the males.

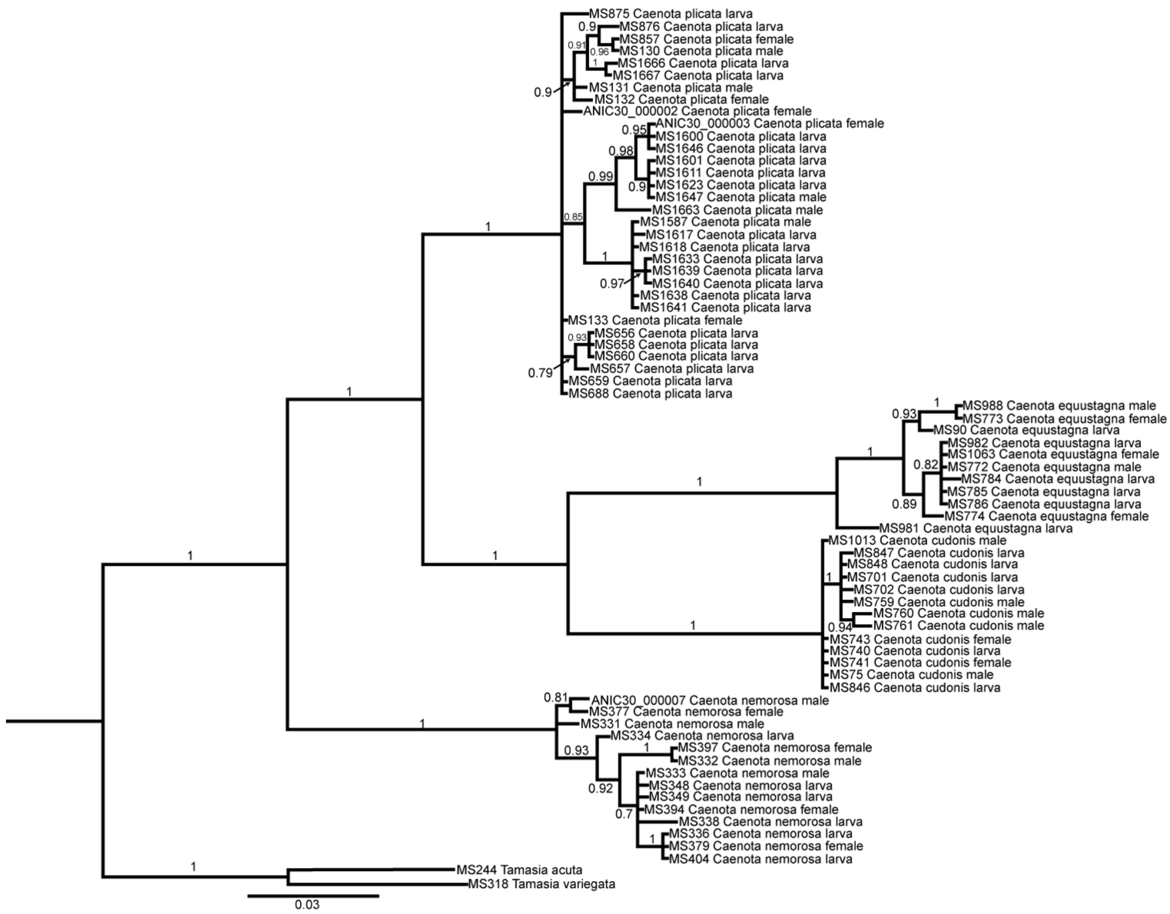

FIGURE 1. COI gene tree as produced by MrBayes 3.1 (Ronquist & Huelsenbeck 2003).

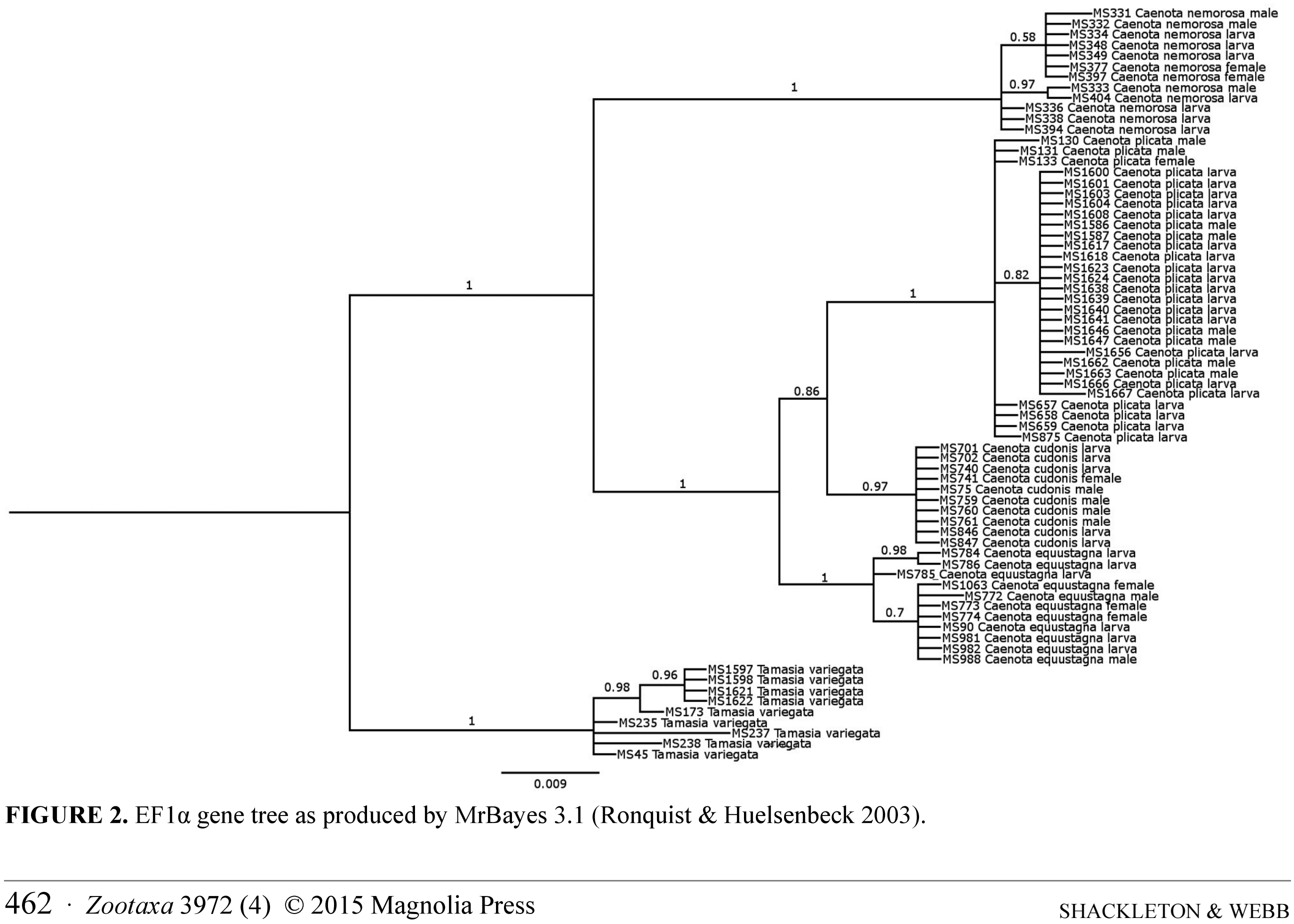

FIGURE 2. EF1α gene tree as produced by MrBayes 3.1 (Ronquist & Huelsenbeck 2003).

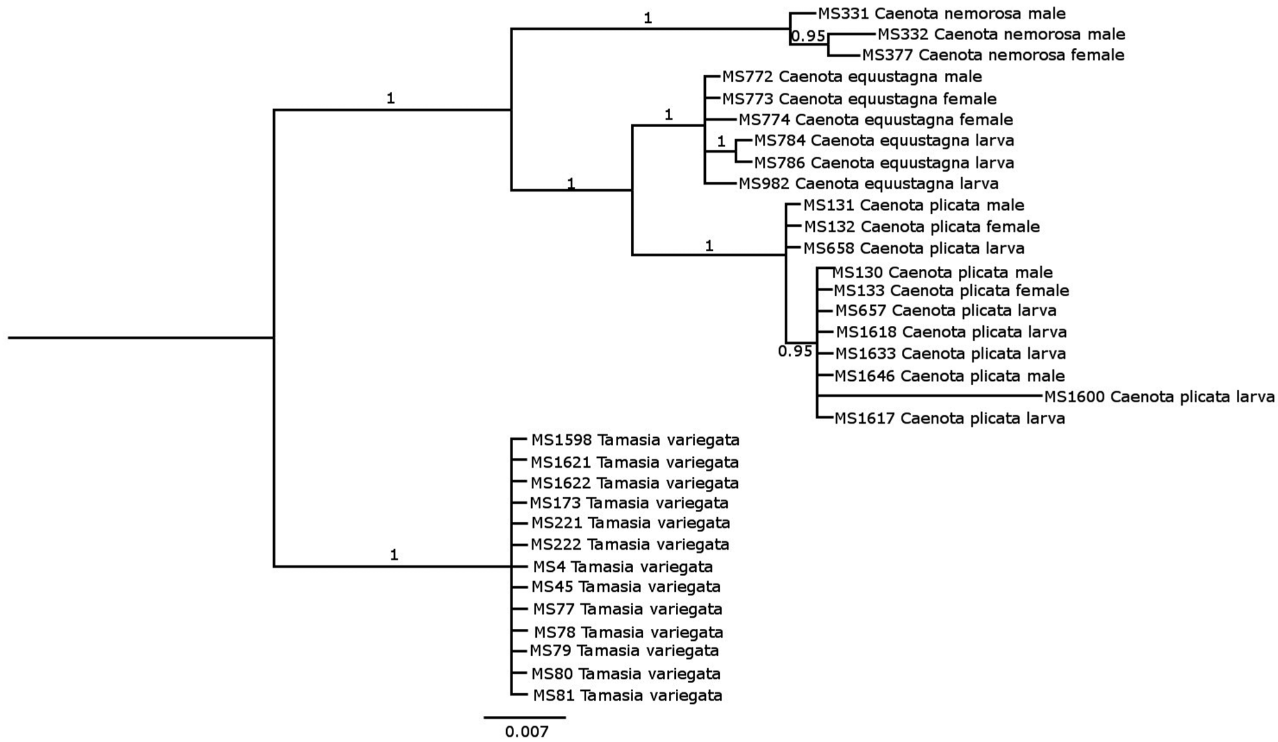

FIGURE 3. POL2 gene tree as produced by MrBayes 3.1 (Ronquist & Huelsenbeck 2003).

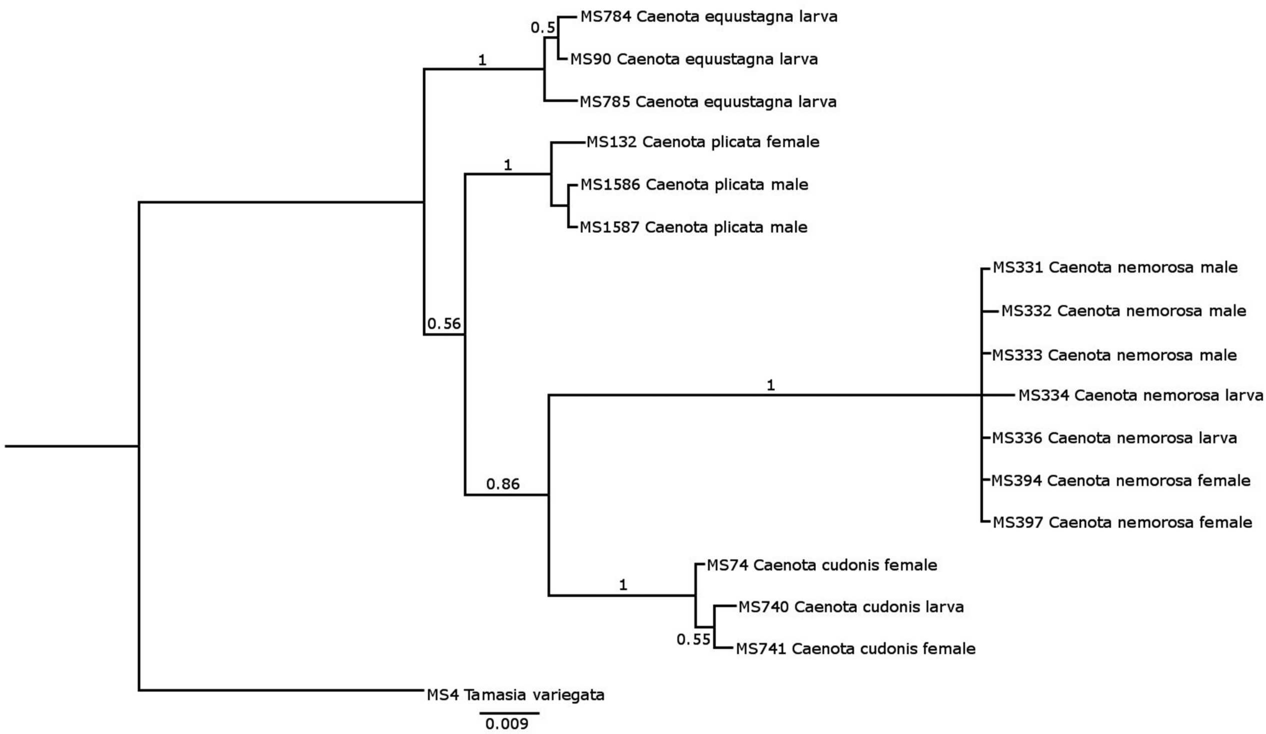

FIGURE 4. CAD gene tree as produced by MrBayes 3.1 (Ronquist & Huelsenbeck 2003).

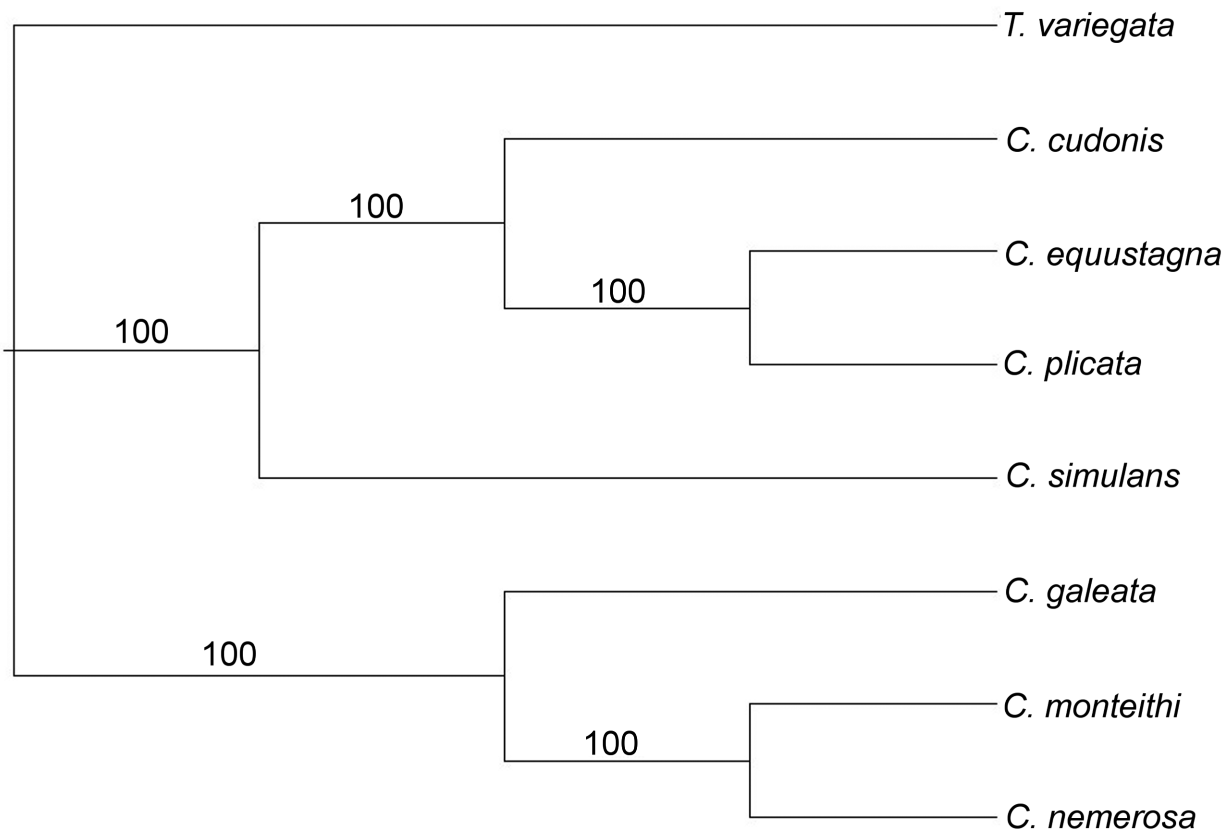

FIGURE 5. Maximum Parsimony majority rule consensus tree from 33 morphological characters of 7 species of *Caenota* and 1 species of *Tamasia*. Values on the branches are bootstrap values calculated from 1000 bootstrap replications.

In the EF1α gene tree, included larval specimens of *C. nemorosa* were nested with adult male specimens and identical sequences were shared between at least 1 larva and 1 adult male. All members of the *C. cudonis* clade shared identical sequences. Three larvae of *C. equustagna* (MS90, MS981, and MS982) shared identical sequences with a male specimen (MS988).

A larva of *Caenota nemorosa* (MS336) shared an identical CAD gene sequence with 2 males (MS331 and MS333). No associations could be inferred from the POL2 gene tree.

The MP analysis of morphological characters resulted in a single best tree (Fig. 5) from 144 rearrangements. The analysis revealed two distinct clades: one composed of the more southern species (*C. cudonis*, *C. equustagna*, *C. simulans* and *C. plicata*) and one composed of the three northern species (*C. nemorosa*, *C. monteithi*, and *C. galeata*). All branches were supported by 100% bootstrap values. However, the analysis failed to resolve the relationships among the southern clade, northern clade and the out-group, resulting in a trichotomy.

Antennae and maxillary palpi. The males of *Caenota* spp. possess structures associated with the maxillary palpi and antennae that are diagnostic for the genus and its included species (Mosely & Kimmins 1953; Neboiss 1984).

Two processes are associated with each antennal scape, both arising from a sheath that encloses the scape (Fig. 10). The first of these is a large membranous expansion, somewhat rounded in lateral view, which rises above the head, meeting its counterpart along the midline, to form a cap. This structure is attached to the posterior margin of the scape. The inner surface is concave and contains a large number of setae. Its size and shape and area of attachment to the scape vary among species. This structure is referred to as the posterior antennal projection.

The second process is usually much smaller, often finger-like and projecting from the anterior surface of the scape. However, in *C. cudonis* it is the larger of the 2 antennal processes. Its length, width, and area of attachment to the scape also vary among species. This structure is referred to as the anterior antennal projection.

The maxillary palpi are highly modified. Segments I and II are greatly expanded, protruding forward from the head capsule and projecting towards the antennae. They are somewhat laterally compressed and meet along the midline to form a cup in front of the head. The inner surface of segment I contains a dense mat of fine setae, which is dark or pale depending on the species. While other setation is usually sparse, 1 species possesses a dense fringe of setae along the ventral surface and another species bears a large disk of setae protruding from the anterior surface. A translucent flange extends along all the dorsal margin of segment II. In some species this flange can be rather deep, while in others it is reduced.

Maxillary palp segments III, IV, and V are greatly reduced and are directed posterad. Segments III and IV are bulbous and short. The shape of segment V varies among species from being short and pointed to long and slender. It is covered with dense pale setae, which can make the segment appear longer than it is. In most species this segment extends posterad to be held within the structures of the antennal scape. The length of this extension appears to be species specific.

Family CALOCIDAE

Genus *Caenota* Mosely 1953 (in Mosely & Kimmins 1953)

Type species: *Caenota plicata* Mosely, by original designation.

Mosely (in Mosely & Kimmins 1953) supplied a description of the genus based on adult males of *C. plicata* and *C. simulans*. Neboiss (1977) added to this description and described the females of *C. plicata*. These descriptions indicated that the maxillary palpi likely each consists of 3 segments. After clearing in potassium hydroxide and viewing under greater magnification than that which would have been available to Mosely and Kimmins, we conclude that the maxillary palpi have 5 segments, the 3rd and 4th being greatly reduced. The inclusions of *C. cudonis* and *C. equustagna* in the genus do not alter previous diagnoses except that, in these species, the fold in each posterior wing is greatly reduced.

Caenota larvae can be distinguished from other Calocidae by the presence of a dark sclerotised ridge medially on the metanotum and a case composed of leaf panels arranged in 2 dorsal and 2 ventral rows (Jackson 1998; Shackleton 2013). There are few differences among the larvae of *C. plicata*, *C. nemorosa, C. cudonis*, and *C. equustagna*, the distinguishing features being the shape of the lateral margins of the anterior section of the frontoclypeus and the presence or absence of a row of setae along the dorsal margin of each foretrochantin.

Revised generic description. Adult. Head with eyes positioned near anterolateral corners of head capsule; posterior setal warts large in females, absent in males. Antennae each with scape normal in females, in males with either small or large projection on anterior surface and large membranous projection on posterior surface. Maxillary palpi each 5-segmented, normal in females, irregular in males with first 2 segments expanded, mesal surface with dense pale or dark, fine setae, segments III and IV reduced, segment V either reduced or elongate. Labial palpi each 3-segmented. Wing venation similar in male and female; each forewing with discoidal cell present, forks I, II, III, and V present; each hind wing without discoidal cell, vein R_1 parallel to Sc until just beyond midpoint of wing, then fusing for short distance before separating to approach wing margin.

Pupa. Head with mid dorsal area having 2 dark setae; frons with pair of 2 dark setae on anterolateral corners; labrum as wide as long, lateral margins with distally projected lobe at about 1/3rd length from base, anterior margin angular or convex; mandibles each either with or without small tooth, with pair of dark setae near base of lateral margin; maxillary palpi of male broad and rounded basally, each abruptly constricted and tapering to long point, unmodified in female; antennae as long as body, expanded basally in male. Abdomen with paired anterodorsal hookplates on segments III to VI; posterodorsal hookplates on segment V only; lateral abdominal fringe extending on each side from anterolateral margin of segment VI to anterolateral margin of segment VIII, small tuft on anterolateral margin of segment V; terminal processes slender, apically acute and turned outward, with long dark setae. Pupal case similar to larval case, posterior and anterior apertures narrow.

Larva. Head dark brown except for pale area on each gena posterior to ventral apotome; frontoclypeus widening abruptly at about mid distance, with paired setae 6 either close to constriction or halfway between constriction and anterior margin, 2 primary setae at each anterolateral corner, 1 pale secondary seta on each lateral margin of anterior half about mid length directed mesad. Antennae situated close to eye. Pronotum dark brown; anterior margin with 2 distinct types of setae, 1 type more slender, bent mesad and sometimes lighter in colour; dorsum with long dark setae in anterior half. Mesonotum pale, with slightly darker muscle scars in anterior half, around 25 dark setae in each anterolateral corner; each sclerite with 4 to 6 long dark setae subapically along anterior margin, 1 seta posterior to these and nearer to the median ecdysial line, 2 long and 1 or 2 short setae at approximately mid sclerite. Metanotum pale, scleritisation weak and restricted to anterior half, medial line of each sclerite with darkly pigmented ridge; each setal area 1 (*sa*1) with about 5 setae, each setal area 2 (*sa*2) with 1 seta, each setal area 3 (*sa*3) with 2 long setae and 2 or 3 smaller setae. Abdomen having segment I lateral humps without sclerites; abdominal gills present on segments II and III, absent or present on segments I and IV; tergite IX with 4 long and 6 short setae; anal lateral sclerites each with about 12–15 long dark setae along posterior margin; abdominal claws each with 1 accessory tooth. Case composed of panels of plant material arranged in 2 rows dorsally and 2 rows ventrally.

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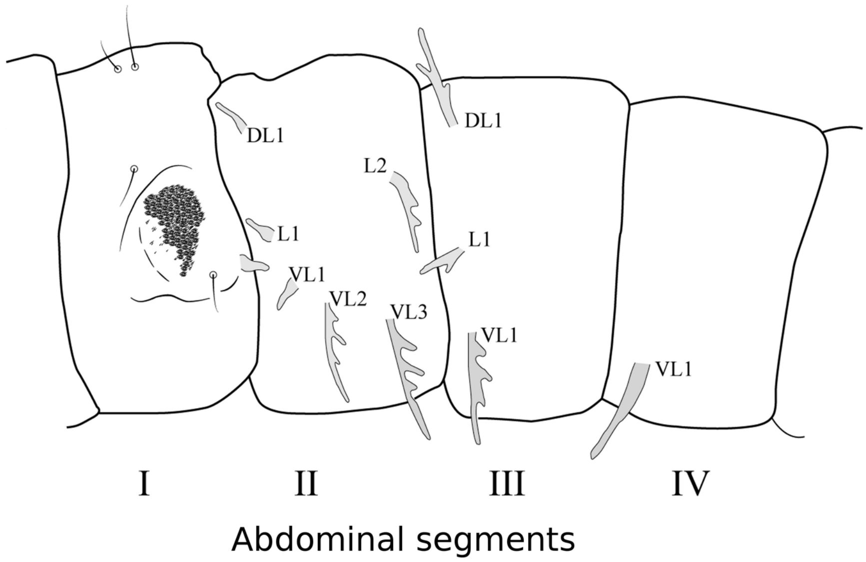


FIGURE 6. Stylised schematic of abdominal segments I to IV showing the placement of gills. Gills are numbered according to their placement along either the dorsal (DL), lateral, (L), or ventrolateral (VL) lines and their position from anterior to posterior.

***Caenota galeata* Neboiss 1984**
Figs 7, 8

Descriptions of the adult male and female were given by Neboiss (1984).

Adult. Male head capsule as in Figs 7, 8. Antennae each with anterior antennal projection slender, arising about 1/2 length of scape, terminating at distal margin of scape; posterior antennal projection with dorsal and posterior margins rounded in lateral view; inner surface concave with fringe of dense pale setae around distal margin, tuft of pale setae in distal area of anterodorsal corner. Maxillary palpi held closely together; each with segments I, II, and III pigmented; segments IV and V fleshy; segments I and II with sparse setae on outer surface, with dense, pale, setae on inner surface, their dorsal and ventral margins with fleshy flange; segment II ventral flange with tuft of pale setae close to distal margin; segment III small, arising before apex of segment II; segment IV small, translucent, bulbous; segment V slender, slightly longer than length of segments I and II combined, extending to posterior margins of posterior antennal processes, basal 2/3rds covered with dense pale setae, distal 1/3rd with sparse setae.

Material examined. AUSTRALIA: North Queensland, 25 km along Mt Lewis Rd, SW of Mossman, 25 Dec 1980, M.S & B.J. Moulds, 5 males (MV WTH-0788). North Queensland, Upper Little Mossman Riv. nr. Mt Lewis, 10 Dec 1974, M.S. Moulds, 1 male (MV WTH-0938).

Distribution. Australia (northern Queensland, Neboiss 1984)

Ecology. This species has been recorded only from the wet tropical area around Mount Lewis National Park, northern Queensland. No ecological information was provided with the species description by Neboiss (1984) and specific water bodies are not mentioned. Furthermore, no new material was collected as part of this present study.

For this reason no specific within-stream ecological information is provided here. However, the altitude at which one specimen, mentioned by Neboiss (1984), was collected was indicated as 1100 m. At this altitude the Mt Lewis National Park is dominated by cloud forest. The area has a high annual rainfall and the rivers are characterized by large boulders, abundant moss and a dense riparian zone (pers. obs.).

Caenota monteithi Neboiss 1984

Figs 9, 10

Descriptions of the adult male and female were given by Neboiss (1984).

Adult. Male head capsule as in Figs 9, 10. Antennae each with 1st segment of flagellum greatly elongated; anterior projection slender, arising from first 1/2 of scape, gradually tapering to slender point, terminating close to distal margin of scape; posterior projection dorsal and posterior margins rounded in lateral view, inner surface concave, with fleshy area along distal margin, dense pale setae along subapical area of distal margin. Maxillary palpi held closely together; each with segments I, II, and III pigmented, segments IV and V fleshy; segments I and II with outer surfaces sparsely setose, inner surfaces with dense, pale, setae, their ventral and dorsal margins each with transparent flange of medium depth; segment III small, arising before apex of segment II; segment IV small, translucent, bulbous; segment V obscured by brush of dense pale setae, slender, about as long as segment II, brush of setae expanding apically, peripheral margin longer than medial margin, extending just beyond apex of segment V.

Material examined. AUSTRALIA: North Queensland, Bellenden, Ker Range, Summit Tv Stn, 1560 m, 1–7 Nov 1981, Earth Watch/QLD Museum, 3 males (MV WTH-1125).

Distribution. Australia (northern Queensland, Neboiss 1984)

Ecology. Specimens listed in the original description by Neboiss (1984) were collected from around the Bellenden Kerr Range and Wooroonooran National Park to as far west as Mareeba, north Queensland. No ecological information was given by Neboiss (1984).

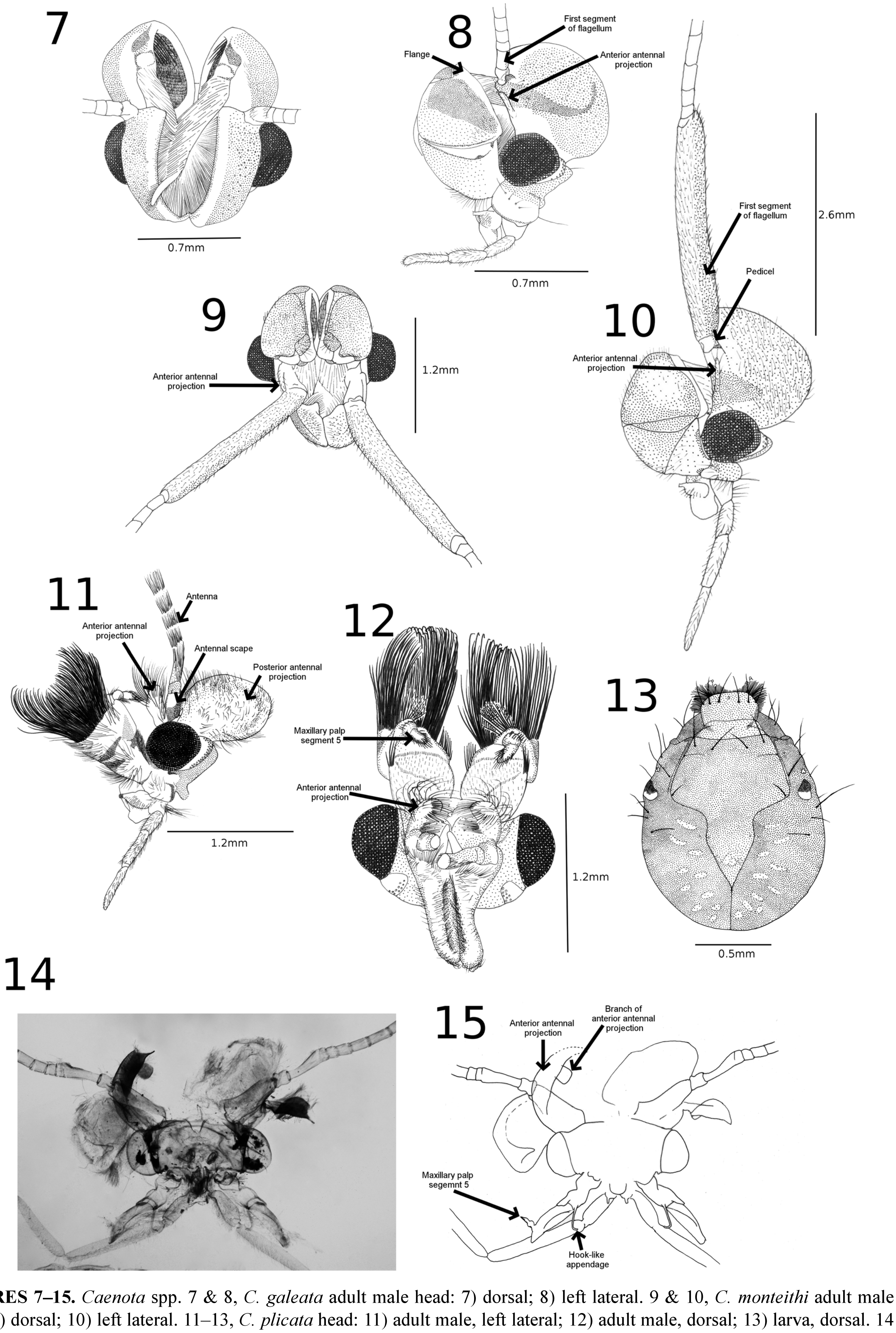
Caenota plicata Mosely 1953

Figs 11–13

A description of the adult male was given by Mosely in Mosely & Kimmins (1953). The female was described by Neboiss (1977).

Adult. Male head capsule as in Figs 11, 12. Antennae each with anterior projection arising from base of antennal scape and extending nearly to distal margin of pedicel, outer surface covered in pale setae, becoming darker on distal margin, inner surface concave, with small patch of golden and dark setae towards anterior edge of concavity; posterior projection relatively small, about size of head in lateral view, ovoid, anterodorsal corner extending anterad into slender, finger-like projection, outer surface covered with dark and pale setae, denser patch of dark setae on anterodorsal corner, inner surface concave and having this cavity filled with thick golden scale-like setae, distal margin with dense band of dark setae, becoming paler towards posterior corner and along posterior edge. Maxillary palpi rotated 90 degrees, not held closely together; each with segments I and II pigmented; segments III, IV, and V fleshy; segments I and II outer surfaces with dark setae, inner surfaces with dense pale setae, each with small flange along dorsal and lateral margins; segment II with large circular brush of dark setae, directed anterad; segment III arising before apex of segment II, with small brush of setae on anterior surface; segment IV bulbous, about 1/2 size of segment III, with small brush of setae on ventral surface; segment V small, abruptly tapering, setose.

Larva. Approximate length 12 mm at maturity. Head (Fig. 13) having frontoclypeus with lateral margins of anterior section relatively straight, converging towards anterior margin; setae 6 positioned at constriction; posterolateral corners at constriction somewhat rounded. Pronotum with narrow transverse line of setae, one or two setae deep, at about 1/3rd distance from anterior margin (as in Figs 44, 66). Legs having each foretrochantin with single, long, dark setae about mid-length on anterodorsal margin (as in Fig. 45). Abdomen with gills either simple or branched on segments II and III only; segment II gills VL2 either present or absent, VL3 present, L2 either present or absent, DL1 either present or absent; segment III gills VL1 present, DL1either present or absent.



FIGURES 7–15. *Caenota* spp. 7 & 8, *C. galeata* adult male head: 7) dorsal; 8) left lateral. 9 & 10, *C. monteithi* adult male head: 9) dorsal; 10) left lateral. 11–13, *C. plicata* head: 11) adult male, left lateral; 12) adult male, dorsal; 13) larva, dorsal. 14 & 15, *C. simulans* adult male head, anterior: 14) original photo provided by the BMNH; 15) line drawing adapted from photo.

Material examined. [AUSTRALIA:] Lucky Hit Ck site 2 on Lucky Hit Ck Rd, near Lucyvale, Victoria, 36º 18' 36"E 147º 35' 9.6"S, 13 Jan 2010, M. Shackleton, 2 males (MV MS130, MS131), 8 larvae (MV MS137, MS174–MS180). Lucky Hit Ck, Lucky Hit tk, near Lucyvale, Victoria (EPA site-AFC), 24 Nov 2009, EPA Victoria, 2 larvae (MV MS232, MS233). Chalet Ck at Mt. Buller, Victoria, -37º 8' 60"E 146º 26' 59.64"S, M. Shackleton, 2 larvae (MS MS267, MS268). White Bridge on Mt Buller Rd, Victoria, M. Shackleton, 7 larvae (MS MS250–MS256).

Distribution. Australia (southeast, Neboiss 1986).

Ecology. No ecological information was given with the original description provided by Mosely in Mosely & Kimmins (1953) nor in subsequent publications. From the collection of specimens for the current study it appears that *Caenota plicata* larvae inhabit a range of flow conditions from small creeks to large rivers. As larvae, they are often found in slower flowing areas, attached to the underside of boulders, where they feed on vegetable matter. In smaller streams they can be found in areas of shallow water and have been collected from near vertical conditions. Pupae are generally found more towards the middle of rivers in more permanently flowing areas.

Caenota simulans Mosely 1953

Figs 14, 15

A description of the adult male was given by Mosely in Mosely & Kimmins (1953). The only known specimen of *C. simulans* is housed at the BMNH and has been dissected and mounted in Canada Balsam. The following description was made based on photographs of this specimen and the original drawings by Mosely and Kimmins (1953). Due to the poor condition of the specimen, some features are difficult to distinguish.

Adult. Male head capsule as in Figs 14, 15. Antennae each with anterior antennal projection long, about length of scape, pedicel, and 1st antennal segment combined, strongly angled towards midline, with rounded branch subapically on ventral surface; posterior antennal projection large, rounded, with fringe of setae around distal margin. Maxillary palpi relatively small; each with segments I and II much larger than segments III–V; segment I with long, hooked projection subapically on medial surface, dorsal margin projecting anterad over first 1/5th of segment II; segment II about as long as segment I, medial surface with enclosed setal area; segments III and IV short; segment V short, abruptly tapering.

Material examined. [AUSTRALIA:] Queensland, National Park, 3000 ft, 2 Jan 1922, British Museum of Natural History, Tillyard Collection, 1 male (BMNH(E) 250245).

Distribution. Australia (southern Queensland, Mosely and Kimmins 1953). The southern Queensland status is assumed given that the location provided by Mosely and Kimmins (1953) was simply "Queensland, National Park, 3000 ft, 2.i. 1922" and that the most likely candidate from this time is Lamington National Park.

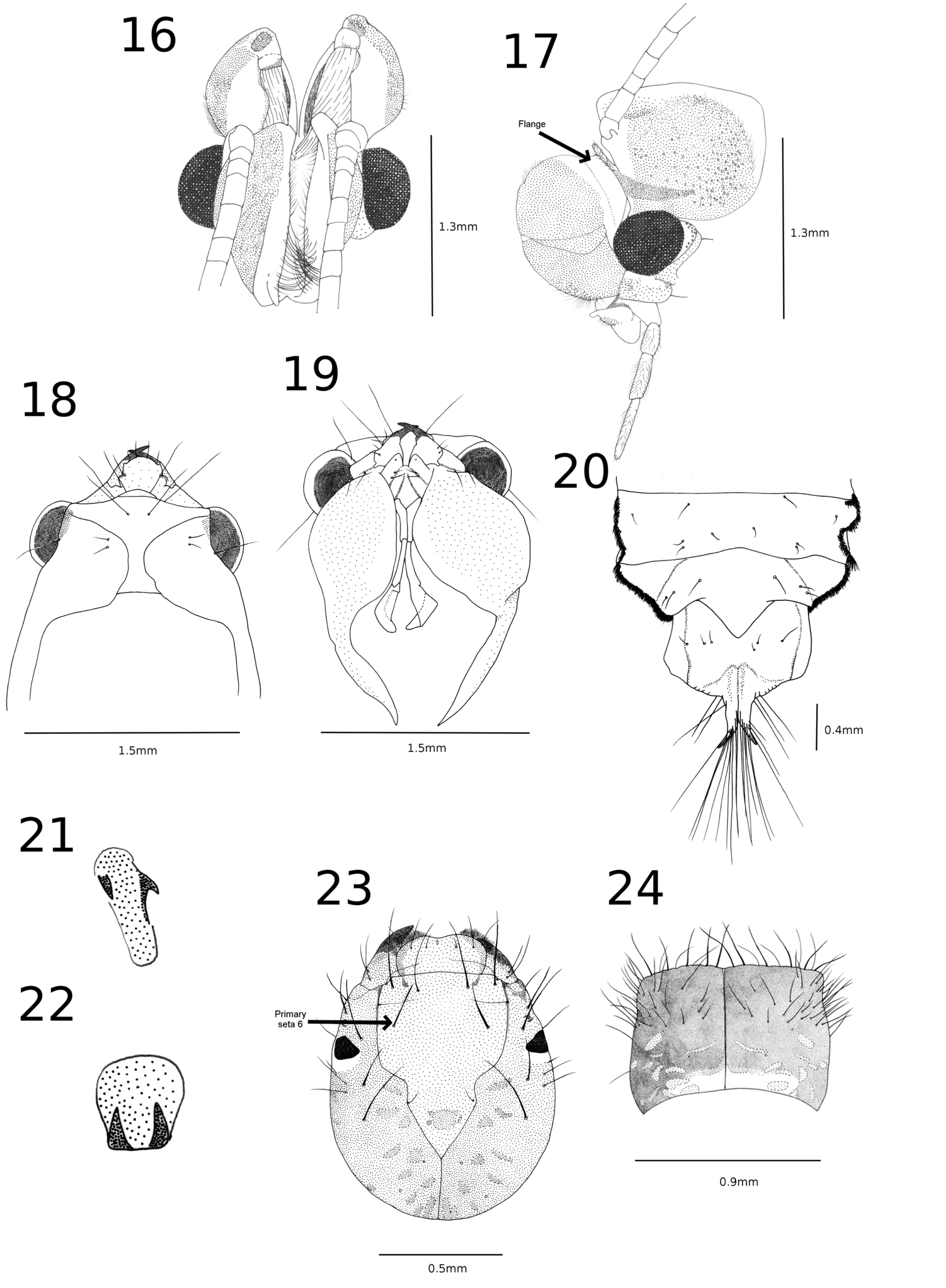
Ecology. No ecological information was given with the original description provided by Mosely (in Mosely & Kimmins 1953) and no subsequent specimens have been collected in order to ascertain the likely habitat preferences of this species.

Caenota nemorosa Neboiss 1984

Figs 16–24

Descriptions of the adult male and female were given by Neboiss (1984).

Adult. Male head capsule as in Figs 16, 17. Antennae each with anterior projection slender, arising from first 1/3rd of scape and terminating bluntly before distal margin of scape; posterior projection with dorsal and posterior margins usually rounded in lateral view; inner surface concave, having ventral surface of this concavity with dense setae; distal margins of inner surface fleshy, with fringe of pale setae along dorsal and posterior margins; dorsoposterior corner of fleshy margin with tuft of darker setae, sometimes produced distally and giving angled appearance to posterior and dorsal margins of posterior projection in lateral view. Maxillary palpi held closely together; each with segments I, II, and III pigmented; segments IV and V fleshy; segments I and II each having outer surface with sparse setae, inner surface with dense pale setae, their dorsal and ventral margins each with fleshy flange; segment II dorsal flange large, about 2/3rds depth of segment, lateral flange with tuft of dark setae



FIGURES 16–24. *Caenota nemorosa*. 16 & 17 adult male head: 16) dorsal; 17) left lateral. 18–22 pupa: 18) head, dorsal; 19) head, ventral; 20) terminal segment, dorsal; 21) anterior hook plate, dorsal; 22) posterior hook plate, dorsal. 23 & 24, larva: 23) head, dorsal; 24) pronotum, dorsal.

close to distal margin; segment III small, arising before apex of segment II; segment IV small, translucent, bulbous; segment V of moderate length, about as long as segments I and II combined, slender, having dorsal and ventral surfaces and basal area clothed with long, dark, setae extending beyond apex of segment.

Pupa. Male head as in Figs 18, 19. Mandibles each with small, indistinct subapical tooth mesally. Labial palpi each with segment III expanded. Abdomen having 1 pair of anterior hookplates on tergites III to VI and 1 pair of posterior hookplates on tergite V; anterior hookplates (Fig. 21) with 2 or 3 hooks; posterior hookplates (Fig. 22) with 2 hooks; segment IX (Fig. 20) relatively square, without lateral projections, with raised triangular area dorsally; abdomen terminating in pair of tapering sclerotized processes curved dorsolaterad to acute apices, each with single basolateral setae, three basoventral setae (only two figured) and around 10 subapical setae; ventral surface with three pairs of long setae arranged close to one another near mid-line and directed towards lateral margin, one pair of shorter setae positioned more lateral to these.

Larva. Approximate length 7.5–8.5 mm at maturity. Head (Fig. 23) having frontoclypeus anterior section relatively square, with lateral margins parallel towards anterior margin; setae 6 positioned halfway between constriction and anterior margin of frontoclypeus. Pronotum (Fig. 24) with scattered setae in anterior half. Each foretrochantin with single long, dark seta at about mid-length of anterodorsal margin. Abdomen with gills either simple or branched; segment I on each side with gill either absent or present laterally posterior to spiny patch; segment II gills VL1 and VL2 either present or absent, VL3 present, L1 and L2 either present or absent, DL1 either present or absent; segment III gills VL1 present, DL1 either present or absent; segment IV gill VL1 present or absent, unbranched.

Material examined. [AUSTRALIA: North Queensland] Huntersbrook Ck on Gordonvale–Atherton Hwy, 17º 10' 38.6"S 145º 41' 30.8"E, 20 May 2010, J.M. Webb and M. Shackleton, 3 males (QM MS388–390), 10 females (QM MS391–MS400), 11 larvae (QM MS401–411 and MS590), 1 pupa (QM MS346). Granite seep on Gordonvale–Atherton Hwy, 20 May 2010, J.M. Webb and M. Shackleton, 4 larvae (QM MS576–579). Upper Freshwater Ck, Whitfield Ra. nr Cairns, 3 Apr 1975, M.S. Moulds, 2 males (MV WTH-1121). Lock Davies Ck Rd, Lamb Ra. Mareeba dist., 10 Nov 1974, M.S. Moulds, 2 males (MV WTH-1122).

Distribution. Australia (northern Queensland, Neboiss, 1984).

Ecology. The habitat for the larva of *C. nemorosa* appears to be very specific. Of the areas that were visited along the Gordonvale–Atherton Highway, only 2 sites yielded *C. nemorosa* larvae. At each site, most of the larvae were found attached to, or near, tree roots and organic matter in areas of very shallow, but relatively fast flowing water. Larvae were always submerged and never found in the splash zone. At the Huntersbrook Creek site, a few larvae were collected from boulders in fast flowing water to a depth of about 30 cm. Among the specimens examined by Neboiss (1984) is one that was collected from Bamaga, Cape York. This locality seems anomalous in regards to the other, wet tropical, sites around the Cairns region, in being tropical savannah with very low elevation.

Caenota cudonis **sp. nov.**

urn:lsid:zoobank.org:act:F18F39A2-1212-4944-81A2-3C625341B21A

Figs 25–45

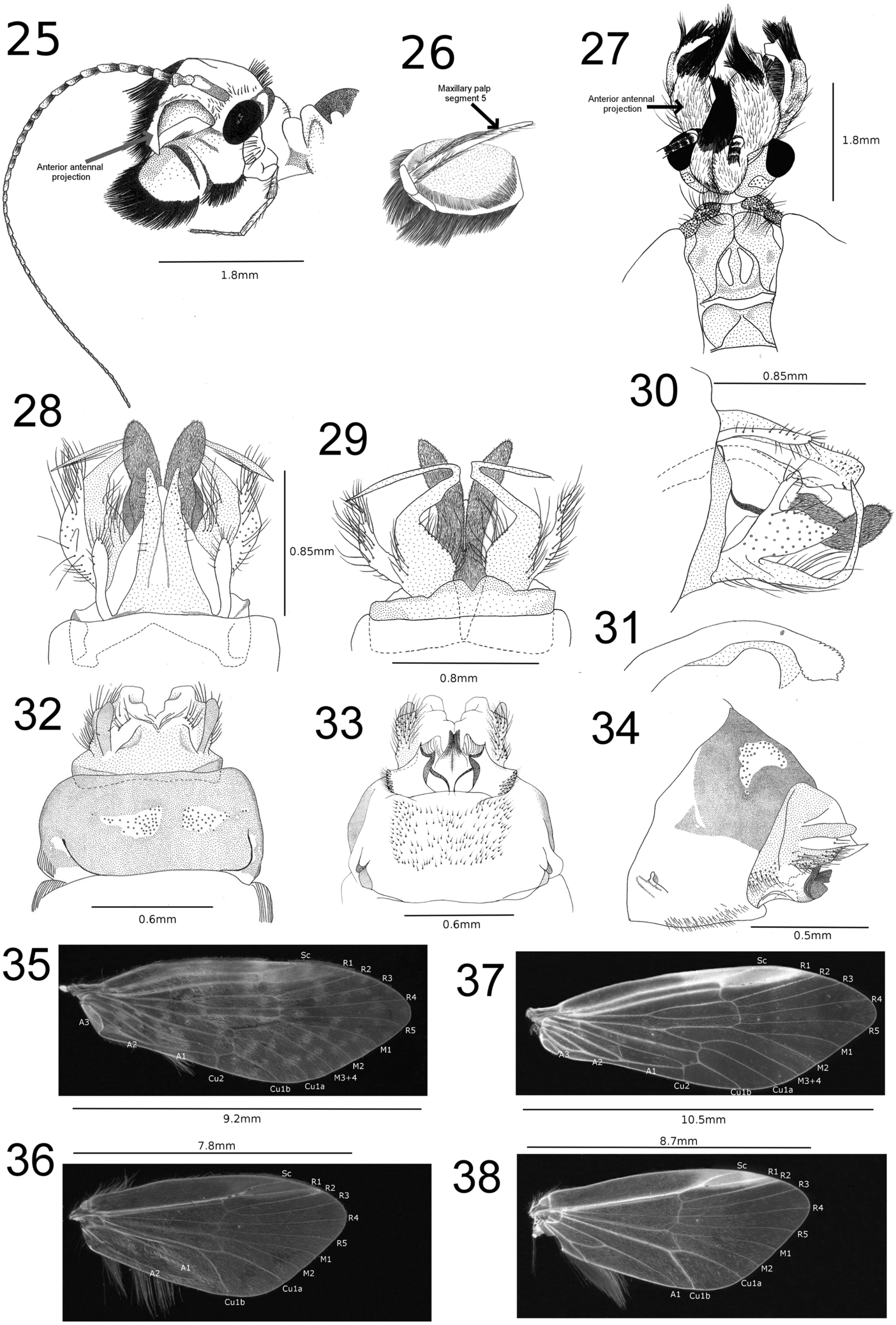
Diagnosis. *Caenota cudonis* is unique among the species of this genus in that the male anterior antennal process is very large, with a fringe of dark setae on the dorsum of its anterior 1/3rd, and the male maxillary palpi each have the anterior margin of segment II rounded, with a dense fringe of dark setae. The genital structures of the males of *C. cudonis* share similarities with those of *C. plicata*, *C. equustagna* **sp. nov.** and *C. simulans*, with the presence of a large pair of lobes associated with the phallocrypt, and the inferior appendages having a similar shape. However, in this species each inferior appendage has a broad dorsal projection as opposed to the more slender projections of *C. equustagna* **sp. nov.** and *C. simulans*. Lobes associated with the male phallocrypt are also present in *C. galeata* but are much smaller. Females of *C. cudonis* can be distinguished from other *Caenota* species by the broad, rectangular setal patch of sternite VIII as well as the 2 pairs of intricate, sclerotised folds on the ventrolateral margins of this same segment. Of the four species for which the larvae are known, the larva of *C. cudonis* differ from that of *C. nemorosa* in having setae 6 positioned at the posterolateral corners of the anterior section of the frontoclypeus rather than mid-way along the lateral margins of this section. The larva of *C. cudonis* differs from *C. equustagna* **sp. nov.** in having only a single seta on the dorsal margin of each foretrochantin and from both *C.*

equustagna and *C. plicata* in that the lateral margins of the anterior section of the frontoclypeus do not strongly converge anteriorly.

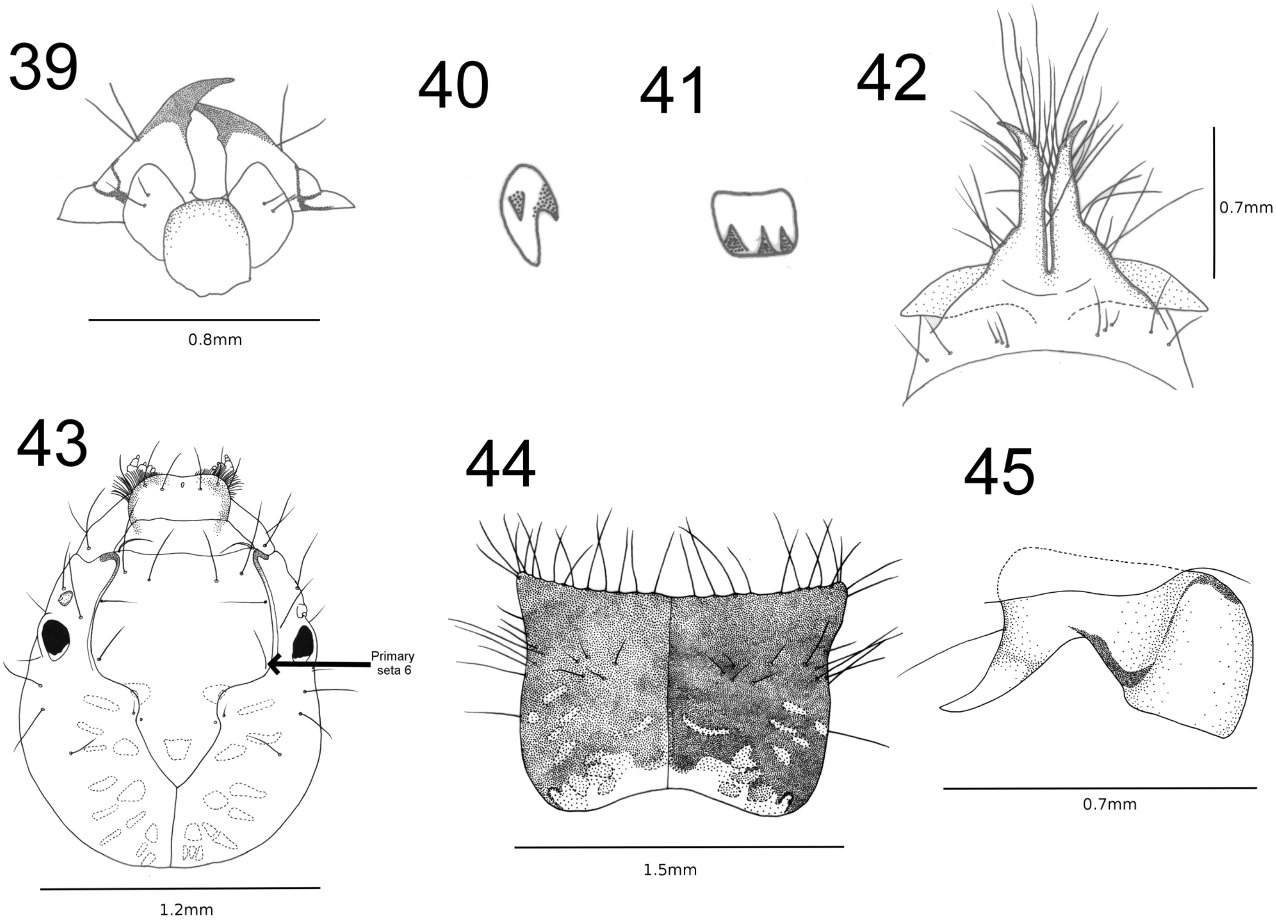
Description. Male. Length of each forewing 8–12 mm, n=13. Head (Figs 25 and 27) with dorsum depressed anteriorly, capsule relatively short and wide, width about twice length; eyes positioned anteriorly on lateral margins; postocular setal warts present, wider dorsally, tapering ventrally; small pair of setal warts on anterior margin of head capsule just above maxillary palpi, translucent, raised; no other setal warts present on head. Antennae slightly shorter than forewings, banded by darker setae on base of each segment of flagella; anterior antennal processes large, broad, tapering anteriorly, each with dense fringe of long dark setae on dorsum of anterior 1/3rd, inner surface concave, opposing inner margins of each pair not quite abutting, diverging anteriorly; posterior antennal processes each with anterior margin projecting forward as far as distal margin of pedicel, dense long dark setae on dorsum anteriorly, sparse setae elsewhere, inner surface concave, small semicircular process arising from posterior margin of each antennal scape medial to posterior antennal process. Maxillary palpi (Fig. 26) each 5-segmented; segments I and II lightly pigmented; segments III, IV, and V fleshy; segments I and II large, their ventral margins each with dense fringe of long dark setae, inner surfaces with dense golden-brown setae, small flanges along dorsal and ventral margins; segment II anterior margin rounded with dense fringe of long dark setae, some setae with golden-brown tips; segment III small, densely setose; segment IV about 1/2 length of segment III, width greater than length, without setae; segment V longer than segments I and II combined, slender, with dense setae along 3/4ths of lateral surface. Labial palpi each 3-segmented, unmodified, covered in pale medium-length setae. Pronotum (Fig. 27) with 1 pair of long, relatively large, warts. Wings irregularly mottled brown and white. Forewings (Fig. 35) brown with white mottling, each with discoidal cell relatively long, forks I and II sessile, fork III on short pedestal, fork IV absent, crossvein *r* concave, crossvein *cu* (joining Cu_{1b} to Cu_2) above arculus, nygmata in thyridial cell and fork II. Hind wings (Fig. 36) relatively broad; each lacking discoidal cell; fork I on very short pedestal, fork II sessile, fork III on long pedestal, fork V large; nygma in fork II; crossvein *m-cu* present; vein A_2 joining A_1 within apical quarter of vein A_1. Forelegs each with fringe of long dark setae extending from femur to 2nd tarsal segment; setae dorsally on femur, dorsally and laterally on tibia, dorsally on tarsal segments; tarsal segments each with distal posterior margin bearing 2–4 spines. Mid- and hind legs unmodified, each with 2 rows of spines along ventral surfaces of tarsal segments. Genitalia (Figs 28–31) with segment X in dorsal view broadest anteriorly, tapering posteriorly, strongly incised in apical 1/3rd; lateral margins with short strong setae; dorsum with sparse strong setae; lateral surface with subapical projection directed anterolaterad. Preanal appendages slender along basal 1/2 and broader in apical 1/2, broadest about 2/3rds from base, rounded apically, 1/2 length of segment X. Inferior appendages each broad in basal 1/3rd, branching into slender ventral and broad dorsal processes, ventral process tapering to point, strongly angled mesad about 1/3rd from base, then strongly angled dorsolaterad at 2/3rds from base; dorsal projection broad, abruptly tapering apically, with slender projection arising from dorsal margin at about 1/2 length of process. Pair of large projections covered with fine, short, pale setae arising from phallocrypt, angled dorsolaterad in apical 1/2 and diverging apically; lateral margins each with weakly sclerotised ridge extending from base of segment IX to halfway along length of projection. Phallus dorsally with faint keel-like structure (visible in cleared specimen).

Female. Length of each forewing 9.50–12.05 mm, n=15. Head with anterior dorsal section between antennae slightly depressed; postocular area relatively large, eyes positioned anteriorly on lateral margins; postocular setal warts present, broader dorsally, tapering ventrally; posterior setal warts present, long; anterior setal warts present, teardrop-shaped, separated; pair of setal warts present on head capsule medial and anterior to scape. Antennae slightly shorter than forewings; antennal scape relatively broad and long, about length of antennal flagellar segments 1–3 combined. Maxillary palpi each 5-segmented, unmodified. Labial palps each 3-segmented. Pronotum with 2 pairs of warts, mesal pair smaller than lateral. Forelegs without dense setae. Wings as in Figs 37 and 38. Wing venation and colouring similar to those of males except that in hind wing fork II sessile and vein A_2 joining A_1 in basal half of A_1. Abdominal sternite VIII with 2 pairs of intricate, sclerotised folds on ventrolateral margins, forming shallow groove on each side. Genitalia as in Figs 32–34. Preanal appendages stout, relatively uniform in width. Sclerotised keel ventrally along midline.

Pupa. Head having frons with pair of rounded lobes along midline of head capsule; labrum with 3 setae on each of pair of distally projected lobes, 5 dark setae along each anterolateral margin, small pale setae located slightly lateral and ventrally to the most medial dark setae; mandibles each with small subapicomesal tooth distinct (Fig. 39); antennae broad, basal section with prominent angle on lateral margin before constriction, with about 5 setae in



FIGURES 25–38. *Caenota cudonis*. 25) adult male head, left lateral; 26) right maxillary palp, right mesal surface; 27) adult male head, dorsal. 28–31: adult male genitalia: 28) dorsal; 29) ventral; 30) left lateral; 31) phallus, left lateral. 32–34, adult female genitalia: 32) dorsal; 33) ventral; 34) left lateral. 35–38, wings: 35) right male forewing, dorsal; 36) right male hind wing, dorsal; 37) right female forewing, dorsal; 38) right female hind wing, dorsal.



FIGURES 39–45. *Caenota cudonis*. 39–42, pupa: 39) mandibles, ventral; 40) right anterior hook plate of abdominal segment VI, dorsal; 41) right posterior hook plate of abdominal segment V, dorsal; 42) terminal segment of abdomen, dorsal. 43–45, larva: 43) head, dorsal; 44) pronotum, dorsal; 45) left foretrochantin, left lateral.

line dorsally. Abdominal segment I with pair of friction pads dorsally; with 1 pair of anterior hookplates on tergites III to VI and 1 pair of posterior hookplates on tergite V; anterior hookplates (Fig. 40) with 2 or 3 hooks; posterior hookplates (Fig. 41) with 3 hooks; segment IX (Fig. 42) of male with pointed projections arising from ventrolateral margins, directed dorsolaterad; abdomen terminating in pair of tapering sclerotized processes curved dorsolaterad to acute apices, each with 3 basolateral setae, and around 18 subapical setae; ventral surface with single pair of ventrolateral setae at about 1/5 length of segment, single pair of ventrolateral setae at about 1/2 length of segment, single pair of ventrolateral setae at about 2/3 length of segment, and three pairs of closely grouped setae near mid-line at about 1/2 length of segment.

Larva. Approximate length 13 mm at maturity. Head (Fig. 43) having frontoclypeus with lateral margins of anterior section slightly rounded, converging slightly near anterior margin; setae 6 positioned at posterolateral corners of anterior section of frontoclypeus. Pronotum (Fig. 44) having anterior margin with alternating dark and light brown setae; dorsum with narrow transverse line of setae, of one or two setae deep, at about 1/3rd distance from anterior margin. Foretrochantins (Fig. 45) each with single long, dark seta about mid-length on anterodorsal margin. Abdomen with gills either simple or branched; segment I without gills; segment II gills VL1 and VL2 either present or absent, VL3 present, L2 either present or absent, DL1 either present or absent; segment III gills VL1 present, L1 either present or absent, DL1 present; segment IV without gills.

Holotype. Male, AUSTRALIA: New South Wales, Wilson River at Wilson River Road, 31° 12'S 152° 29'E, 29 Sept 2008, J. Dean and D. Cartwright; deposited in the Australian Museum, New South Wales (MS76).

Paratypes. [AUSTRALIA: New South Wales] Collected with holotype, 2 males (AM MS73 & MS75), 1 female (AM MS54). Trib of Williams River, Rocky Crossing, 32° 07'S 151° 29'E, 3 Oct 2008, J. Dean and D. Cartwright, 1 pupae (AM MS85). Williams R, Rocky Crossing 32° 07’S 151° 29’E, 3 Oct 2008, J. Dean and D.

Cartwright, 1 pupa, 1 larva (AM MS91). Williams River, Rocky Crossing, 32° 07'S 151° 29'E, 29 Sept 2007, A. Glaister, J. Dean, and R. St Clair, 7 pupae (AM MS86, MS88, MS89, MS92, and MS95) 5 larvae (AM MS93, MS98, MS100); 32º 6' 59.99"S 151º 29' 0.01"E, 24 Feb 2011, J. Mynott and M. Shackleton, 4 males, 1 female (AM MS952). Wilson River, Wilson River Rd, 31° 12'S 152° 29'E, 30 Sept 2008, J. Dean and D. Cartwright, 1 larva (AM MS84). Wilson River, Wilson River Rd, 31° 12' 25.38"S 152° 28' 46.2"E, 25 Feb 2011, J. Mynott and M. Shackleton, 1 male (AM MS1013), 2 females (AM MS741 and MS742). Trib. of Wilson River, 100 m u/s Wilson River Road, 31° 12'S 152° 29'E, 29 Sept 2008, J. Dean and D. Cartwright, 1 pupa (AM MS97). Trib. of Wilson R, Wilson R Res, 4 Dec 2007, A. Glaister, J. Dean and R. St Clair, 1 pupa (AM MS94). Sharpes Ck, Gloucester River camping area, 32° 03'S 151° 41'E, 2 Oct 2008, J. Dean and D. Cartwright, 1 pupa, 1 larva (AM MS87). Coppernook ck, 30º 17' 33.18"S 152º 49' 3.73"E, 26 Feb 2011, J. Mynott and M. Shackleton, 2 males, 10 females (AM MS1250). Never Never River at Whitney's Rd, 30º 19' 48.06"S 152º 51' 43.98"E, 10 Nov 2010, J. Mynott and M. Shackleton, 3 males (AM MS759, MS760 and MS762), 1 female (AM MS761).

Etymology. From the Latin *cudonis*, a masculine noun in apposition to *Caenota*, meaning "a cap made of raw skin."

Caenota equustagna **sp. nov.**

urn:lsid:zoobank.org:act:E41D5326-C154-4BF2-8044-3764A58AB7BE
Figs 46–67

Diagnosis. This species is most nearly resembles *C. cudonis*. However, the male anterior antennal process, while relatively large, is smaller than the posterior antennal process; the male maxillary palpi have their segments directed anterad and each segment II anteriorly has a whorl of long, dark setae. The female head has 2 to 5 pairs of setose punctures on the head capsule medial and anterior to the scapes. The larval frontoclypeus has the lateral margins of the anterior section relatively straight, converging as they approach the anterior margin; the larval foretrochantins each have many setae along the anterodorsal margin.

Description.Male. Length of each forewing 10–11.5 mm, n=3. Head (Figs 46, 47) with anterior surface depressed, capsule short and wide; eyes positioned anteriorly on lateral margins; postocular setal warts present, wider dorsally, tapering ventrally; no other setal warts on head capsule. First flagellar antennal segment modified, its anterior surface somewhat concave with brush of short dark setae basally, produced anteriorly; anterior antennal process relatively large but smaller than posterior antennal process, broad, flattened, anterior margin with dense, thick, dark setae; posterior antennal process large, rounded in lateral view, with scattered dark setae, posterior and anterior margins with dense dark setae, inner surface concave, with fringes of setae on basal and dorsal margins, 2 clumps of long, dark setae in basal anterior and posterior corners, antennal scape protruding through anterior surface. Maxillary palpi each 5-segmented; segment I broad, ventral surface with large pigmented area and densely scattered setae, lateral surface with narrow area of pigmentation elongated laterally in dorsal 1/2, inner surface densely covered with short yellow setae, anterodorsal corner with brush of long, dark setae; segment II broad, lateral surface with area of pigmentation near posterior margin elongate transversely, ventral surface with dense, long, dark setae, anteriorly with whorl of long, dark setae, inner surface with long pale setae along dorsal margin; segment III arising from dorsal 1/2 of anterior margin of segment II, short, bulbous, inner surface with pale setae dorsally, long dark setae on ventral surface; segment IV shorter than segment III, squat; segment V elongate, slightly shorter than segment II, with brush of long pale setae directed anterad. Labial palpi (broken in specimen) setose. Pronotum with 1 pair of broad setal warts. Forewings (Fig. 56) brown/grey with some white mottling; each with forks I and II sessile, fork III on pedestal, fork IV absent, crossvein *r* concave, crossvein *cu* (joining Cu_{1b} to Cu_2) above arculus, nygmata in thyridial cell and fork II. Hind wings (Fig. 57) relatively broad; each with discoidal cell absent; forks I and II sessile, fork III on pedestal; nygma in fork II; crossvein *m-cu* (joining Cu_{1a} to M) present; anal veins terminating in basal 1/8th of wing, not at wing margin. Foreleg tarsal segments with short, dark setae dorsally; tibiae covered in dense, long, dark setae dorsally and laterally; femora with long, pale setae on dorsal and inner lateral surfaces; costae with inner margins covered in long pale setae; mid- and hind legs unmodified. Genitalia (Figs 49–52) having segment X in dorsal view with lateral margins concave in anterior 1/2, convex in posterior 1/2, tapering posteriorly, strongly incised in apical 1/3rd, with scattered, strong, dark setae, dorsal surface with line of strong, dark setae from about 1/3rd length to near apex; in lateral view broad, rounded apically, with small anteroventral protrusion subapically. Preanal appendages slender, apically rounded, about 1/2 length of segment X. Inferior appendages broad in basal 1/3rd, each branching into slender ventral and broad dorsal processes; ventral process tapering to point, strongly curved mesad at about 1/3rd from base, then strongly curved dorsolaterad at 2/3rds from base; dorsal process extending beyond segment X, tapering to point, with slender, posteriorly directed process arising about 1/2 length on dorsal surface and tapering to point. Pair of large projections covered with fine, short, pale setae arising from phallocrypt, in dorsal and ventral views angled laterad, extending just beyond segment X; in lateral view lateral surface concave, with slender, sclerotised ridge extending from base of segment IX to less than 1/3rd length of projection. Phallus (Fig. 52) in lateral view gradually curved ventrad, dorsal surface convex, lateral surfaces concave, lightly sclerotised along length except for membranous apex, phallotremal sclerite somewhat triangular, positioned dorsolaterally about 3/4ths length.

Female. Length of each forewing 11–13.0 mm, n=4. Head (Fig. 48) with anterior dorsal section between antennae slightly depressed; postocular area relatively large, eyes positioned anteriorly on lateral margins; postocular setal warts present, broader dorsally, tapering ventrally; posterior setal warts present, long; anterior setal warts present, teardrop-shaped, separated; 2 to 5 pairs of setose punctures on head capsule medial and anterior to scapes. Antennae slightly shorter than forewing length; antennal scapes relatively broad and long, each about as long as its pedicel and flagellar segment I combined. Maxillary palps each 5-segmented, unmodified. Labial palps each 3-segmented. Pronotum with 2 pairs of warts, mesal pair smaller than lateral. Wings (Figs 58, 59) with venation and colouring similar to males except that in hind wing fork II sessile and vein A_2 joining A_1 before 1/2 length of A_1. Abdominal segment VIII with single sclerotised fold on ventrolateral margin. Foreleg tibiae and tarsi with short, dark setae. Genitalia (Figs 53–55) with preanal appendages relatively slender, widening posteriorly, apically rounded; sclerotised keel present ventrally along midline.

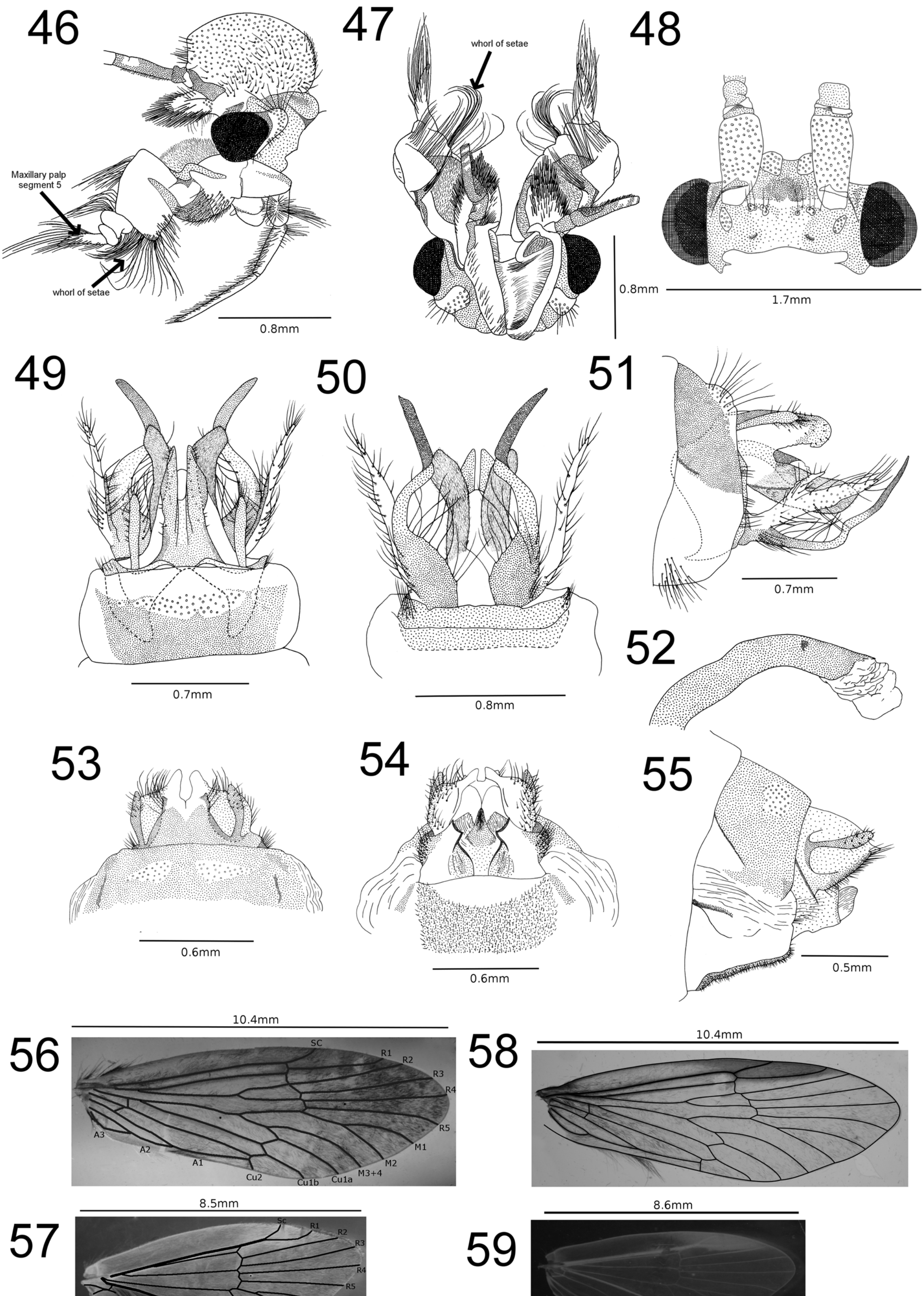
Pupa. Head (Fig. 60, 61) having frons with pair of rounded lobes along midline of head capsule; labrum with 3 setae on each distally projected lobe, each anterolateral margin with 4, long dark setae and 2 small pale setae on anterior margin; mandibles without small subapicomesal teeth; antennae broad basally, each with about 5 setae in line dorsally. Abdominal segment I with pair of friction pads dorsally; tergites III to VI each with 1 pair of anterior hookplates, tergite V with 1 pair of posterior hookplates, anterior hookplates (Fig. 63) with 2 hooks; posterior hookplates (Fig. 64) with 3 hooks; segment IX (Fig. 62) of male with pointed projections arising from ventrolateral margins, directed dorsolaterad; abdomen terminating in pair of tapering sclerotized processes curved dorsolaterad to acute apices, each with 4 basolateral setae, and around 16 subapical setae; ventral surface with three pairs of closely grouped setae near mid-line at about 1/2 length of segment, one pair of setae basad of posterior projections.

Larva. Approximate length 9.5–11.0 mm at maturity. Head (Fig. 65) having frontoclypeus with lateral margins of anterior section relatively straight, converging near anterior margin; setae 6 positioned at constriction; posterolateral corners at constriction relatively sharply angled. Pronotum (Fig. 66) having anterior margin with dark setae; dorsum with narrow transverse line of setae, 1 or 2 setae deep, about 1/3rd distance from anterior margin. Foretrochantins (Fig. 67) each with row of long, dark setae along anterodorsal margin. Abdomen with gills either simple or branched; segment I without gills; segment II gills VL1 and VL2 either present or absent, VL3 present, L1 absent, L2 present or absent, DL1 either present or absent; segment III gills VL1 present, L1 present or absent, DL1 present; segment IV without gills.

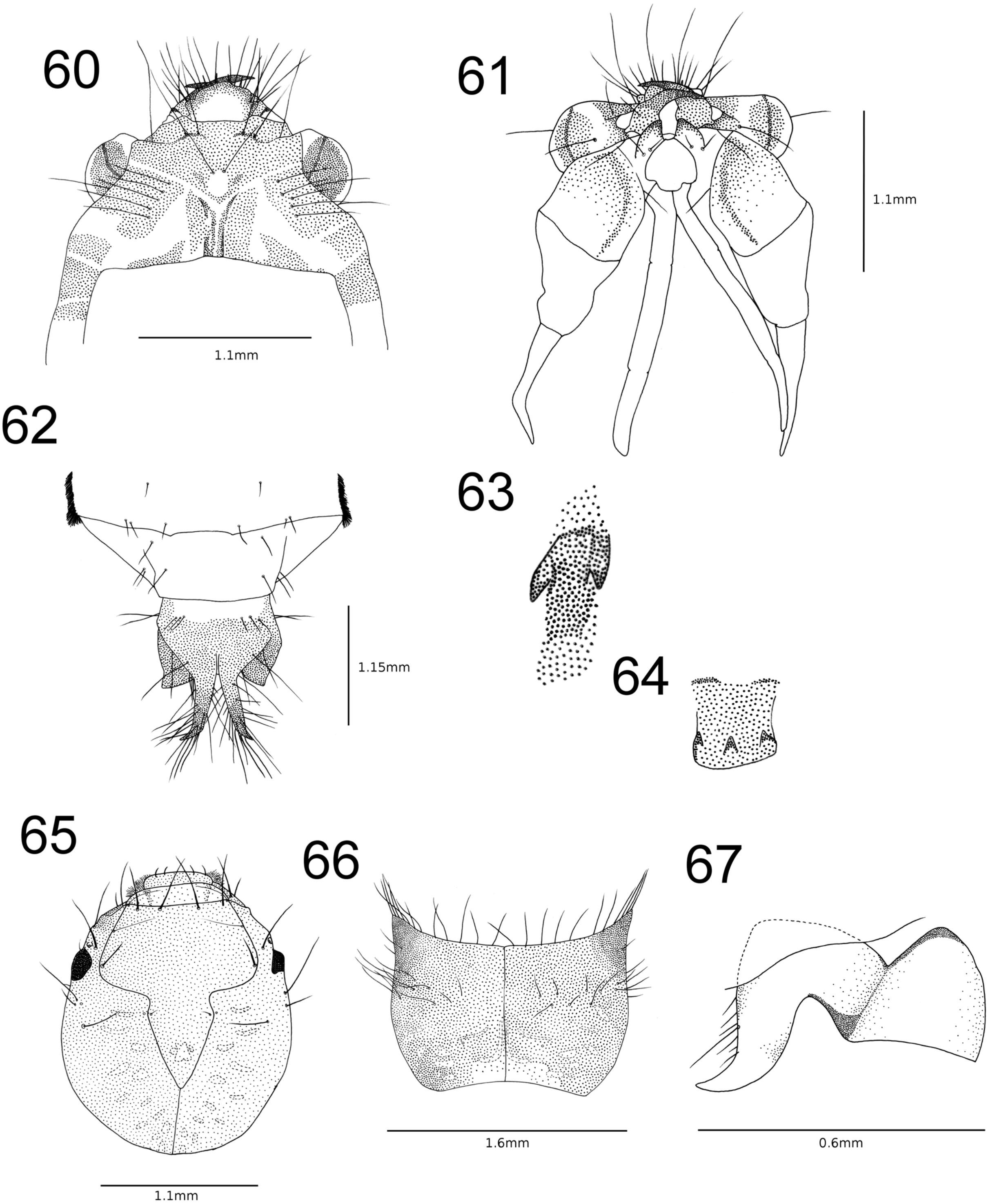
Holotype. Male, [AUSTRALIA: New South Wales] Horse Swamp Ck at Horse Swamp campground, -31° 55' 35.68"S 151° 23' 10.62"E, 24 Feb 2011, J. Mynott and M. Shackleton (AM MS988).

Paratypes. [AUSTRALIA: New South Wales] collected with holotype, 3 females (AM MS773–MS775), 3 male pupae (AM MS99, MS789, MS790), 3 larvae (AM MS786–MS788. Collected at same site as holotype, 11 Nov 2010, J. Mynott and M. Shackleton, 1 male (AM MS772); 24 Feb 2011, J. Mynott and M. Shackleton, 2 larvae (AM MS981 and MS982). New South Wales, Horse Swamp Ck, up stream of Horse Swamp, 31° 56'S 151° 25'E, 2 Oct 2008, J. Dean and D. Cartwright, 3 larvae (AM MS307, MS90, MS96), 1 March 2011, J. Mynott and M. Shackleton, 1 female (AM MS1063). Kunderang Brook on Racecourse Trail, Werrikimbe NP, 31° 8' 8.77"S 152° 17' 19.31"E, 28 Feb 2011, J. Mynott and M. Shackleton, 1 male (AM MS1049).

Etymology. From the Latin *equus* and *stagna*, combined as a pleural neuter noun in apposition to *Caenota*, meaning "the pools of the horse," pertaining to the type locality.



FIGURES 46–59. *Caenota equustagna*. 46 & 47, adult male head: 46) left lateral; 47) dorsal. 48: female head, anterior. 49–52, adult male genitalia: 49) dorsal; 50) ventral; 51) left lateral; 52) phallus, left lateral. 53–55, adult female genitalia: 53) dorsal; 54) ventral; 55) left lateral. 56–59, wings: 56) male right forewing, dorsal; 57) male right hind wing, dorsal; 58) female right forewing, dorsal; 59) female right hind wing, dorsal.



FIGURES 60–67. *Caenota equustagna*. 60–64, pupa: 60) head, dorsal; 61) head, ventral; 62) terminal abdominal segments, dorsal, 63) right anterior hook plate of abdominal segment V, dorsal; 64) right posterior hook plate of abdominal segment V, dorsal. 65–67, larva: 65) head, dorsal; 66) pronotum, dorsal; 67) left foretrochantin, left lateral.

Discussion

Genetic analyses of the 4 genes clearly supported the morphological delimitation of each of the 4 (of 7) species analysed, indicating that the morphological differences used to distinguish among these species do in fact represent true species boundaries.

Associations of larvae with adults were primarily based on the morphological characters of the genitalia of pharate male pupae along with the presence of identifiable larval sclerites in the pupal case. In addition the presence of both adult males and larvae of a single species at the same localities provides further evidence for these associations.

The genetic analyses of the COI and EF1α gene fragments supported the association of larvae and adult males. In both gene trees the larvae, for each species, either occurred nested within the adults, shared identical sequences with a male specimen, or both. The evidence, in total, supports the association of the *C. nemorosa* adult male with the larva collected at the same northern Queensland locality, and the adult males of the 2 new species with larvae collected from their respective localities.

The genus *Caenota* now contains 7 species and descriptions of larvae are available for 4 species. Further investigation may produce a complete knowledge of the larval fauna, which will enable correct identification of these immature aquatic stages.

Key to males of *Caenota* from Australia

1 First segment of each antennal flagellum elongate, much longer than depth of head (Figs 9 and 10). . . . . *C. monteithi*

\- First segment of each antennal flagellum normal, much shorter than depth of head (Figs 8 and 11). 2

2(1) Inferior appendages each with inwardly directed apical spine (Neboiss 1984, figs 23 & 28); anterior projection of each antenna slender (Figs 8 and 17) 3

\- Inferior appendages without inwardly directed spines (Figs 29 and 50); anterior projection of each antenna expanded (Figs 11, 15, 25 and 46) 4

3(2) Segment X with apices curved inward, rounded, and without lateral spines (Neboiss 1984, fig. 26); Maxillary palps each having dorsal margin of segment II with large flange (about 1/3rd depth of segment II) (Fig. 17). . . . . *C. nemorosa*

\- Segment X with apices divergent, angular, and with lateral spines (Neboiss 1984, fig. 22); maxillary palps each having dorsal margin of segment II with small flange (less than 1/3rd depth of segment II) (Fig. 8) . . . . *C. galeata*

4(2) Anterior antennal projections larger than posterior antennal projections (Figs 25 and 27); last segment (segment V) of each maxillary palp long (Fig. 26). . . . . *C. cudonis*

\- Anterior antennal projections smaller than posterior antennal projections (Figs 11, 12 and 45); last segment of each maxillary palp short (Figs 11, 12, 14, 15, 46, 47) 5

5 (4) Hind wings each with fold in posterior margin (Mosely & Kimmins 1953, fig. 38a); anterior antennal projections each with small rounded branch on lateral surface subapically; 1st segment of each maxillary palp with hook-like appendage on apico-medial margin (Figs 14, 15); abdomen, dorsally with dense setae along midline . . . . *C. simulans*

\- Hind wings each with or without fold; anterior antennal projections without small rounded subapical branches; 1st segment of each maxillary palp without hook-like appendage; abdominal terga without dense setae 6

6(5) Second segment of each maxillary palp with circular brush of large dark setae (Figs 11, 12). *C. plicata*

\- Second segment of each maxillary palp without circular brush of large dark setae, instead with sparser whorl of setae (Figs 46, 47) . . . . *C. equustagna*

Key to the known larvae of *Caenota* from Australia

1 Anterior section of frontoclypeus with lateral margins either parallel to each other or slightly rounded outwards (Fig. 23 and 43) 2

\- Anterior section of frontoclypeus trapezoid, with lateral margins relatively straight and converging towards anterior margin (Figs 13 and 65). 3

2(1) Primary setae 6 of head capsule positioned about halfway between constriction and anterior margin of frontoclypeus (Fig. 23) . . . . *C. nemorosa*

\- Primary setae 6 of head capsule positioned in posterolateral corners of anterior section of frontoclypeus (Fig. 43) . . . . *C. cudonis*

3(1) Foretrochantins each with single seta on anterodorsal surface at mid length (Fig. 45) . . . . *C. plicata*

\- Foretrochantins each with more than 1 seta on anterodorsal surface (Fig. 67). . . . . *C. equustagna*

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