

Systematics and biology of the iconic Australian scribbly gum moths *Ogmograptis* Meyrick (Lepidoptera : Bucculatricidae) and their unique insect–plant interaction

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Abstract. Many smooth-barked *Eucalyptus* spp. in south-eastern Australia bear distinctive scribbles caused by the larva of some *Ogmograptis* spp. However, although these scribbles are conspicuous, the systematics and biology of the genus is poorly known. This has been addressed through detailed field and laboratory studies of the biology of three species (*O. racemosa* Horak, sp. nov., *O. fraxinoides* Horak, sp. nov., *O. scribula* Meyrick) in conjunction with a comprehensive taxonomic revision supported by a molecular phylogeny utilising the mitochondrial *Cox1* and nuclear 18S genes. In brief, eggs are laid in bark depressions and the first-instar larvae bore into the bark to the level where the future cork cambium forms (the phellogen). Early-instar larvae bore wide, arcing tracks in this layer before forming a tighter zig-zag-shaped pattern. The second-last instar turns and bores either closely parallel to the initial mine or doubles its width, along the zig-zag-shaped mine. The final instar possesses legs and a spinneret (unlike the earlier instars) and feeds exclusively on callus tissue that forms within the zig-zag-shaped mine formed by the previous instar, before emerging from the bark to pupate at the base of the tree. The scars of mines then become visible scribbles following the shedding of the outer bark. Sequence data confirm the placement of *Ogmograptis* within the Bucculatricidae, suggest that the larvae responsible for the ‘ghost scribbles’ (raised scars found on smooth-barked eucalypts) are members of the related genus *Tritymba* Meyrick, and support the morphology-based species groups proposed for *Ogmograptis*. The formerly monotypic genus *Ogmograptis* Meyrick is revised and divided into three species groups. Eleven new species are described: *Ogmograptis fraxinoides* Horak, sp. nov., *Ogmograptis racemosa* Horak, sp. nov., and *Ogmograptis pilularis* Horak, sp. nov., forming the *scribula* group with *Ogmograptis scribula* Meyrick; *Ogmograptis maxdayi* Horak, sp. nov., *Ogmograptis barloworum* Horak, sp. nov., *Ogmograptis paucidentatus* Horak, sp. nov., *Ogmograptis rodens* Horak, sp. nov., *Ogmograptis bignathifer* Horak, sp. nov., and *Ogmograptis inornatus* Horak, sp. nov., as the *maxdayi* group; *Ogmograptis bipunctatus* Horak, sp. nov., *Ogmograptis pulcher* Horak, sp. nov., *Ogmograptis triradiata* (Turner), comb. nov., and *Ogmograptis centrospila* (Turner), comb. nov., as the *triradiata* group. *Ogmograptis notosema* (Meyrick) cannot be assigned to a species group as the holotype has not been located. Three unique synapomorphies, all derived from immatures, redefine the family Bucculatricidae, uniting *Ogmograptis*, *Tritymba* (both Australian) and *Leucoedemia* Scoble & Scholtz (African) with *Bucculatrix* Zeller, which is the sister group of the Southern Hemisphere genera. The systematic history of *Ogmograptis* and the Bucculatricidae is discussed.

Additional keywords: callus, *Eucalyptus*, *Leucoedemia*, mine, phellogen, phylogeny, *Tritymba*.

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Introduction

The gum-tree stands by the spring

I peeled its splitting bark

And found the written track

Of a life I could not read

(Judith Wright 1955)

The ‘scribbles’ on the bark of some smooth-barked *Eucalyptus* species in south-eastern Australia are quintessentially Australian and gained an iconic status as a result of the classic children’s books by May Gibbs (1918 and later) and the poem ‘Scribbly-Gum’ by Judith Wright (1955). These scribbles were first thought to be caused by beetle larvae, a misconception still alive today (e.g. Flannery 2010). Upton (1997) detailed the discovery by Greaves in 1934 that a very small moth is responsible.

Meyrick (1935) described the moth, reared from larvae emerging from *Eucalyptus pauciflora* Sieber ex Spreng, in the mountains west of Canberra, as *Ogmograptis scribula* Meyrick, but he found it difficult to assign the new genus to a family. He included it in the Elachistidae but stated that the longitudinally ribbed cocoon 'suggests the cocoon of a *Bucculatrix*, but there is no real relationship'. The position of *Ogmograptis* remained so enigmatic that Common (1990) omitted the genus in his authoritative *Moths of Australia*.

In 1958, I. F. B. Common collected several pupae of *O. scribula* from *E. pauciflora* at the type locality west of Canberra, but elucidation of the life history producing these unique tracks was never attempted as they are generated beneath the bark and therefore not easily observable while the larva is present. Cooke and Edwards (2007) analysed the pattern of scribbles on three species of *Eucalyptus* in the Australian Capital Territory, and concluded that there was more than one species of *Ogmograptis*. Obvious differences in wing pattern among the specimens recognised as *Ogmograptis* in the Australian National Insect Collection (ANIC) supported this supposition.

This study is the result of collaboration between entomologists and botanists, guided over several years by one of us (M. F. Day), and aimed at elucidating the phylogeny, taxonomy and biology of the scribbly moth system, as described by Whitten (2012). We describe the interaction between *Ogmograptis* larva and the tree that produces bark scribbles and we show that the related genus *Tritymba* is responsible for 'ghost scribbles', mines in the vascular cambium that result in raised scars visible on smooth-barked *Eucalyptus* spp. Our studies show that *Ogmograptis* comprises numerous species that are newly accommodated in three species groups, the *scribula* group (which produces the bark scribbles) and the *maxdayi* and *triradiata* groups (whose larval biology is not known). Finally, the systematics of *Ogmograptis* and the Bucculatricidae are discussed in the light of synapomorphic behaviours and structures identified in the course of this study.

Material and methods

Material studied and preparation

The taxonomic revision was largely based on specimens in the ANIC or reared during the present study. Because differences among species are often subtle, type series were usually restricted to a single population. Genitalia preparations were made following Robinson (1976) and Common (1990), and wing preparations followed the method developed by Common (1990).

Scanning electron microscopy

Cryo-scanning electron micrographs of the larvae and the surrounding tissue were produced by CB. In the field, sections of bark were removed from the trunk to expose *Ogmograptis* larvae in their tracks. The part of the track containing a larva was excised from the tree trunk with a razor blade, flash frozen in a dry shipper previously cooled with liquid N₂ to -196°C and stored at -196°C until examined. Scanning electron microscopy was performed on a Cambridge 360 SEM equipped with a cryo-stage and cryo-transfer unit. Samples were removed from the vials mounted onto brass stubs using colloidal graphite paste (Agar

Aids) and transferred via the cryo-transfer unit into the column of the SEM. Under observation, samples were slowly warmed to, and held at, -90°C to sublime surface frost, returned to the preparation chamber of the cryo-transfer unit for sputter coating with gold and then placed back into the SEM column for observation. Micrographs of larval legs and abdominal structures were taken using conventional SEM. Larvae were fixed in 70% ethanol, dehydrated through a graded ethanol series, critical-point dried, mounted on stubs and sputter coated with gold. Images were captured with a JEOL 6400 SEM.

Light microscopy

Cross-sections of eucalypt bark for light microscopy were produced by CB. In the field small pieces of bark from *Eucalyptus racemosa* ssp. *rossii* R. Baker & H.G. Smith (~4 cm²) were removed from trees, and, from the centre of each, small strips (~2 mm × ~4 mm) were cut using single-edged razor blades. The strips were placed in a fixative solution of 3% glutaraldehyde in 25 mM sodium phosphate buffer pH 7.2 and stored at 4°C. In the laboratory the fixative solution was discarded, the samples washed with several changes of the phosphate buffer, dehydrated through an ethanol series and infiltrated with LRWhite resin (London Resin Co.). The samples were infiltrated for 1–2 weeks in pure resin and polymerised in flat aluminium foil dishes in a 70°C oven under nitrogen. Sections 1–2 μm thick were cut with glass and diamond knives on a Reichert ultracut microtome, dried onto glass slides, stained with a solution of 0.1% Toluidine Blue O and examined under an optical microscope.

Molecular methods

Whole genomic DNA was extracted from thoracic muscle tissue with the DNeasy Blood and Tissue kit (QIAGEN). Two genes were amplified, a portion of the mitochondrial cytochrome c oxidase subunit 1 (= *cox1*) and the nuclear small subunit rRNA gene (18S). A 659-bp portion of the 5' end of *Cox1* was amplified with the LCO/HCO primers (Folmer *et al.* 1994). Almost the entire 18S gene was amplified (1798 bp) using the primers 1.2F, b3.0, a0.7, bi, a2.0 and 9R (Whiting 2002). PCRs and sequencing reactions were conducted as in our previous studies (Cameron *et al.* 2009; Dowton *et al.* 2009); sequencing trace files were generated on an ABI3730 capillary sequencer (Applied Biosystems) at the John Curtin Medical Centre, Biomolecular Resource Facility (Australian National University). Raw sequence files were edited and assembled into contigs in Sequencher ver. 4.9 (GeneCodes Corporation).

Alignments of each gene were undertaken in Sequencher ver 4.9 by eye using *Bucculatrix* as an outgroup. Alignments were trivial as *Cox1* included no indels and 18S only 5 single-base indels. Alignments of each gene were concatenated in MacClade ver 4.06 (Maddison and Maddison 2003). Models for each partition were chosen using AIC as implemented in ModelTest (Posada and Crandall 1998). Phylogenetic analysis was performed using parsimony (MP) and likelihood (ML) methods using PAUP 4.0b10 (Swofford 2002) and Bayesian analysis (BA) using MrBayes ver 3.1.2 (Huelsenbeck and Ronquist 2001). Bootstrap supports for MP and ML trees were calculated with PAUP 4.0b10 with 1000 replicates. Phylogenetic

analyses were performed using either a single (MP, ML) or two (BA) data partitions based on each gene region. All Bayesian analyses were run with unlinked partitions using two independent runs, each run consisting of four chains (three hot and one cold chain), for 3 million generations with sampling every 1000 generations; convergence was achieved by all analyses within 3 million generations, as determined using Tracer ver. 1.4 (Rambaut and Drummond 2007). Completed Bayesian analyses were examined for asymptotic behaviour of each parameter and of total tree likelihood; trees collected before this asymptotic point were treated as burn-in and discarded (generally the first 30 000–60 000 generations). Bayesian and ML run files are available for each analysis from SLC upon request.

Abbreviations

AMSA	Australian Museum, Sydney, Australia
ANIC	Australian National Insect Collection, CSIRO, Canberra
BMNH	The Natural History Museum, London (British Museum of Natural History)
DEM V	Department of Entomology, Museum of Victoria, Melbourne
GS	genitalia slide
NP	National Park
SAMA	South Australian Museum, Adelaide
SEM	scanning electron micrograph

Biology

Life history of the Ogmograptis scribula group

The life history of the *scribula* group was studied in *O. racemosa* Horak, sp. nov., and, in lesser detail, in *O. scribula* Meyrick, 1935, and *O. fraxinoides* Horak, sp. nov. The layout of larval tracks in the *scribula* group follows a general pattern that is summarised in Table 1, with crucial points in the track marked from A to D as explained in Table 1 and indicated in the relevant illustrations (Figs 4, 9). There are, however, differences in the arrangement of the track components between different species, as discussed below. In a one-year life cycle, in autumn, rarely in winter, eggs are laid singly on the bark surface in small depressions or crevices (Figs 20, 21). Eggs often occur in the narrow ledge along the

edges of the most recently shed outer bark. The first-instar larva chews through the underside of the egg directly into the bark, filling the empty egg shell with its droppings. When the larva reaches the depth at which next year's cork cambium (phellogen) will be formed, it makes a 90° turn (Table 1: A), usually associated with a widening of the track to about double its previous width. From there the larva bores tangentially near the future phellogen layer. The initial entry track is much narrower than its continuation beyond the turn, suggesting that the larva may be moulting into the second instar at this point. No head capsule has, however, been found among the droppings in this section of the track in the 10 samples examined. The tangential track (Table 1: A–B) is typically at an angle between 90° and 120° to the axis of the trunk, usually forming a few long, quite loose zig-zags, always beneath bark that will be shed in the following year. Each time the track reaches the margin of the bark to be shed in the next year, it turns back and remains within the confines of the bark to be abscised (Fig. 9). The track is distinctly wider in the second half of this section, suggesting that the larva moults into the third instar about halfway.

At some point, usually after making a particularly long, possibly 'exploratory' loop, the larva moults into what is likely to be its fourth and penultimate instar, and the track changes into a more regular pattern of shorter zig-zags within the confines of the width of the last loop (points B–C). This set of shorter and more regular zig-zags varies in two ways between taxa. First, this final set of zig-zags either follows in the same direction (either downward or upward) as the narrow, initial zig-zags (Figs 1–4), or, as in *O. pilularis* Horak, sp. nov., it changes direction and is superimposed over the second half of the earlier track (Figs 5, 6). Second, there are two different patterns with regard to the return track from the turning loop (Table 1: C–D). In *O. scribula*, *O. fraxinoides*, *O. pilularis* and other unidentified *Ogmograptis* species of the *scribula* group, the returning larva follows the first track in a closely parallel but separate track (Figs 1–3, 12, 15). In contrast, the larva of *O. racemosa* re-enters the first track after a small turning loop, enlarging the track to double width on its return passage (Figs 4, 9).

Observations of scribbles on various eucalypt species suggest that the track of *O. racemosa* is the exception, with most larvae of the *scribula* group returning in a closely parallel track rather than in the same track after the turning loop. Up to this point the larva is

Table 1. Generalised description of tracks of *Ogmograptis* larvae of the *scribula* group (bark scribbles)

The track description applies to all the species except where noted for a specific species. See Figs 2, 4, 5, 9

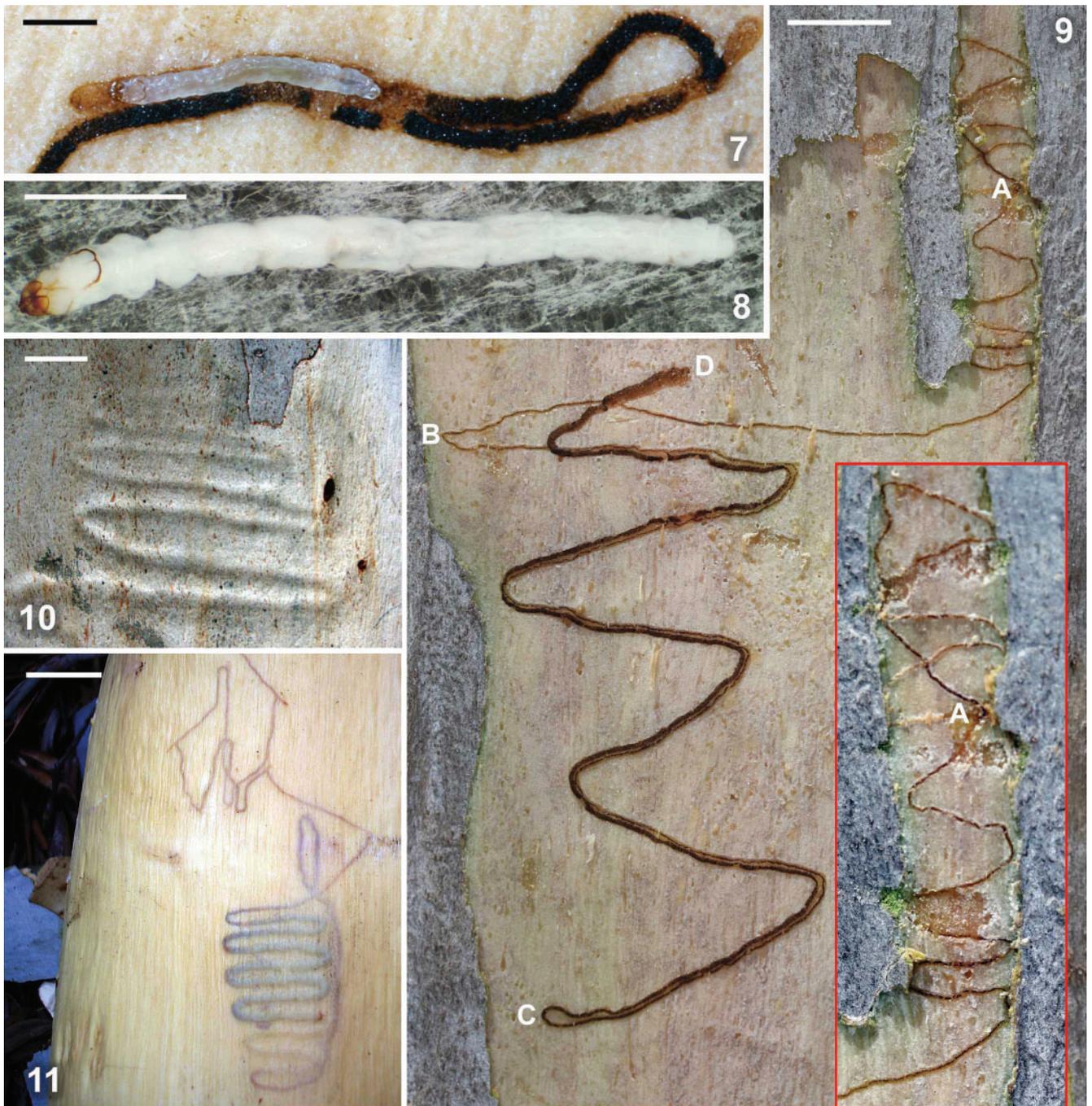
Point A	Larva chews through underside of egg and through outer bark to reach, at point A, the bark layer where the future cork cambium (phellogen) will form. There it turns to bore along this layer, possibly moulting to 2nd instar
Track A–B	Track narrow, irregular, often meandering and occasionally crossing itself. Larva feeds on bark tissue, apparently moulting partway between A and B
Point B	Beginning of series of regular track zig-zags; larva moults near point B
Track B–C	First pass of doubled zig-zags which don't cross each other; larva feeds on bark tissue
Point C	First turning loop of doubled track
Track C–D	Return track of doubled zig-zags, either closely parallel in separate track (<i>O. scribula</i>) or joining and enlarging initial track (<i>O. racemosa</i>); larva feeds on bark tissue
Point D	Second turning loop; larva (after turning) moults at point D to final instar with legs
Track D–(E)	Larva returns towards point C along the doubled track. It feeds on callus filling the track, with both the callus and the incorporated frass from the earlier passage(s) eaten
(Point E)	Emergence hole where mature larva bores to the surface somewhere between points D and C. E not visible after outer bark has abscised



Figs 1–6. Bark scribbles of the *Ogmograptis scribula* group on *Eucalyptus* spp. 1, 2, *O. scribula* on *E. pauciflora*, Bulls Head, Brindabella, ACT. 3, *O. fraxinoides* on *E. fraxinoides*, Piper’s Lookout, Brown Mt, NSW. 4, *O. racemosa* on *E. racemosa* ssp. *rossii*, nr Gunning, NSW. 5, 6, *O. pilularis* on *E. pilularis*, S of Guerilla Bay, NSW, inner side of fallen outer bark. Explanation for A–D, see Table 1. Scales = 10 mm.

extremely long and slender, lacks legs, has a particularly shaped prothoracic shield, lacks a spinneret and lives as a true borer, feeding on the bark tissue it excavates to form its mine (Fig. 7). In *O. racemosa* the return track ends in a second turning loop (Point D) at the opposite end of the set of shorter, more regular loops. In this second turning loop the caterpillar moults into the last, probably fifth, instar with well developed legs and a

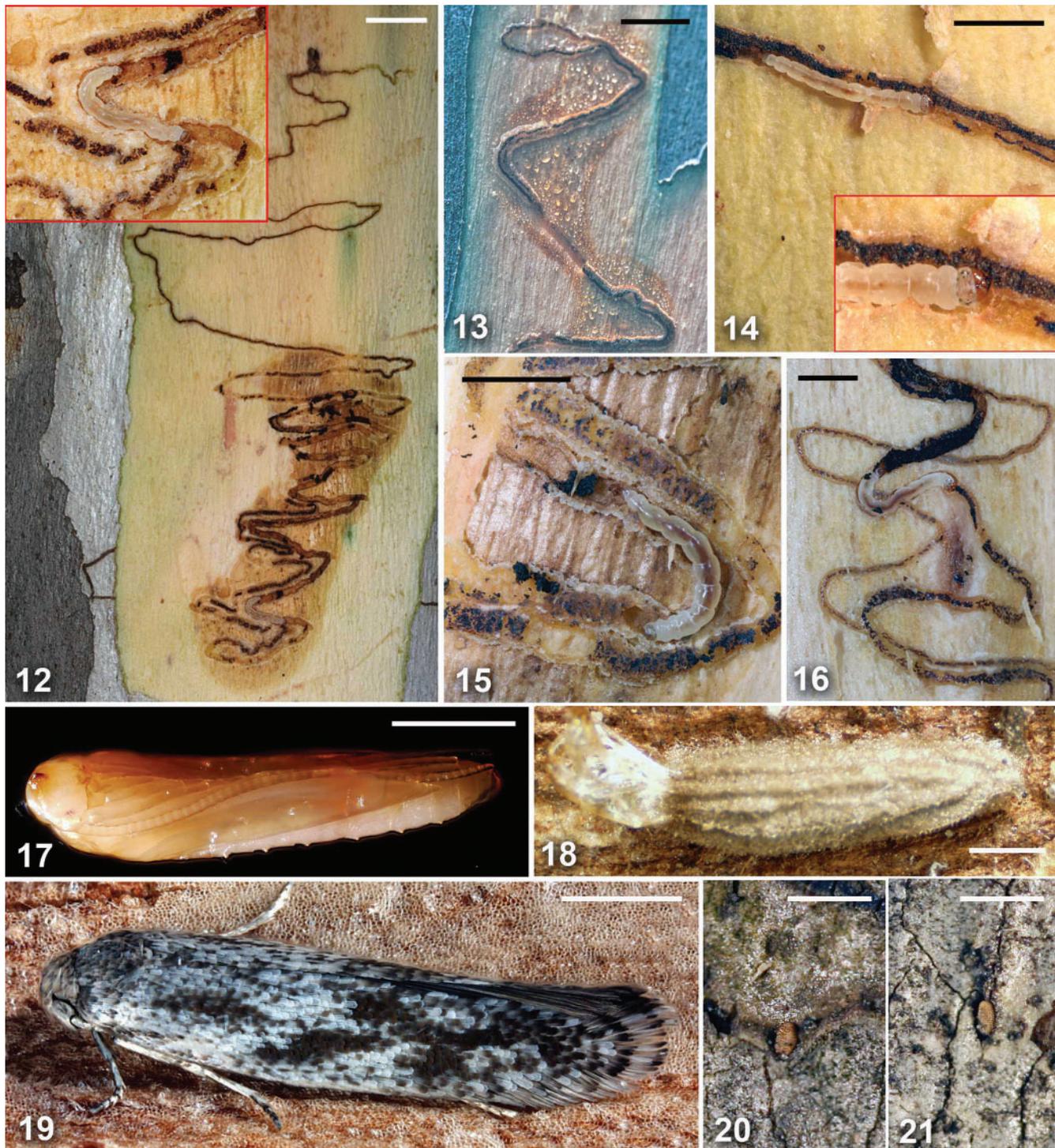
spinneret. The location of this turning point varies from track to track, with the larva turning before reaching the beginning of the set of tight loops (Fig. 4) or extending the track beyond the onset of the tight loops before turning (Fig. 9). The synchronisation of larval development within a given side of a eucalypt trunk as well as the feeding behaviour of the last-instar larva suggest that the stimulus for this last turn and for moulting may be growth activity



Figs 7–11. 7, Penultimate, legless larva of *Ogmograptis racemosa* in track after first turning loop. 8, Penultimate, legless larva of *O. racemosa*, in process of moulting to final instar. 9, Exposed track of *O. racemosa* with enlarged detail of early track as inset (explanation for A–D, see Table 1). 10, 'Ghost scribble' on *Eucalyptus rubida*, Warrandyte, Vic. (Photo: D. J. Hilton). 11, Exposed track of *Tritymba* sp. in cambium layer of *Eucalyptus racemosa*. Scales = 1 mm (Figs 7, 8), 20 mm (Figs 9–11).

of the cork cambium rather than the larva having reached a certain spatial position in its track. Evidence from tracks of *O. scribula*, *O. fraxinoides* and *O. pilularis* is ambiguous as to whether the larva, either before or after moulting into the last instar, returns in the same track or sometimes crosses over into the parallel track.

While the larva makes the final turn and moults into the fully legged last-instar caterpillar, the set of double tracks fills with callus tissue, and the bark in the vicinity usually becomes discoloured (Figs 12, 13). The final-instar larva feeds exclusively on this turgid callus (Figs 12, 14–16, 28) which includes the frass left by the larva while boring the track.



Figs 12–21. 12, Exposed track of *Ogmograptis scribula* with inset of enlarged detail of final-instar larvae feeding on callus tissue. 13, Exposed track of *O. racemosa* with protruding callus tissue incorporating two frass lines. 14, Final-instar larva of *O. racemosa* feeding on callus tissue with enlarged detail of larva as inset. 15, Final-instar larva of *O. scribula* feeding on callus tissue. 16, Final-instar larva of *O. racemosa* feeding on callus tissue in narrow, atypical part of usually doubled track. 17, Pupa of *O. racemosa*. 18, Cocoon of *O. racemosa*. 19, Adult of *O. racemosa*. 20, 21, Eggs of *O. scribula*, vacated and filled with frass by first-instar larva. Scales = 10 mm (Figs 12, 13), 5 mm (Figs 14–16), 1 mm (Figs 17–21).

In *O. scribula*, *O. fraxinoides* and *O. pilularis*, where the return track is parallel but separate, there is only one frass line embedded in the callus (Fig. 15), in contrast to *O. racemosa* which returns in the same track and thus produces two frass lines (Fig. 14) (Table 1: D–E). The final instar lasts only a few weeks with the larva growing rapidly, eating callus along the track until it has reached full size, and boring to the outside of the bark, producing a narrow, slit-like exit hole (Table 1: E) not visible in exposed scribbles as the outer bark has abscised. The larva descends to the bottom of the tree and pupates at its base behind loose bark or in the topmost layer of the surrounding soil. The longitudinally ribbed cocoon (Fig. 18), characteristic of bucculatricids, is usually attached to a firm substrate, either the base of the tree or a stone or piece of bark in the soil adjacent to it. The caterpillar first spins a larger, loose outer layer of silk, which is then pulled in, forming longitudinal folds (the ribs of the finished cocoon) fixed to the dense inner layer. The cocoon has a preformed exit flap, and the pupa pushes itself partly out of the cocoon before the adult emerges from the pupal shell. Cocoon formation is surprisingly fast, with a caterpillar of either *O. scribula* or *O. fraxinoides* collected whilst boring out of its track found within a perfect cocoon six hours later in the laboratory.

In addition to *O. racemosa*, we collected the two morphologically distinct larval forms of both *O. scribula* and *O. fraxinoides*. For both species we found a penultimate legless instar which is a genuine borer feeding on bark tissue and a final instar with legs feeding exclusively on the callus produced within the gallery excavated by the penultimate instar. Furthermore, the similarities in the complex pattern of surface scribbles on other smooth-barked eucalypts suggest that this life history applies to all *Ogmograptis* species feeding in the cork cambium layer.

Histological results

SEM images of early- and last-instar larvae of *O. racemosa* and their tracks show the different tissues the larva is feeding on during the early borer and the later callus feeder phases. Whereas the last-instar larva is surrounded by callus tissue of large, spherical, thin-walled cells (Figs 28, 29), the track of the legless larva exposes normal bark tissue without callus cells (Figs 26, 27). Cross-sections of preserved eucalypt bark across recent *O. racemosa* tracks show in detail the mass of large, spherical, thin-walled callus cells at the site of the larval track, in contrast to the normal cork layer with a basal row of thick-walled phellem cells followed by numerous rows of flat phellem cells (Figs 22, 23). The stacks of cells are contiguous across the phellogen and phellogen, into the orderly columns of the phellem as well as into the proliferating mass of callus cells (Fig. 22), suggesting that the callus is produced by the phellogen. If this observation is confirmed, it means that within the area of the double track the phellogen produces callus instead of cork tissue at the site of larval activity. The tracks become filled with callus which remains attached to the tree after the outer bark is removed at the level of the newly formed cork cells produced by the phellogen elsewhere (Figs 13, 15, 22). Particularly obvious is the termination of the row of thick-walled phellem cells at the edge of the callus (Fig. 22). These observations provide strong support for the hypothesis that the callus within the double track is generated

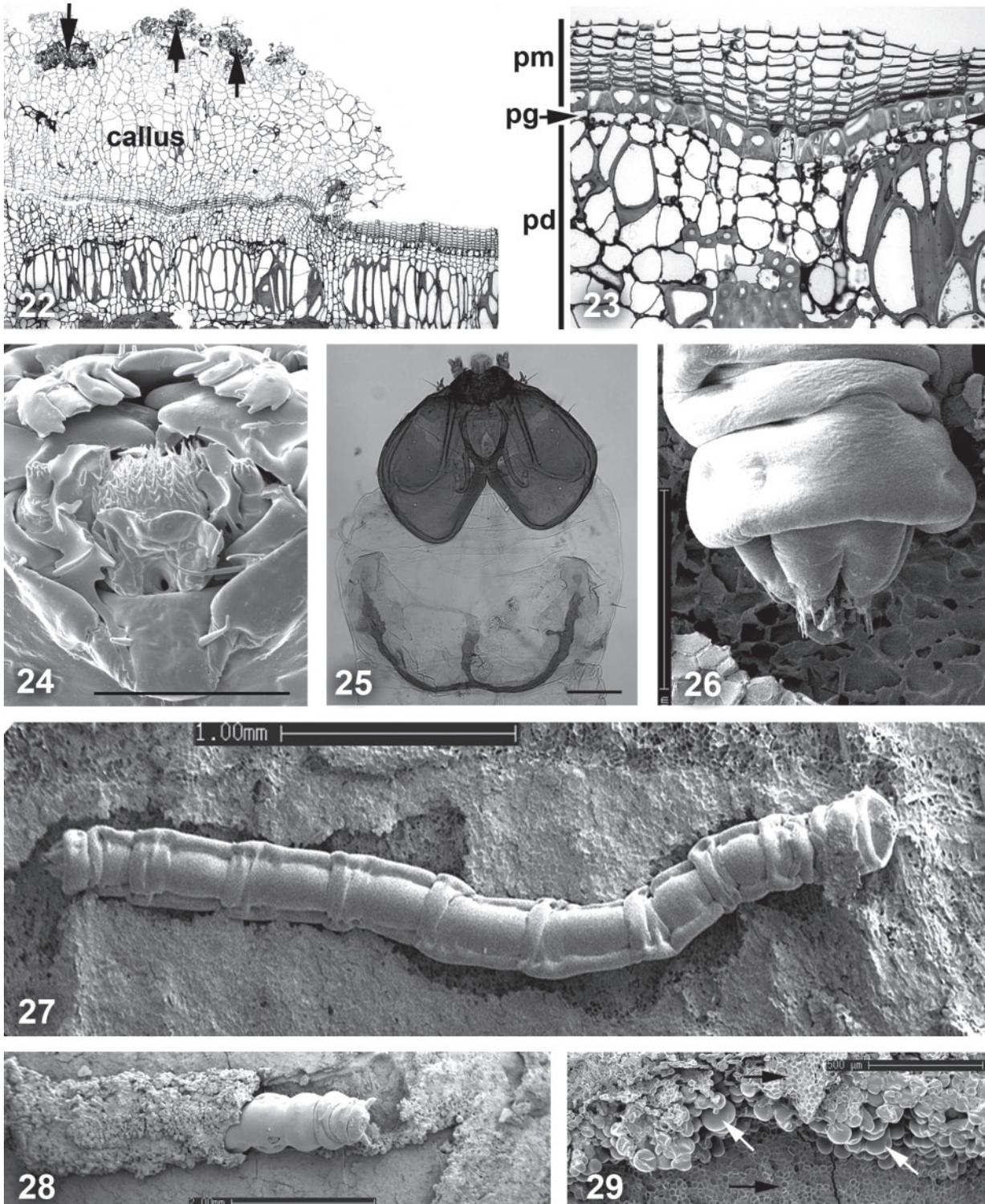
by the phellogen, but more detailed studies are required to confirm this.

Phenology

The duration of the various life stages has to be inferred as the entire development takes place beneath the surface of the bark. The bark may be forcibly split off at the cork cambium only during later stages of larval development, when the larva has started the set of double tracks. This probably coincides with the onset of activity in the cork cambium providing a discontinuous layer that allows the forced removal of the outer bark. Eventually, once a new cork layer is fully established, the outer bark falls off and the track is exposed. At this point the larva has already left and pupated. *O. racemosa* is the only species for which we have sufficient data to roughly time the life history. Adults emerged from collected larvae or pupae or were attracted to light from 28 March to 15 May in the wider Canberra region, Jervis Bay and Wedderburn, New South Wales, with most on the wing during April. We found legless larvae of the penultimate instar on the southern, cooler side of *E. racemosa* spp. *rossii* near Gunning, New South Wales, on 1 December 2008. On the northern side of the same trees the larvae were already in their final instar with legs, feeding on callus tissue. Several of the legless larvae were still near the beginning of the double track, not far beyond the first turning loop (Fig. 7) whilst several were found at the crucial point just after the second turning loop (D in Fig. 9), in the penultimate instar and about to moult into the final instar with legs, which were clearly visible beneath the soon-to-be-shed larval skin. Pupae were collected at the base of *E. racemosa* spp. *rossii* in Canberra and Gunning from the end of December through to January. These dates allow no exact timing, but suggest that the larva grows only slowly over many months, feeding on the bark tissue in the widely looping narrow track that precedes the set of double tracks. The fact that on 1 December 2008 on the same tree the least developed larvae on the southern side of the tree were still at the beginning of boring the return track whilst those on the northern side were already last-instar larvae, suggests that the last two phases, the boring of the set of double tracks and the last instar callus feeding, must occur rapidly, probably in weeks rather than months. Pupation time varies, with pupae of *O. racemosa* collected in mid-January emerging from late March to mid-April, spanning the summer months. On the other hand, six mature larvae of *O. scribula* extracted from their tracks on 6 and 10 February 2010 pupated in 6–48 h and emerged 26–33 days after the collection date. They were all females, which, given that in over 50% of the tracks the larva had already left, suggests that the males may have emerged earlier. However, eight pupae of *O. fraxinoides* collected on 8 March 2010 yielded five males which emerged between 12 March and 4 April 2010 and three females between 21 and 24 March 2010. The emergence of these *O. scribula* and *O. fraxinoides* specimens coincided with the passage of low-pressure weather systems.

Biology of *Tritymba*

Observations of fresh *Tritymba* tracks suggest that this genus has a similar biology to that of *Ogmograptis*. The track of a *Tritymba* larva also forms a closed loop, with the larva re-entering the terminal part of its track (Fig. 11). The raised contour of fresh



Figs 22–29. 22, Cross-section of outer bark of *Eucalyptus racemosa* ssp. *rossii* with callus-filled track of *Ogmograpteis racemosa* larva on left (arrows: larval frass), normal bark on right. 23, Enlarged cross-section of outer bark of *E. racemosa* ssp. *rossii*, showing details of outer bark not disturbed by *Ogmograpteis* track (pg, phellogen; cork cambium (arrow); pm, phellem; pd, phelloderm). 24, Mouthparts of probably third instar of *O. racemosa* larva, showing simple opening of silk gland without spinneret. 25, Head capsule and thoracic shield of penultimate instar of *O. racemosa*. 26, Enlarged last segment of probably third instar of *O. racemosa*, in ventral view. 27, Probably third instar of *O. racemosa*, ventral view, with head to the right. 28, Last instar of *O. racemosa* surrounded by callus. 29, Enlarged detail of large, thin-walled callus cells (white arrows) associated with double-tracked section of *O. racemosa*, bordered by normal phellem cells (black arrows). Scales = 0.05 mm (Fig. 24), 0.1 mm (Figs 25, 26).

tracks (Fig. 11) and the strong welts of their scars when they reach the surface of the bark (Fig. 10) both suggest that the tracks of *Tritymba* also become filled with callus on which the last-instar larva feeds. Whereas the tracks of the *O. scribula* group are located in the cork cambial layer, those of *Tritymba* are in the deeper vascular cambium. Their scars become visible only after years of growth have brought their impression to the surface of the bark. Unlike the bark scribbles where one sees the scribbles themselves, in the *Tritymba* scribbles it is only the reaction to mining, the displaced tissue, which becomes visible. The vascular cambium is persistent and keeps producing tissue, pushing the scar inward and outward.

Molecular systematics

A molecular systematic study (Table 2) was conducted in concert with the morphological investigations to match larval and adult forms in the absence of rearing, to test species-group assignments based on morphology (see below) and to help identify the vascular cambium-mining larvae responsible for the 'ghost scribbles'. Preliminary trees (not shown) supported the inclusion of *Ogmograptis* plus the vascular cambium-mining species within Gracillarioidea and as sister to *Bucculatrix*, results later confirmed by Mutanen *et al.* (2010), who referred *Tritymba* to the Bucculatricidae. *Bucculatrix* was thus chosen as the outgroup for subsequent analyses. These results (Fig. 30) suggest that the 'ghost scribble'-producing species are members of the large genus *Tritymba*, although there is a significant molecular divergence between the confirmed adult specimens and the larval specimens, comparable to that between the *maxdayi* and *scribula* species groups within *Ogmograptis*. While sequences were obtainable from only two of the three *Ogmograptis* species groups, the phylogenetic results support the morphology-derived species group assignments (see below). For both *O. fraxinoides* and *O. scribula*, molecular sequences match for larvae and adults, thus confirming their utility for identifications. While both *O. fraxinoides* and *O. scribula* were found to be monophyletic, nodal support for their monophyly was weak due to the limited molecular divergence between the two species.

Taxonomy

Genus *Ogmograptis* Meyrick, 1935

Type species: *Ogmograptis scribula* Meyrick, 1935.

Diagnosis

Head. Scaling smoothly appressed; frons short; antennal scape with strong anterior extension by broad scales to form a partial 'eye cap'; labial palpus with 3 segments, straight; maxillary palpus with 1 segment.

Wings. Venation reduced; forewing with M-stem weak, costa and Sc fused into marginal vein, radius 4-branched, all ending anterior to apex, R(4+5) and M1 stalked in wingtip with M1 posterior to apex, altogether three M and CuA veins; CuP weak, 1A+2A without basal loop; hindwing with Sc+R1 as marginal vein, Rs and two M-branches on weakly developed vein along middle of wing, cell open, CuA well developed, unbranched.

Abdomen. Apodemes of sternum II long, slender.

Male genitalia. Tegumen hood-shaped, fused with band-shaped vinculum; uncus deeply bifid, pointed; socii at most an elongate patch of bristles; gnathos arms fused into distally fringed process; saccus long to very long, slender; valva long, slender, simple; transtilla two slender lateral processes; juxta a sclerotised band usually with a dorsally strongly projecting central portion; aedeagus long and slender, with a slightly bulbous base, straight or with a bent base or with a large basal loop.

Female genitalia. Ovipositor with slender apophyses; ovipositor lobes usually membranous, closely appressed to each other, with scattered bristles on outer surface, rarely sclerotised, spinulose and posteriorly oriented. Ostium at base of S8, without sclerotised sterigma; ductus bursae slender, with sclerotised, funnel-shaped distal portion or with a minute sclerite somewhat below ostium and a lightly sclerotised bursa neck; ductus seminalis originating from neck of corpus bursae, with large, diverticulate bulla seminalis close to corpus bursae; usually with scobination across part of corpus bursae.

Larva. Strongly polymorphic: last instar with thoracic and abdominal legs and spinneret present, but anal prolegs reduced and without crochets; earlier instars without legs and spinneret. Larva with last abdominal segment modified with posterolaterally strongly protruding lobes supported by internal rod-shaped skeleton. Last-instar larva with polymorphic tarsi: prothoracic tarsus with distal setae unmodified but slender tarsal claw, meso- and metathoracic tarsi with two distal setae greatly enlarged, spatulate to cone-shaped but with strong normal claw.

Pupa. Aedecticous, protruded from longitudinally ribbed cocoon on emergence.

Description

Adult (Figs 19, 58–83)

Head (Figs 58–61). Scales smoothly appressed; frons short, ventrally narrowing, triangular, scaling not extending below eyes; lateral tufts on vertex flattened, appressed, their tips meeting medially. Eye large, naked, with interocular index ~0.85. Ocelli and chaetosema absent. Antennae filiform, 0.75–0.95 × length of forewing, entirely scaled with two rings of scales per segment; scape expanded into a dense 'eye-cap' by large broad scales extending anteriorly far beyond scape; first segment not 'notched'. Pilifers well developed. Labial palpus 3-segmented, slender, straight, drooping, as long as vertical diameter of eye, ratio of segments from base 1 : 0.7 : 1.4, third segment with apical vom Rath's organ. Proboscis short, 1.5 × length of labial palpus, naked, with small, 1-segmented, knob-shaped maxillary palpus with few large scales.

Wingspan. 8–13 mm.

Thorax. Scaling smooth. Metafurca with posterior apophyses elongate, straight, slender, free.

Forewing (Fig. 36). Lanceolate, pointed; W/L index 0.20–0.21; cell closed; M-stem weak, to base of R(4+5) and M1; costa and subcosta fused into strong marginal vein, retinaculum a hook from its base; R 4-branched, weak up to R1; R1 from below middle; R2 from 3/5, R3 from just before end of cell, R(4+5) fused into single vein (stalked in *Tritymba* Meyrick) and stalked with M1 from end of cell; R(4+5) to before

Table 2. Data for DNA samples

LEP No	DNA No	Genus	Species	Stage	<i>Eucalyptus</i>	Locality, date, collector	18S #	<i>cox1</i> #
LEP001		<i>Ogmograptis</i>	<i>racemosa</i>	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW	JX312222	JX312250
LEP002		<i>Ogmograptis</i>	<i>racemosa</i>	Larva		Royal National Park, Uloola Falls Track, 20.xi.2008, D. Lewis	JX312223	JX312251
LEP003		<i>Bucculatrix</i>	sp.	Larva	<i>Commersonia</i>	Bot. Garden, ACT, em. Jan. 2009, M. Horak	JX312224	JX312252
LEP004		<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Bull's Head, ACT, coll. 8.iii.2008	JX312225	JX312253
LEP005		<i>Ogmograptis</i>	<i>maxdayi</i>	Adult	?	Warrandyte, Vic., 1-15.xi.2008, D. J. Hilton	JX312226	JX312254
LEP006	3008	<i>Ogmograptis</i>	<i>scribula</i>	Adult	<i>pauciflora</i>	Bull's Head, ACT, coll. 12.ii.2009, em. 8.iii.2009, M. Horak, Y. N. Su and P. Macnicol	JX312227	JX312255
LEP007	3009	<i>Ogmograptis</i>	<i>racemosa</i>	Adult	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, em. 20.iv.2009, C. Barlow	JX312228	JX312256
LEP009	3011	<i>Ogmograptis</i>	<i>racemosa</i>	Adult	<i>racemosa</i>	3 km E Wedderburn, NSW, 18.iv.2007, D. Britton	JX312229	JX312257
LEP010	3012	<i>Ogmograptis</i>	<i>fraxinoides</i>	Adult	<i>fraxinoides</i>	Piper's Lookout, Brown Mt, NSW, pupa coll. 14.iii.2009, em 5.iv.2009, M. Horak	JX312230	JX312258
LEP011	3013	<i>Ogmograptis</i>	<i>scribula</i>	Adult	<i>pauciflora present</i>	Tallaganda, NSW, 11.vi.2008, G. Cocking and E. Edwards	JX312231	JX312259
LEP012	3014	<i>Tritymba</i>	sp.	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, 31.vii.2009, C. and P. Barlow	JX312232	JX312260
LEP013	3015	<i>Tritymba</i>	sp.	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, 31.vii.2009, C. and P. Barlow	JX312233	JX312261
LEP014	3016	<i>Tritymba</i>	sp.	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, 3.viii.2009, C. and P. Barlow	JX312234	JX312262
LEP015	3017	<i>Tritymba</i>	sp.	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, 31.vii.2009, C. and P. Barlow	JX312235	JX312263
LEP190	4017	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>fraxinoides</i>	Piper's Lookout, Brown Mt, NSW, 8.ii.2010, M. Horak	JX312236	JX312264
LEP191	4018	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>fraxinoides</i>	Piper's Lookout, Brown Mt, NSW, 8.ii.2010, M. Horak	JX312237	JX312265
LEP192	4019	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>fraxinoides</i>	Piper's Lookout, Brown Mt, NSW, 8.ii.2010, M. Horak	JX312238	JX312266
LEP193	4020	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>fraxinoides</i>	Piper's Lookout, Brown Mt, NSW, 8.ii.2010, M. Horak	JX312239	JX312267
LEP194	4021	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>pauciflora</i>	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010, Horak <i>et al.</i>	JX312240	JX312268
LEP195	4022	<i>Ogmograptis</i>	<i>fraxinoides</i>	Larva	<i>pauciflora</i>	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010, Horak <i>et al.</i>	JX312241	JX312269
LEP196	4023	<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010, Horak <i>et al.</i>	JX312242	JX312270
LEP198	4025	<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Bull's head, ACT, 10.ii.2010, M. Horak and Y. N. Su	JX312243	JX312271
LEP199	4026	<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Bull's head, ACT, 10.ii.2010, M. Horak and Y. N. Su	JX312244	JX312272
LEP200	4027	<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Bull's head, ACT, 10.ii.2010, M. Horak and Y. N. Su	JX312245	JX312273
LEP201	4028	<i>Ogmograptis</i>	<i>scribula</i>	Larva	<i>pauciflora</i>	Bull's head, ACT, 10.ii.2010, M. Horak and Y. N. Su	JX312246	JX312274
LEP204	4031	<i>Ogmograptis</i>	<i>barloworum</i>	Adult	?	Gilwell Pk., Melbourne, Vic., 30.x.2009, A. Kallies, P. Marriott and D. Hilton	JX312247	JX312275
LEP207	4034	<i>Tritymba</i>	sp.	Adult	?	8 km NE Nerriga, NSW, 6.xii.2008, E. D. Edwards and A. Kallies	JX312248	JX312276
X1		<i>Tritymba</i>	sp.	Larva	<i>ssp. rossii</i>	Barlow property, Gunning, NSW, 30.viii.2008, C. and P. Barlow	JX312249	JX312277

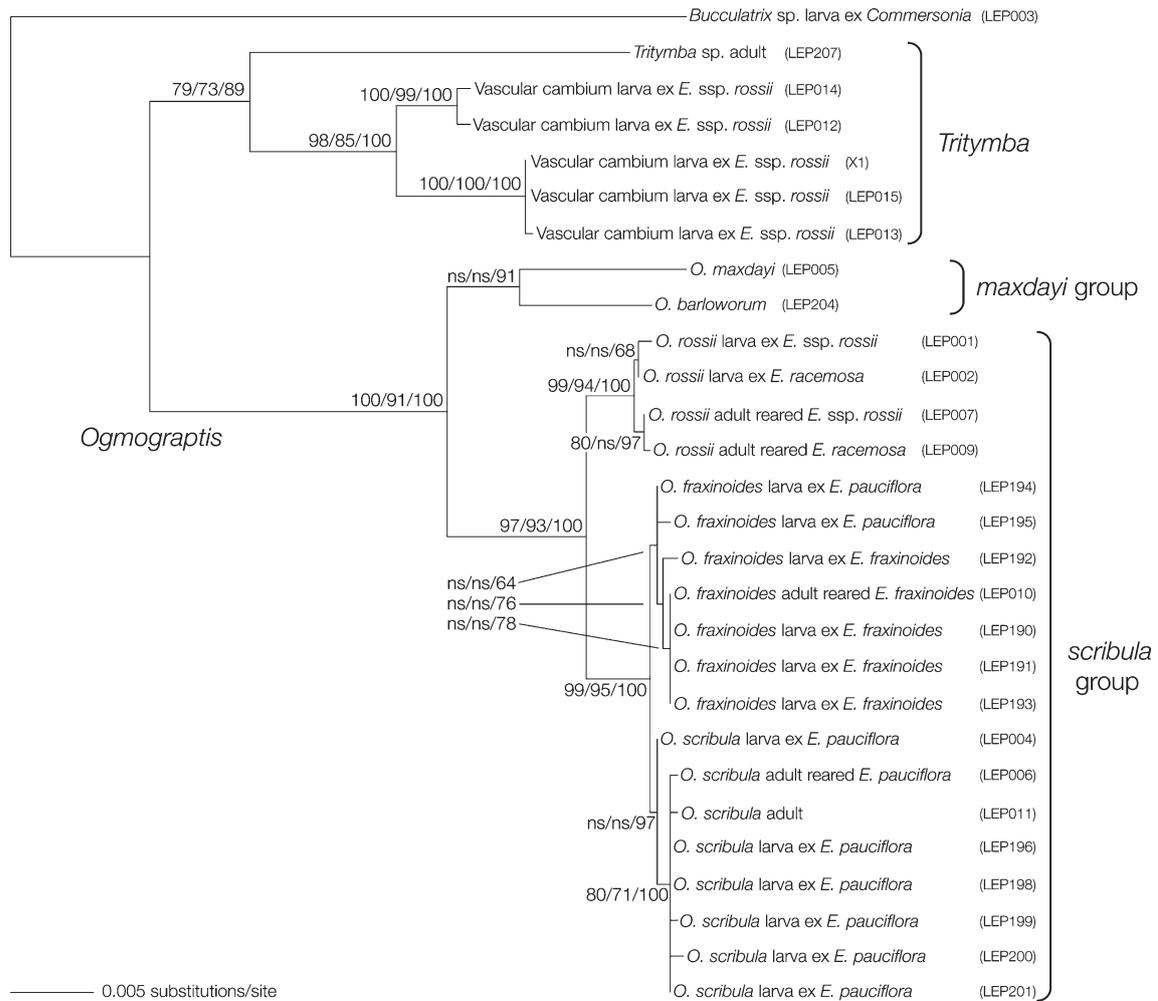


Fig. 30. Molecular phylogeny based on concatenated *coxI* and 18S sequences. The Bayesian phylogram is presented as the most resolved tree with support values from other methods mapped to each node. Nodal support is summarised for each analytical method: parsimony bootstrap/likelihood bootstrap/Bayesian posterior probability. ns, not significant.

and M1 to behind apex in tip of wing; M2 closely approximated to stalk of R(4+5) and M1, CuA1 more distant; CuP weak; 1A+2A to about middle of wing, without basal loop, no trace of 3A.

Hindwing (Fig. 36). Lanceolate, widest just before middle; ~2/3 width of forewing; W/L index 0.16–0.17; frenulum in male a single strong bristle, in female two bristles (rarely one only); venation reduced with Sc+R1 as marginal vein, Rs and two M-branches on weakly developed vein along middle of wing which anastomoses at 1/3 wing length with strongly curved weak vein remnant (?base of Rs) running to near base parallel to costa and with trace of a crossvein to costa (?R1); cell open; CuA well developed, unbranched; A hardly discernible trace.

Legs. Forelegs with epiphysis well developed, approximately half length of foretibia; tibial spurs 0–2–4; hindtibia in both sexes with very long loose hair scales along dorsal and ventral margins.

Abdomen. Unmodified in both sexes, without scale tufts. Paired sternal apodemes of A2 long, slender; sternal rods indicated as pigmented traces across S2.

Male genitalia (Figs 84–119). Tegumen well sclerotised, broad, hood-shaped, fused with band-shaped vinculum. Uncus well developed, two parallel, short, pointed processes. Socii elongate lateral patches of bristles, sometimes only 2–3 bristles. Gnathos paired arms, apically fused into a paddle-shaped to pointed process, with distal fringe or teeth. Saccus a moderately to very long, slender, straight process. Valva long, slender, simple; transtilla incomplete, two slender, curved processes from base of costa. Anellus membranous, very flimsy; juxta well developed, sclerotised, a transverse band usually with a central shield-shaped and dorsally protruding portion, often diagnostic. Aedeagus long and slender, with a slightly bulbous base, either entirely straight, with a bent base or with a large basal loop; sometimes 1–2 indistinct needle-shaped structures in vesica.

Female genitalia (Figs 120–133). Ovipositor with both apophyses well developed, slender; ovipositor lobes usually membranous, ovate, leaf-like, parallel and closely appressed to each other, with scattered bristles on outer surface, rarely

spinulose and sclerotised, posteriorly oriented (in *triradiata* group). Ostium at base of S8, without sclerotised sterigma. Bursa copulatrix differentiated into ductus bursae and corpus bursae, with ductus seminalis originating from neck of corpus bursae, with a large, diverticulate bulla seminalis close to corpus bursae; ductus bursae very slender, with either a sclerotised, funnel-shaped distal portion or with a minute sclerite somewhat below ostium and a lightly sclerotised bursa neck; corpus bursae with scobination across part of corpus bursae except in *triradiata* group.

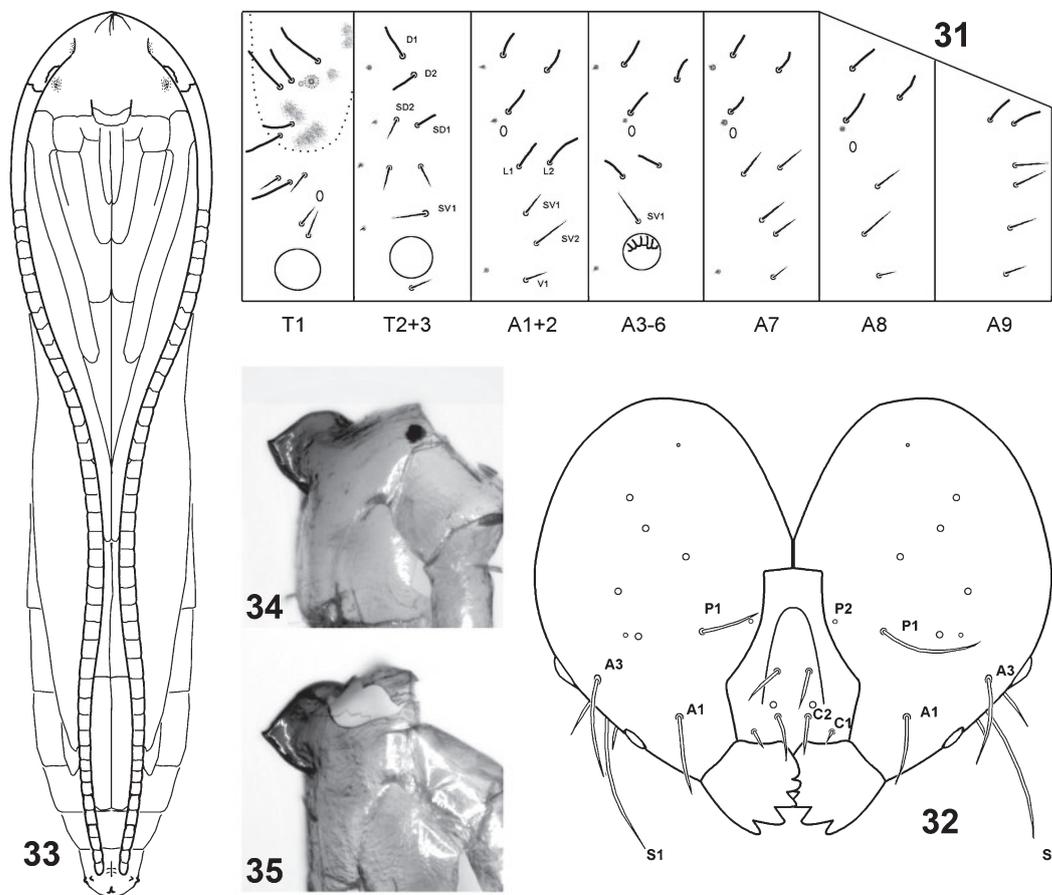
Egg (Figs 20, 21)

Length: 0.41–0.50 mm, width 0.17–0.25 mm; elongate-ovate, narrower at one end, usually somewhat apple-pip-shaped, but exact shape depending on depression in which the egg has been deposited; chorion weakly reticulate.

Larva (Figs 7, 8, 12, 14–16, 24–28, 31, 32, 37–56)

Final-instar larva (Figs 12, 14–16, 28, 31, 32, 37–55). Maximum length 11 mm. Head prognathous, dorso-ventrally flattened, reddish ochreous to reddish brown; epicranial notch extending 1/3 length of head; frontoclypeus subtriangular, apex

not quite reaching epicranial notch; 6 stemmata on each side, with the 6th not visible except in macerated head capsule: 1 and 2 close to touching each other, 3 close to usually partially fused with fused 4 and 5, and 6 strongly reduced, not protruding, narrow and posteriorly attenuated (Figs 37, 49, 50); length of many cranial setae reduced to that typical of proprioceptors and their interpretation questionable, with one of the anterior group (A) absent and only one long setae of the posterior group (P) present (Fig. 32). Thoracic legs well developed, with polymorphic tarsus, prothoracic tarsus with two unmodified distal setae and a long, slender claw (base obliterated by fluid in all SEM preparations) (Fig. 40), meso- and metathoracic tarsus with the two distal setae strongly modified, spatulate to cone-shaped, with a strong, distally curved claw (Figs 42, 43, 45, 46, 53, 54). Prothoracic shield pale, with some greyish marks, with five setae and one pore; T1 with L series trisetose, SV bisetose, no V setae; T2+3 with D, SD and L series all bisetose, SV and V unisetose; A1+2 with L and SV series bisetose, V unisetose; A3–6 with L series bisetose, SV unisetose, no V seta; A7 with L and SV series usually bisetose (SV sometimes unisetose), V unisetose; A8 with L, SV and V all unisetose; A9 with 4–6 setae on each side, with position even of the two dorsal ones very variable (Fig. 31). Prolegs present on A3–6, 10; ventral prolegs rather short, with a semicircle of 5–6



Figs 31–35. Larva and pupa of *Ogmograptis* spp. 31, Diagram of chaetotaxy of last-instar larva of *O. racemosa*. 32, Head capsule of last-instar larva of *O. racemosa*. 33, Pupa of *O. racemosa*, ventral view. 34, 35, Frontal process of pupa of *O. racemosa* male (34) and *O. fraxinoides* female (35), lateral view.

crochets along the inner side of each proleg (Fig. 41); anal prolegs reduced, without crochets (Figs 39, 47, 48, 52). A10 modified (Figs 39, 47, 48, 51, 52), with distally strongly protruding lateral lobes crowned by 4 setae each along vertical posterior margin, covered by flat, hand-shaped protuberances on inner surface (anal region); each lobe supported by an internal skeleton of two rods: one much larger, horizontally along lateral margin, widening into a vertical, flat, triangular lobe in apical tip, ventrally joined by a sharply inwardly and downwardly angled, much shorter, thinner and lightly sinuate second rod, with both these ventral rods meeting in a V-shaped connection below anal opening (Fig. 55).

Penultimate larval instar (Figs 7, 8, 24–27, 56). Maximum length 4.5 mm. Extremely long and slender, without legs; head prognathous, dorsoventrally strongly flattened, without spinneret (Fig. 24), mandibles with blunt teeth; prothorax with well developed setae, dorsal shield with a narrow dark band along lateral and posterior margin, with an antero-median extension, forming a transverse, rounded E-shape (Fig. 25); except on head capsule, prothorax and last segment no setae visible; anal segment modified (Fig. 26), with internal skeleton of two longitudinal, posteriorly widened rods (Fig. 56).

Pupa (Figs 17, 33–35)

Length: 3.8–4.4 mm. Aedeagus, with appendages free. Frontal process pointed and blade-shaped (Figs 34, 35). Labial palpi visible. Antennae to tip of abdomen, forewings nearly concealing hindwings, to middle of A7. Abdomen with dorsum of segments 3–7 in female and 3–8 in male with a transverse band of scattered spines in anterior half; A10 with 6 wart-like projections around its base.

Cocoon (Fig. 18)

Length: 5–8 mm. Elongate-ovate to spindle-shaped, wider and more domed at one end, longitudinally ribbed; higher end with a preformed, roughly semicircular exit flap, usually beneath a projecting, loosely spun apron.

Remarks

Genitalia morphology in both sexes suggests three discrete species groups within *Ogmograptis*, two of which are also supported by the molecular data. The *scribula* group, *O. scribula* and all other species reared from bark scribbles,

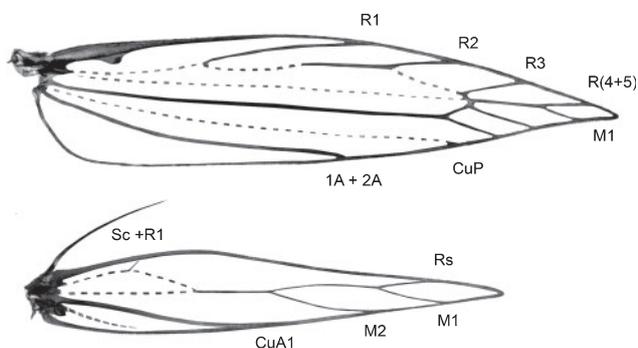


Fig. 36. Wing venation of *Ogmograptis racemosa*, male.

i.e. with tracks in the cork cambium layer, have the base of the aedeagus bent at up to 90°, a moderately long saccus, a sclerotised funnel at the entrance to the ductus bursae and a pale and dark mottled wing pattern. The *maxdayi* group of six species including *O. maxdayi*, with unknown larval biology, has the base of the aedeagus forming a nearly complete loop, a very long, slender and distally lightly clubbed sacculus, a ductus bursae with a small sclerite somewhat below the ostium and a sclerite at the entrance to the corpus bursa. Both these groups have modified, leaf-like ovipositor lobes appressed to each other. *O. triradiata* (Turner), *O. centrospila* (Turner) and two newly described species, *O. bipunctatus* Horak, sp. nov., and *O. pulcher* Horak, sp. nov., all with snow white ground colour, few black-sprinkled yellowish streaks and a black line around the termen, form the apparently more plesiomorphic *triradiata* group. Their larval biology is unknown. They have a straight aedeagus, shorter saccus, an unmodified ovipositor with posteriorly oriented, spinulose lobes, and a sclerotised funnel at the entrance to the ductus seminalis. The modified ovipositor lobes of the *maxdayi* and *scribula* groups suggest a different biology from the *triradiata* group. The level of divergence in the DNA data between the *scribula* group and the two species sequenced from the *maxdayi* group would justify different subgenera, but formalising this is premature until molecular data for the *triradiata* group and biological information for all three subsets of *Ogmograptis* are available.

Checklist of species

scribula group

- Ogmograptis scribula* Meyrick, 1935.
- Ogmograptis fraxinoides* Horak, sp. nov.
- Ogmograptis racemosa* Horak, sp. nov.
- Ogmograptis pilularis* Horak, sp. nov.

maxdayi group

- Ogmograptis maxdayi* Horak, sp. nov.
- Ogmograptis barloworum* Horak, sp. nov.
- Ogmograptis paucidentatus* Horak, sp. nov.
- Ogmograptis rodens* Horak, sp. nov.
- Ogmograptis bignathifer* Horak, sp. nov.
- Ogmograptis inornatus* Horak, sp. nov.

triradiata group

- Ogmograptis triradiata* (Turner, 1926) (*Cateristis*), comb. nov.
- Ogmograptis centrospila* (Turner, 1923) (*Opostega*), comb. nov.
- Ogmograptis bipunctatus* Horak, sp. nov.

Unassigned to species group

- Ogmograptis notosema* (Meyrick, 1922) (*Cryphioxena*).

The *scribula* group

This group is characterised by a moderately long saccus and a moderately long aedeagus with a bent base, by appressed, leaf-shaped ovipositor lobes, and a sclerotised funnel below the ostium. All species have speckled wings with five roughly longitudinal dark streaks, and they are so similar that they cannot be distinguished externally. Interspecific genitalia differences also are subtle, confined to the relative width of the

teeth on the gnathos fringe, the ribs of the juxta, the relative length of the apophyses and the shape of the sclerotised funnel below the ostium and of the corpus bursae. This group comprises the scribbly moths feeding in the cork cambium layer, with the shape of the scribble often taxonomically indicative. There is considerable correlation between *Ogmograptis* species and eucalypt host species, but it is not exclusive, with two of the four species studied sometimes found on the same eucalypt species (see Discussion).

***Ogmograptis scribula* Meyrick**

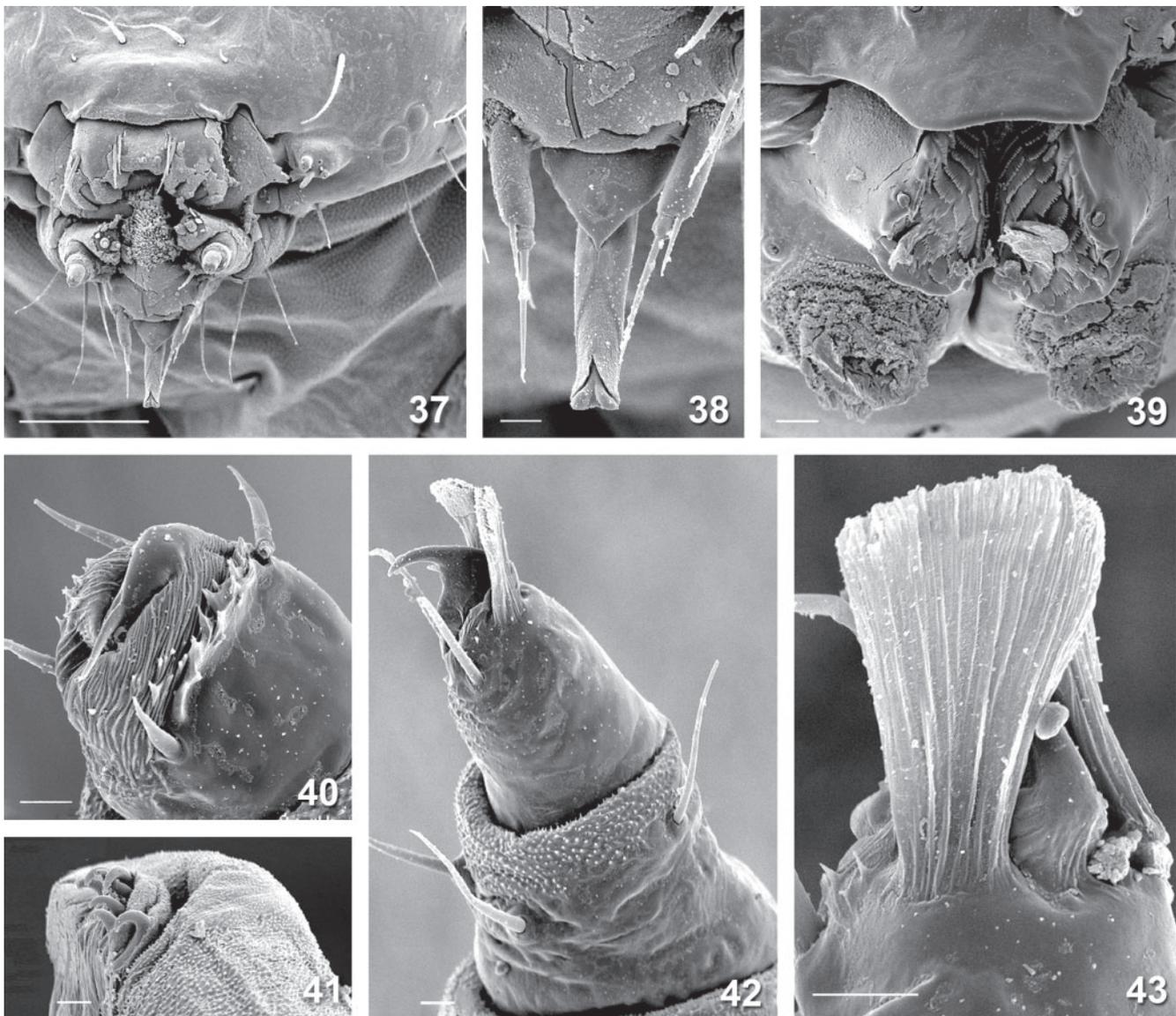
(Figs 1, 2, 12, 15, 20, 21, 37–43, 62, 63, 84–86, 120–122)

Ogmograptis scribula Meyrick, 1935: 600.

Material examined

Holotype. ♂: ‘Scribble Insect, larvae on *Eucalyptus coriacea* [= *E. pauciflora*], Pupated 8–12 Feb[ruar]y [19]35, Emerged 11 March [19]35, Lee’s Springs, Brindabella Range [35.23S 149.103E], FCT [Federal=Australian Capital Territory], Australia, coll. T. Greaves.’; ‘ANIC 31-035161’ (ANIC).

Other material examined. **Australian Capital Territory:** 4 ♂, same label data as holotype, ANIC 31-035162 to 31-035165, ANIC GS 14775 ♂, 14839 ♂; 1 ♀, 35.55S 148.77E, Lee’s Springs, 1.ii.1933, W. Bruce & F. G. Holdaway, ANIC 31-035170; 4 ♀, Canberra [Brindabella Range, coll. T. Greaves], em. Brisbane, 13–18.iii.1934 [Turner’s handwriting], ANIC 31-035181 to 31-035184, ANIC GS 14776♀, 14791♀; 2 ♂, 2 ♀, 35.55S 148.77E, Lee’s Springs, 4000 ft, em. 18.ii.1958, I.F.B. Common, ANIC 31-035166 to 31-035169, ANIC GS H57 ♂, H58♀; 2 ♂, 6 ♀, 35.38S



Figs 37–43. Last-instar larva of *Ogmograptis scribula*, Sawpit Creek, Kosciuszko NP, NSW. 37, Head, frontal. 38, Spinneret. 39, Last abdominal segment, posterior view, note square margin of anal shield. 40, Prothoracic tarsus with modified slender claw (basal part obliterated by undetermined fluid) and two normal distal setae. 41, Proleg with short row of crochets on inner side. 42, Mesothoracic tarsus with modified distal setae and normal claw. 43, Enlarged detail of modified, flattened distal seta. Scales = 0.1 mm (Fig. 37), 0.01 mm (Figs 38–43).

148.80E, Brindabella, Bull's Head, larvae coll. 10 & 12.ii.2010 on *E. pauciflora*, em. 8–20.iii.2010, Horak & Su, Horak & Su & Macnicol, ANIC 31-035171 to 31-035178, ANIC GS 14864♀; (ANIC, AMSA, BMNH).

Diagnosis

Forewings evenly speckled, somewhat darker along dorsum, with five well defined longitudinal dark streaks, the two distal streaks usually connected. Male genitalia: base of aedeagus lightly curved and saccus rather short and stout, with tip of gnathos broadly rounded and with long, slender fringe; central juxta plate dorsally triangularly projecting, with dorsally converging ribs. Female genitalia: appressed, leaf-like, elongate-ovate ovipositor lobes, with short posterior apophyses and with sclerotised narrow funnel below ostium less wide than long; corpus bursae bottle-shaped.

Description

Adult (Figs 62, 63)

Wingspan: (7.5 mm) 10–12 mm.

Head and thorax. Grey-brown, speckled with white scales; upper frons and anterior part of eye cap white.

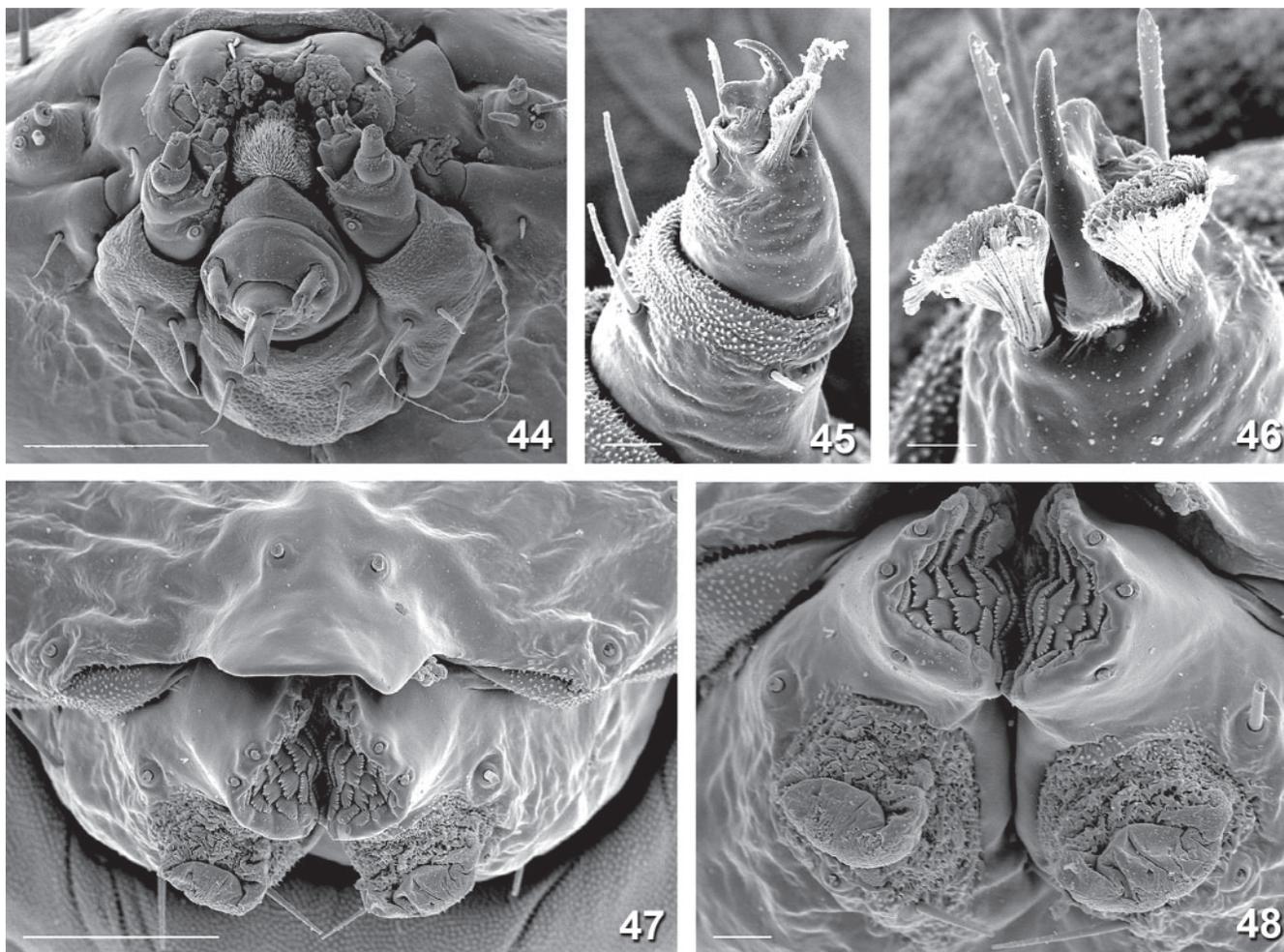
Forewings. White, finely and evenly speckled with grey-brown scales, somewhat denser near dorsum; with five well defined, longitudinal, slender grey-brown streaks, one along midline in basal third, two subparallel and distally slightly converging between 1/3 and middle of wing, the more dorsal of these along fold, the fourth at 3/5 of wing and 1/4 of wing width below costa and the fifth at 2/3 along midline, the last two usually connected in the middle, sometimes a less well defined grey-brown spot at base of apical cilia; terminal cilia white with grey-brown tips, forming two parallel dark bands around apex and termen, dorsal cilia grey.

Hindwings. Pale grey, cilia concolorous.

Legs. White, variably speckled with grey, anterior pair mostly grey, middle pair with tarsi ringed with grey.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 84–86). Gnathos tip broadly rounded, with full apical fringe of long, slender teeth, 4–5 times as long as wide; valva long and sides nearly parallel, widest near apex; saccus rather short; juxta dorsally deeply sinuate band with a



Figs 44–48. Last-instar larva of *Ogmograptis fraxinoides*, Brown Mt, NSW. 44, Mouth parts, frontal view. 45, Mesothoracic leg with modified distal setae and normal claw. 46, Enlarged detail of mesothoracic tarsus with cone-shaped modified distal setae. 47, Last abdominal segment, posterior view, note square margin of anal shield. 48, Enlarged detail of anal prolegs, note absence of crochets. Scales = 0.1 mm (Figs 44, 47), 0.02 mm (Figs 45, 48), 0.01 mm (Fig. 46).

projecting dorsally triangular, shield-shaped median plate with a prominent ventral bar and 2–3 strongly converging ribs running towards dorsal tip of central plate; aedeagus moderately long, straight except for smoothly curved, short, lightly bulbous base; vesica with an indistinct needle-shaped cornutus.

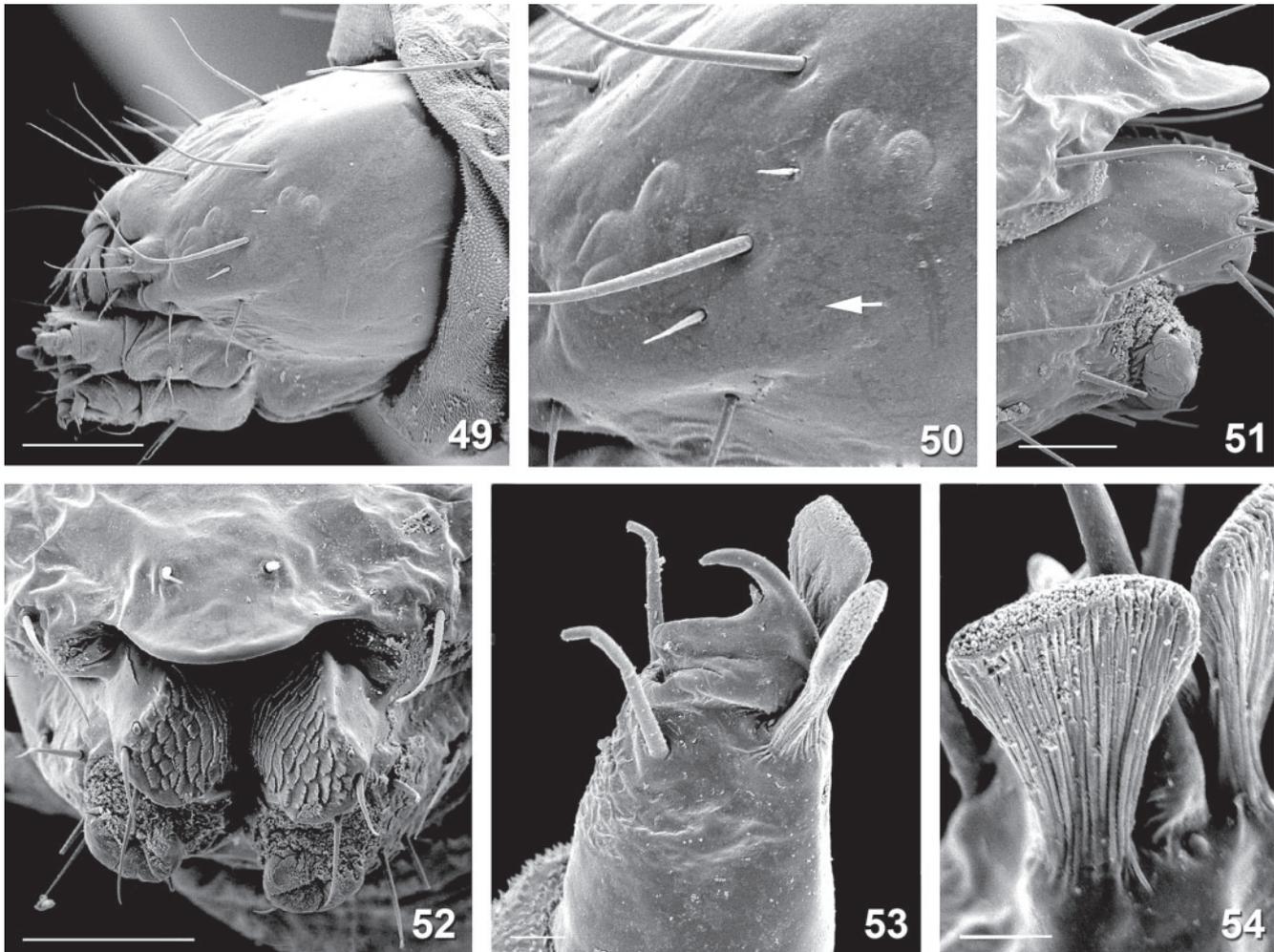
Female genitalia (Figs 120–122). Ovipositor lobes membranous, appressed; elongate-ovate; posterior apophyses, short (1.2–1.3 × length of sclerotised dorsal margin of ovipositor lobe). Ductus bursae membranous, with narrow sclerotised funnel below ostium; corpus bursae bottle-shaped, with posterior 1/3 much narrower and parallel-sided, with large central area of scobination.

Biology

Snow gum, *E. pauciflora* Sieber ex Spreng., is the host of *O. scribula*, with scribbles on the trunk and large branches. According to our observations, scribbles are found only up to an altitude of 1400 m in the Brindabella Ranges and up to the same

altitude in the Kosciuszko National Park, suggesting that *O. scribula* might be restricted to ssp. *pauciflora*. The track of *O. pauciflora* (Figs 1, 2, 12, 15) consists of initial slender, long and rather irregular loops followed by the final set of thicker, shorter and moderately closely approximated zig-zags, with the terminal turns often shorter and/or more widely spaced, giving the doubled track set a somewhat triangular outline. The returning track is parallel but rather distant, with the space between the two tracks usually wider than the width of each track. In some localities (e.g. Sawpit Creek, Kosciuszko NP), *E. pauciflora* is host also to *O. fraxinoides*, with the two species often occurring on the same tree.

Adults reared from mature larvae collected on 12 February 2010 at Bull's Head, Brindabella Range, emerged after 26–30 days. Specimens reared from pupae or fully grown larvae have a wingspan from 11–12 mm, smaller larvae extracted from their track produce much smaller adults, from 7.5 mm upwards, if they survive at all.



Figs 49–54. Last-instar larva of *Ogmograptis racemosa*, nr Gunning, NSW. 49, Head, lateral. 50, Enlarged detail of stemmata region (arrow indicating position of reduced 6th stemma). 51, Last abdominal segment, lateral view. 52, Last abdominal segment, posterior view, note rounded margin of anal shield. 53, Mesothoracic tarsus with modified distal setae and normal claw. 54, Enlarged detail of modified, flattened distal seta. Scales = 0.1 mm (Figs 49, 52), 0.02 mm (Fig. 50), 0.05 mm (Fig. 51), 0.1 mm (Fig. 52), 0.01 mm (Figs 53, 54).

Remarks

According to Meyrick's description, there are three paratypes with the same data as the holotype in the BMNH. There are also five males with the same handwritten label as the holotype in the ANIC, but they were not included in the type series. The labels of the type series give *E. coriacea* as the host plant, which is a synonym of *E. pauciflora*.

Ogmograptis scribula and *O. fraxinoides* both have the forewing sprinkled darker along dorsum, a juxta with dorsally converging ribs and a bottle-shaped corpus bursae. However, the male of *O. scribula* has a longer gnathos fringe with narrower teeth, the juxta is dorsally triangular rather than rounded as in *O. fraxinoides*, and the female has much shorter posterior apophyses than *O. fraxinoides*.

Ogmograptis fraxinoides Horak, sp. nov.

(Figs 3, 35, 44–48, 58, 59, 64, 65, 87–89, 123–125)

Material examined

Holotype. ♂: '36.36S 149.27E [36.60S 149.45E], Brown Mt, NSW, pupa coll. 9 Mar 2010, on/nr *E. fraxinoides*, em. 12 Mar 2010, Edwards, Horak, Day & Su', 'ANIC Database No. 31-035185', 'ANIC GS 14863 ♂' (ANIC).

Paratypes. **New South Wales:** 3 ♂, 3 ♀, same label data as holotype, but em. 21–26.iii.2010, ANIC 31-053186, 053188 to 31-053192, ANIC GS 14861 ♂, 14862 ♀; 1 ♂, 36.6S 149.45E, Brown Mt, pupa coll. 2.iii.2009, em. 24.iii.2009, M. Horak & Y.N. Su, ANIC 31-035199, ANIC GS 1482; 3 ♂; 2 ♀, 36.60S 149.45E, Brown Mt, pupa coll. 14.iii.2010, em. 2 & 5.iv.2010, ANIC 31-035197 & 31-035198, ANIC GS 14838 ♀; 2 ♀, Piper's Lookout 18 km ESE of Nimmitabel [Brown Mt], em. 15 & 19.iii.2007, E.D. Edwards & M.F. Day, ANIC 31-035195 & 31-035196, ANIC GS 14750 ♀; (ANIC, AMSA).

Other material examined. **New South Wales:** 2 ♀, 36.10S 148.20E, Kosciuszko National Park, Sawpit Creek, larvae coll. 6.ii.2010 on *E. pauciflora*, em. 11.iii.2010, Horak, Hines, Corbett & Mackenzie, ANIC 31-035179 & 31-035180, ANIC GS 14872 ♀. (ANIC).

Diagnosis

Forewings with dark speckling concentrated along dorsum, with five longitudinal streaks narrow and all separate, the two costal ones often weak or absent. Male genitalia: with base of aedeagus

lightly curved and saccus rather short and stout, with broadly rounded gnathos tip with short fringe, with dorsally projecting margin of central juxta plate semicircular, not triangular as in *O. scribula*, with dorsally converging ribs. Female genitalia: with appressed, leaf-like, elongate-ovate ovipositor lobes, with long posterior apophyses, with sclerotised funnel below ostium as wide as long, and with bottle-shaped corpus bursae.

Description

Adult (Figs 58, 59, 64, 65)

Wingspan: 10–12 mm.

Head and thorax. Grey-brown, speckled with white scales, upper frons and anterior part of eye cap white.

Forewings. White, increasingly speckled with dark grey and blackish scales towards dorsum, which is quite dark. Five longitudinal, slender dark grey to blackish streaks, one along midline in basal third, two subparallel and distally slightly converging between 1/3 and middle of wing, the more dorsal of these along fold, the fourth at 3/5 of wing and 1/4 of wing width below costa, and the fifth, slightly oblique, at 2/3 along midline, with the two more costal streaks often only indicated; terminal cilia white with dark grey tips, forming two parallel dark bands around apex and termen, dorsal cilia grey.

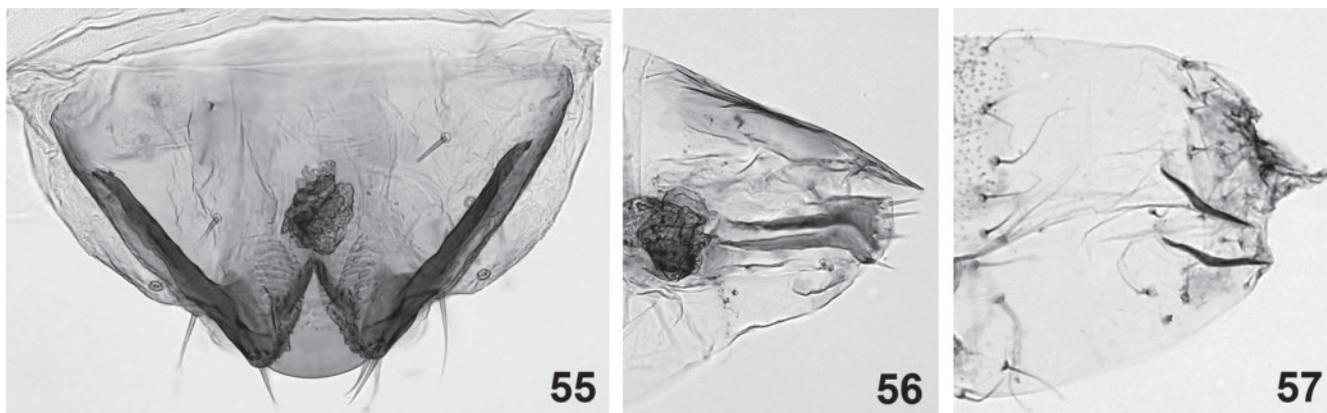
Hindwings. Dark grey, cilia concolorous.

Legs. White variably touched with grey, anterior pair mostly grey, tarsi ringed with grey, darker on anterior and middle pair.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 87–89). Gnathos tip broadly rounded, with full apical fringe of short, relatively broad teeth, 2–3 times as long as wide; valva long and nearly parallel-sided, widest near middle; saccus rather short; juxta a dorsally deeply sinuate band with a dorsally rounded, shield-shaped median plate with a prominent ventral bar and 2–3 dorsally strongly converging ribs; aedeagus moderately long, straight except for short, slightly rounded-angled, lightly bulbous base; vesica with a needle-shaped cornutus.

Female genitalia (Figs 123–125). Ovipositor lobes elongate-ovate, membranous and appressed; posterior apophyses long, 1.6–1.9 × length of sclerotised dorsal margin



Figs 55–57. Internal skeleton in last abdominal segment of larva of *Ogmograptis racemosa* (55, 56) and *Bucculatrix* sp. (57). 55, Dorsal view, last instar. 56, Lateral view, penultimate instar. 57, Lateral view, penultimate instar.



Figs 58–61. Head of *Ogmograptis* spp., male. 58, 59, *O. fraxinoides*. 60, 61, *O. maxdayi*.

of ovipositor lobe. Ductus bursae membranous with wide sclerotised funnel below ostium (as wide as long); corpus bursae bottle-shaped, with posterior 1/3 much narrower and parallel-sided, with large central area of scobination.

Biology

White ash, *Eucalyptus fraxinoides* H.Deane & Maiden, and *E. pauciflora* are both hosts of *O. fraxinoides*, but only material from the former host at Brown Mt is included in the type series. On *E. fraxinoides*, scribbles are on the trunk above the rough bark at the base of the tree and on large branches, often at high density. The track of *O. fraxinoides* (Fig. 3) consists of initial slender, rather irregular and sometimes long zig-zags followed by the final set of thicker, shorter and closely approximated zig-zags, with the returning track separate but usually very closely parallel to the initial track so that the distance between the tracks is hardly more than the width of each track. On mature trees there are often large numbers of scribbles, with the doubled part of the track compressed and usually with a rectangular outline. On *E. pauciflora* scribbles of *O. fraxinoides* were nearly all on the southern face of the trunk and hardly ever in the bottom 1–2 m.

At Pipers Lookout, Brown Mt, Southern Forests NP, larvae were found boring out of their track on 8 February 2010, with about half the larvae having already left the mine. Pupae collected on 9 March 2010 behind bark at the foot of the tree or on leaves in nearby leaf litter emerged between 12 March and 4 April, but mainly 21–24 March. On the slope above Sawpit Creek, Kosciuszko NP, larvae found boring out of their tracks on *E. pauciflora* pupated on 7 February 2010. The first cocoon was found 6 h after the larva was collected, several more formed their cocoons in the next 48 h, and two adults emerged after 33 days.

Remarks

This species occurs together with *O. scribula* on *E. pauciflora* on the slope above Sawpit Creek in Kosciuszko NP, with no *E. fraxinoides* nearby, and photos of scribbles on snow gum on Mt. Kaputar suggest that it is present there as well. *O. fraxinoides* can be separated from the very similar *O. scribula* by a shorter gnathos fringe with wider teeth, a dorsally more rounded juxta in the male, and by much longer posterior apophyses in the female. While the two species have very modest molecular divergences, resulting in the limited nodal support for their

reciprocal monophyly (Fig. 30), genitalic and scribble structure differences support their separation into two species. It is possible that the limited molecular divergences between these species, and their sharing of *E. pauciflora* as a host in some regions, is evidence of their recent speciation.

Etymology

The species name refers to the host tree.

Ogmograptis racemosa Horak, sp. nov.

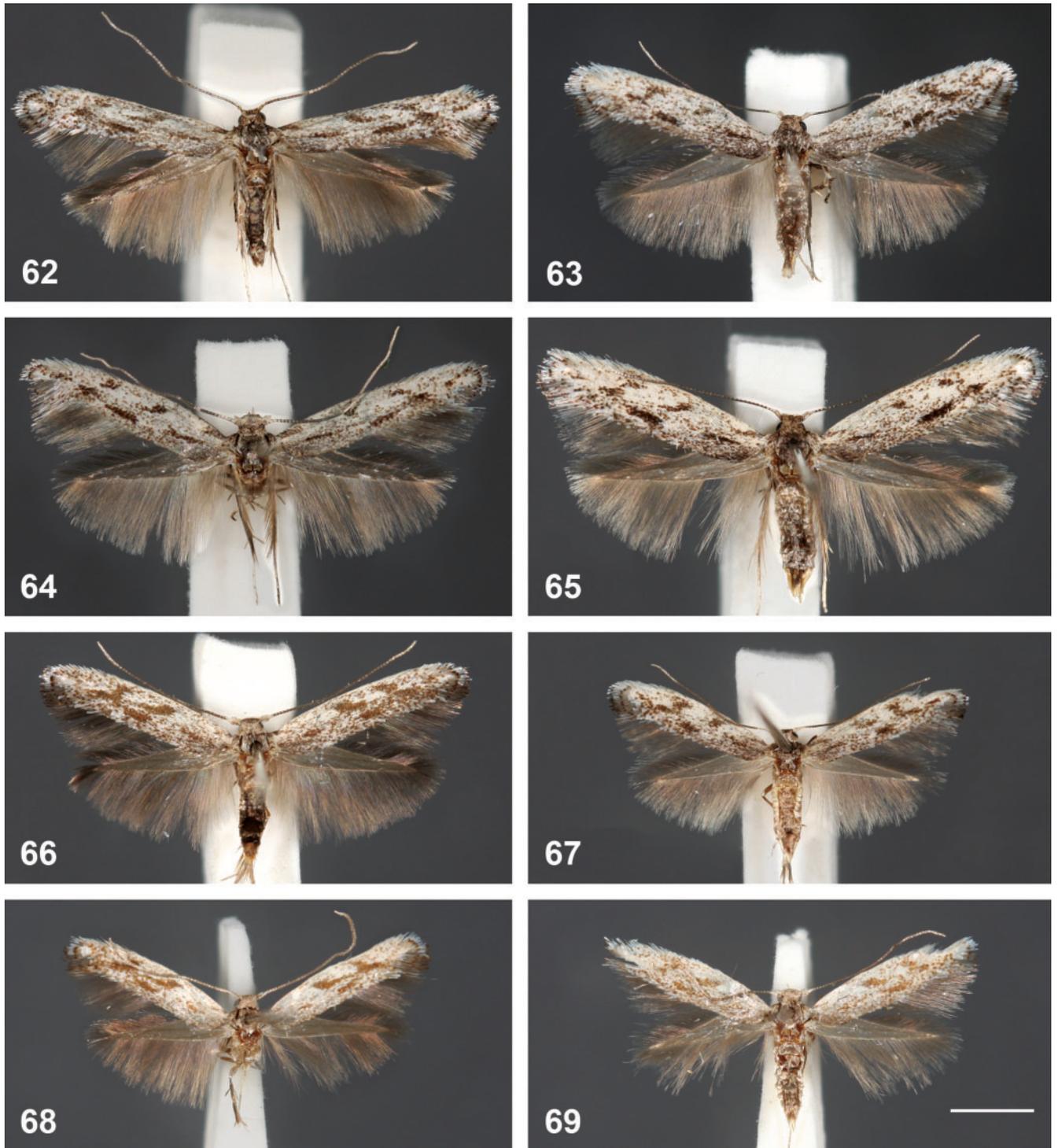
(Figs 4, 7–9, 13, 14, 16–19, 22, 24–28, 31–34, 36, 49–56, 66, 67, 90–92, 126, 127)

Material examined

Holotype. ♂: '35.17S 149.06E [35.28S 149.10E], Botanical Gardens, Canberra, ACT, Emg. 30 Apr 2007, Day, Horak & Edwards'; 'Cocoon in litter beneath *Eucalyptus racemosa*, 'ANIC Database No. 31-035200', 'ANIC Genitalia slide No 14873 ♂' (ANIC).

Paratypes. **Australian Capital Territory:** 4 ♂, 3 ♀, same label data as holotype but em. 2–30.iv.2007, ANIC 31-0352001 to 31-0352007, ANIC GS 14878 ♂; 1 ♂, 2 ♀, 35.28S 149.10E, Botanical Gardens, Canberra, Apr. 2006, M. Day, ANIC 31-035212 to 31-035214, ANIC GS 19315♀; 2 ♂, 35.28S 149.10E, Botanical Gardens, Canberra, 14.iv.2006, M. Day; 3 ♂, 8 ♀, 35.28S 149.10E, Botanical Gardens, Canberra, 28.iii.–19.iv.2007, Day & Edwards, ANIC 31-035215 to ANIC 31-035225, ANIC GS 14784♀; 1 ♂, 35.28S 149.10E, Botanical Gardens, Canberra, pupa on *E. racemosa* ssp. *rossii*, em. 4.iv.2007, Machicol & Horak, ANIC 31-035209, ANIC GS 14751 ♂; 1 ♂, 2 ♀, 35.27S 149.10E, Black Mt, Canberra, 2 & 9.iv.1963, 15.v.1964, I.F. B. Common, ANIC 31-035208, 31-035210 & 31-035211, ANIC GS H59 ♂. **New South Wales:** 5 ♂, 5 ♀, 34.88S 149.12E, Barlow's property nr Gunning, Celia & Peter Barlow, em. Apr. 2006, pupae coll. 23 Jan. em. Apr. 2007, pupae coll. Dec. 2008 em. 7–20.iv.2009, ANIC 31-035226 to 31-035235, ANIC GS 14773 ♀, 14780 ♂, 14788 ♀, 19316 ♂; (ANIC, AMSA, BMNH).

Other material examined. **New South Wales:** 5 ♂, 6 ♀, 34.13S 150.82E, 3 km E Wedderburn, at MV light, 15 & 21.iv.2007, em. 18–28.iv.2007, D. Britton, ANIC 31-035271 to 31-035281, ANIC GS 14782 ♂, 19357 ♂, 19358 ♀; 16 ♂, 16 ♀, 34.23S 150.70E, CSIRO Exp. Farm, Wilton, 18.iv.1974, 28.iv.1974, 8.v.1974, 11.iv.1975, 19.v.1975, 15.v.1977, V. J. Robinson, ANIC 31-035236 to 31-035267, ANIC GS 14754 ♂, 14771 ♂, 14774 ♂, 19329 ♂, 19330 ♀, 19336 ♀; 4 ♂, 35.15S 150.65E, Jervis Bay Nat. Res., 3.iv.1999, L. Kaila, black light, ANIC 31-035282 to 31-035285, ANIC GS 19400 ♂; 2 ♀, 35.15S 150.67E, Jervis Bay Botanical Gardens, cocoon beneath *E. racemosa*, em. 24 & 25.iv.2007, E.D. Edwards & M.F. Day, ANIC 31-035286 & 31-035287, ANIC GS 14748 ♀ (ANIC, AMSA).



Figs 62–69. Adults of the *Ogmograptis scribula* group. 62, 63, *O. scribula*, male, Bull's Head, ACT (62), female, Sawpit Creek, Kosciuszko NP, NSW (63). 64, 65, *O. fraxinoides*, holotype male (64), paratype female (65). 66, 67, *O. racemosa*, holotype male (66), female paratype, nr Gunning, NSW (67). 68, 69, *O. pilularis*, holotype male (68), paratype female (69). Scale = 2 mm.

Diagnosis

Forewings evenly speckled, usually three dark longitudinal marks in basal half of wing and an irregular larger dark mark in distal

half. Male genitalia: base of aedeagus lightly curved and saccus rather short and stout, with rounded-truncate gnathos tip with long fringe of slender teeth, with dorsally projecting pentagonal central juxta plate with vertical ribs, the two flanking the central plate on

each side pronounced and with tips often projecting beyond dorsal margin. Female genitalia: appressed, leaf-like, elongate-ovate ovipositor lobes, with long posterior apophyses and with sclerotised narrow funnel below ostium, less wide than long, and with ovate to slightly hourglass-shaped corpus bursae.

Description

Adult (Figs 19, 66, 67)

Wingspan: 8.5–10.5 mm.

Head and thorax. Grey-brown, speckled with white scales, upper frons and anterior part of eye cap white.

Forewings. White, finely and evenly speckled with grey-brown scales, with four moderately defined grey-brown marks, roughly longitudinal, one along midline in basal third, two subparallel and slightly converging distally between 1/3 and middle of wing, the more dorsal of these along fold, the fourth an irregular dash along middle of distal third of wing with extensions towards costa at both ends, the proximal extension at 2/3 costa and the distal one to just before apex; terminal cilia white with grey-brown tips, forming two parallel dark bands around apex and termen, dorsal cilia grey.

Hindwings. Grey, cilia concolorous.

Legs. White variably touched with grey, anterior pair mostly grey, middle pair with tarsi ringed with grey.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 90–92). Gnathos tip rounded-truncate with full fringe of long, slender teeth; valva moderately long, nearly parallel-sided, widest beyond middle; saccus moderately long; juxta a band with a dorsally projecting, shield-shaped, pentagonal median plate with a prominent bar along ventral margin and some faint vertical ribs, with a shorter, stronger vertical rib with usually dorsally projecting tip flanking the median plate on each side; aedeagus long, straight to faintly sinuate with a curved to weakly angled, lightly bulbous base; vesica with two needle-shaped cornuti.

Female genitalia (Figs 126, 127). Ovipositor lobes elongate-ovate, membranous, appressed; posterior apophyses long, 1.7–2.0 × length of sclerotised dorsal margin of ovipositor lobe; ductus bursae membranous, with narrow sclerotised funnel below ostium; corpus bursae ovate, somewhat hourglass-shaped, with large area of scobination in posterior 2/3 and with a short, narrow neck leading to ductus bursae and ductus seminalis.

Biology

O. racemosa occurs on both inland scribbly gum or white gum, *E. racemosa* ssp. *rossii* R. Baker & H.G. Smith, and narrow-leaved scribbly gum or snappy gum, *E. racemosa* ssp. *racemosa* Cav., supporting the recent decision that the two taxa are merely subspecies (Pfeil and Henwood 2004). Scribble tracks on *E. haemastoma* Smith look exactly like those on *E. racemosa*, and given the close relationship between the two species it would not be surprising if *E. haemastoma* also serves as host for *O. racemosa*. Most of our observations and the type series are based on material from *E. racemosa* ssp. *rossii*. Scribbles are present on the trunk and large branches. The track of *O. racemosa* (Figs 4, 9, 13, 14, 16) is unique as the return track is not parallel to

but adjoining the initial track, enlarging it to double width. This results in initial slender, long and rather irregular zig-zags followed by a final set of much thicker, shorter, single zig-zags with a turning loop at each end.

Remarks

O. racemosa and *O. pilularis* are superficially similar and share a juxta with vertical rather than dorsally converging ribs and an ovate to hourglass-shaped corpus bursae. However, *O. racemosa* has a gnathos fringe with longer, narrower teeth.

Etymology

The species name refers to the host tree.

***Ogmograptis pilularis* Horak, sp. nov.**

(Figs 5, 6, 68, 69, 93–95, 128–130)

Material examined

Holotype. ♂: '[35.63S 150.32E] 1.5 km N of Depot Beach, 16 km NE of Batemans Bay, NSW, 12 Apr. 1975, I.F.B. Common', 'ANIC Database No. 31-035288', 'ANIC genitalia slide No 14867 ♂' (ANIC).

Paratypes. **New South Wales:** 2 ♂, same label data as holotype but ANIC 31-035289 & 31-035290; 6 ♂, 6 ♀, 35.63S 150.32E, Ryans Ck Rd, Depot Beach, 16 km NE of Batemans Bay, 11.iv.1975, I.F.B. Common, ANIC 31-035291 to 031302, ANIC GS 14752 ♀, 14772 ♂, 14840 ♀, 14868 ♀, 19337 ♂ (ANIC, AMSA, BMNH).

Diagnosis

Forewings lightly speckled, usually three dark longitudinal marks in basal half of wing and an irregular oblique dark mark in distal half. Male genitalia: base of aedeagus lightly curved and saccus rather short and stout, with rounded-truncate gnathos tip with moderately long fringe of broad teeth, with dorsally projecting pentagonal central juxta plate with vertical ribs, the two flanking the central plate on each side pronounced and with tips projecting beyond dorsal margin. Female genitalia: appressed, leaf-like, elongate-ovate ovipositor lobes, with long posterior apophyses and with narrow sclerotised funnel below ostium, less wide than long, and with ovate to hourglass-shaped corpus bursae.

Description

Adult (Figs 68, 69)

Wingspan: 8.5–9.5 mm.

Head and thorax. Speckled with white scales tipped with grey-brown, upper frons and anterior part of eye cap white.

Forewings. White, speckled with scales with grey-brown tips, with four irregular grey-brown marks, roughly longitudinal, one along midline in basal third, two subparallel and distally slightly converging between 1/3 and middle of wing, the more dorsal of these along fold and sometimes connected with the fourth mark, the fourth an irregular dash along middle of distal third of wing with extensions towards costa usually at both ends, the proximal extension at 2/3 costa and the distal one to just before apex; terminal cilia white with grey-brown tips, forming two parallel dark bands around apex and termen, dorsal cilia grey.

Hindwings. Grey, cilia concolorous.

Legs. White variably touched with grey, anterior pair mostly grey, middle pair with tarsi ringed with grey.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 93–95). Gnathos tip rounded-truncate with full fringe of rather stout teeth, valva moderately long, nearly parallel-sided, widest beyond middle, saccus moderately long, juxta a band with a dorsally projecting, shield-shaped, pentagonal median plate with a prominent bar along ventral margin and some faint vertical ribs, with a shorter, stronger vertical rib flanking the median plate on each side; aedeagus long, straight to faintly sinuate with a curved to weakly angled, lightly bulbous base; vesica with one needle-shaped cornutus.

Female genitalia (Figs 128–130). Ovipositor lobes elongate-ovate, membranous, appressed; posterior apophyses long. Ductus bursae membranous, with narrow sclerotised funnel below ostium; corpus bursae ovate to somewhat hourglass-shaped, with large area of scobination in posterior 2/3 and with a short, narrow neck leading to ductus bursae and ductus seminalis.

Biology

Blackbutt, *E. pilularis* Sm., is the host of *O. pilularis*, with scribbles only observed high on the larger smooth branches above the entirely rough-barked trunk. The track of *O. pilularis* (Figs 5, 6) is unlike other scribbles examined, having the terminal set of thick zig-zags produced in the reverse direction, superimposed over the initial, slender zig-zags. The initial, widely spaced zig-zag track ends in a sharp turning loop with the conspicuously wider returning track usually closely following back to the previous turning point, then proceeding as the final set of thick, short and closely spaced zig-zags across the zig-zags of the initial track. After a second turning loop at the end of this final set the track returns closely parallel for several zig-zags before joining the original track.

Remarks

O. pilularis can be separated from the closely related *O. racemosa* by the shorter, wider teeth of the gnathos fringe.

Etymology

The species name refers to the host tree.

The *maxdayi* group

This group is characterised by a very long slender saccus, a long crosier-shaped aedeagus, appressed, leaf-shaped ovipositor lobes, and a sclerotised ring somewhat below the ostium. The wing pattern in this group is much more diverse than in the other species groups of *Ogmograptis*. Interspecific genitalia differences also are usually obvious, especially in the shape of the gnathos tip and the juxta. Nothing is known about the larval biology of this group.

Ogmograptis maxdayi Horak, sp. nov.

(Figs 60, 61, 70, 71, 96–98, 131)

Material examined

Holotype. ♂: [35.27S 149.10E] Black Mt, ACT, Light Trap, 15 Oct. 1963, I.F.B. Common', 'ANIC Database No. 31-035303', 'ANIC genitalia slide No 14879 ♂' (ANIC).

Paratypes. 13 ♂, 5 ♀, same label data as holotype but 7.x.–6.xi.1959, 6.xii.1960, 9.x.–25.xi.1963, 22.x.1964, ANIC 31-035304 to 31-035321, ANIC GS 14790 ♂, 14875 ♂, 19327 ♂, 19328 ♀ (ANIC, DEMV, BMNH).

Other material examined. **Victoria:** 1 ♂, 2 ♀, 37°44.1'S 145°13.2'E, Warrandyte, 16–31.x.2004, 1–15.x.2007, 1–15.xi.2008, D.J. Hilton, ANIC GS 14920 ♀, 14822 ♂ (ANIC).

Diagnosis

Forewings white, with a few scattered dark-tipped scales in distal half and in a double row around termen, with five small roughly longitudinal yellow streaks, some sprinkled with dark grey. Male genitalia: very long, crosier-shaped aedeagus; club-shaped saccus; gnathos tip fringed only along central 2/3; valva with costa convex in distal half and apex tapering, narrowly rounded; juxta wide, band-shaped, with a median crease. Female genitalia: appressed, leaf-like, broadly ovate ovipositor lobes; ductus bursae narrow, sclerotised, with a narrow membranous funnel below ostium ending in a small sclerotised ring; corpus bursae ovate with a short, triangular, partly sclerotised neck.

Description

Adult (Figs 60, 61, 70, 71)

Wingspan: 8–12 mm.

Head and thorax (Figs 60, 61). White except for some pale grey scales on lower part of face and anterior edge of eye cap, and a silvery grey antennal flagellum.

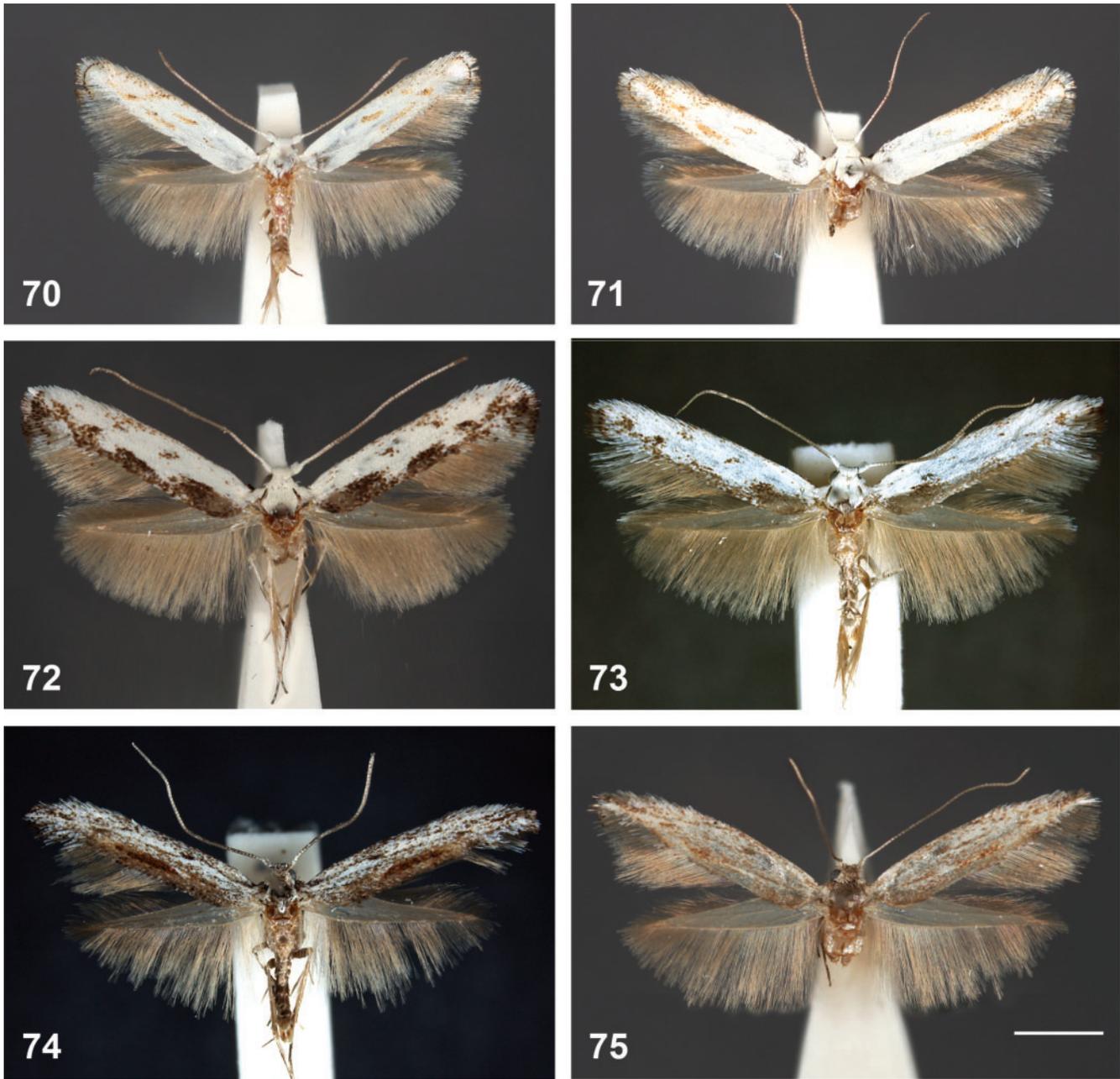
Forewings. White, with widely scattered off-white scales; scales with narrow grey-brown apex in a narrow band along costa from 1/4 to apex, expanded into an irregular wider band beyond middle; far fewer off-white scales scattered along dorsum beyond 1/4, reaching to middle of wing in distal third; four or five longitudinal, deep yellow streaks, the first faint and often absent, a slender line along midline of wing in basal third, the next two subparallel and distally slightly converging near middle of wing, the shorter one just below middle of wing and 1/3 from costa, the longer dorsal one along fold from just below middle to 2/3, the fourth a short, indistinct dash at 2/3, ~1/4 below costa, and the fifth at 3/4 of wing near midline, an oblique dash, distally sometimes extended as a narrow line towards termen; yellow streaks often sprinkled with a few dark-tipped off-white scales, especially the fifth one; terminal cilia white with short dark grey tips, forming two narrow dark bands around apex and termen in perfect specimens, the basal one darker; dorsal cilia pale grey.

Hindwings. Pale grey, cilia concolorous.

Legs. White, variably touched with grey, darker on more anterior legs.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 96–98). Gnathos with rounded tip with moderately long apical fringe only around central 2/3 of apical curvature; valva moderately long, much wider (1.4–1.6×) in distal half with costa lightly convex and apex tapering, sharply rounded; saccus long, slender, club-shaped; juxta a wide band with a strong ventral bar, with dorsal margin long and slightly sinuate, with a weakly beak-shaped vertical median crease; aedeagus very long, with a large basal loop, crosier-shaped, broadest at base, gradually tapering to narrow apex; vesica without obvious cornuti.



Figs 70–75. Adults of the *Ogmograptis maxdayi* group. 70, 71, *O. maxdayi*, paratype male (70), paratype female (71). 72, 73, *O. barloworum*, holotype male (72), paratype female (73). 74, 75, *O. paucidentatus*, paratype male (74), paratype female (rubbed specimen) (75). Scale = 2 mm.

Female genitalia (Fig. 131). Ovipositor lobes membranous, appressed, broadly ovate, with scattered bristles; posterior apophyses 1.7 × as long as anterior apophyses. Ductus bursae with a long, narrow, membranous funnel below ostium ending in a narrow, strongly sclerotised ring, remainder of ductus narrow and lightly sclerotised; corpus bursae ovate, with large area of very sharp and long spinules in anterior 2/3, and with a short, triangular, partially sclerotised neck leading to ductus bursae and ductus seminalis.

Remarks

One male and two females from Warrandyte, Victoria, are conspecific but have not been included in the type series from Black Mt, ACT. Superficially, *O. maxdayi* resembles a species of the *triradiata* group, but the yellow marks in the distal half of the forewing are never joined into a three-branched structure. The band-shaped juxta with a prominent median crease is diagnostic for *O. maxdayi*.

Etymology

This species is named for Max Day who inspired and guided this study.

Ogmograptis barloworum Horak, sp. nov.

(Figs 72, 73, 99–101, 132)

Material examined

Holotype. ♂: 'ACT, Black Mt [35.27S 149.10E], 4 Oct. 1963, I.F. B. Common, light trap; ANIC 31-035322; ANIC GS No. 19332 ♂' (ANIC).

Paratypes. 3 ♂, same data as holotype but 19.ix.1962, 29.ix. & 20.x.1964, ANIC 31-035323 to 31-035325 (ANIC, DEMV).

Other material examined. **Victoria**: 1 ♀, 37.43S 145.64E, Melbourne, Gembrook, Gilwell Park, at light, 30.x.2009, Kallies, Marriott & Hilton, ANIC GS 14874 ♀ (ANIC).

Diagnosis

Forewings mostly white with few scattered dark scales along costa and an irregularly wide dark grey band along most of dorsum, any dark marks in costal half of wing very small. Male genitalia: with crosier-shaped aedeagus and very long, club-shaped saccus, with gnathos tip strongly tapering and fringed around its entire rounded apex, with distally broadly rounded valva tip, and juxta with a dorsally sharply projecting median plate.

Description

Adults (Figs 72, 73)

Wingspan: 10.5–13.5 mm.

Head and thorax. White except for pale grey scales on lower part of face, a silvery grey antennal flagellum and a dark grey posterior tip of thorax.

Forewings. White with a narrow band of unevenly scattered dark grey scales along costa to 2/3 expanding into a triangle reaching towards centre of wing beyond middle; with a broad dark grey band along dorsum to just before tornus, broadly indented nearly to dorsum at 1/3 and at 2/3, distal part of grey band beyond 2/3 mixed with white scales and often connected with a variable patch of mixed white and dark grey scales in middle of termen, often extending as a dark grey triangle across terminal cilia; central white part of wing with a variable spot of mixed white and grey scales at 2/5; terminal cilia white with dark grey tips at least in middle of termen forming two parallel dark grey rows, sometimes cilia in middle of termen entirely dark grey; dorsal cilia grey.

Hindwings. Pale grey, cilia concolorous.

Legs. White, variably touched with grey, darker on more anterior legs.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 99–101). Gnathos strongly tapering to rounded tip with moderately long apical fringe around entire curvature; valva long, much (1.6–1.7×) wider in distal half, apex broadly rounded; saccus long, slender, club-shaped; juxta a narrow band with a dorsally sharply and irregularly projecting shield-shaped median plate with a prominent ventral bar and an outwardly curved rib on each side; aedeagus very long, with a

large basal loop, crosier-shaped, broadest at base, gradually tapering to narrow apex; vesica without obvious cornuti.

Female genitalia (tentatively associated) (Fig. 132). Ovipositor lobes membranous, appressed, ovate, with scattered bristles; posterior apophyses 1.4× as long as anterior apophyses. Ductus bursae with a long, narrow, membranous funnel below ostium ending in a broad, longitudinally ribbed sclerotised ring, remainder of ductus narrow and lightly sclerotised; corpus bursae ovate, with large area of widely scattered minute spinules in anterior 2/3, and with a short, triangular, weakly sclerotised neck leading to ductus bursae and ductus seminalis.

Remarks

Among the described species, *O. barloworum* is characteristic with its bipartite forewing, largely white in the costal half and largely grey-black along the dorsum, but there are somewhat similar undescribed species with additional black marks on the costa. The combination of a strongly tapering gnathos tip and a juxta with a dorsally irregularly or weakly projecting median plate is characteristic of the species. A single female from Gembrook, Victoria, seems to be conspecific and is tentatively described and figured, but not included in the type series.

Etymology

This species is named for Peter and Celia Barlow who both played a crucial role in unravelling the biology of *Ogmograptis*.

Ogmograptis paucidentatus Horak, sp. nov.

(Figs 74, 75, 102–104)

Material examined

Holotype. ♂: '[35.27S 149.10E] Black Mt, ACT, Light Trap, 2 May 1963, I.F.B. Common', 'ANIC Database No. 31-035326', 'ANIC genitalia slide No 19334 ♂' (ANIC).

Paratypes. **Australian Capital Territory**: 4 ♂, 1 ♀, same label data as holotype, but 3.viii.1961, 17 & 27.v.1963, 7.v.1964, ANIC 31-035327 to 31-035331, ANIC GS 19333 ♀, 19334 ♂, 19335 ♂. **New South Wales**: 1 ♂, 35.33S 149.25E, 2.7 km NE of Queanbeyan, 18.v.1974, I.F.B. Common, ANIC 31-035332 (ANIC).

Diagnosis

Forewings white with scattered dark brown scales and usually three brown short streaks in costal half, and largely brown, often partially red-brown in dorsal half, with a long dark mark along fold. Male genitalia: crosier-shaped aedeagus and very long, club-shaped saccus, uncus tips short and blunt, gnathos with acute apex with only a few teeth, valva distally only moderately wider, apex broadly rounded, juxta in slide preparation folded and projecting as a narrow beak. Female genitalia: appressed, leaf-like, broadly ovate ovipositor lobes, ductus bursae narrow, sclerotised, slightly widening near corpus bursae, with a short, sclerotised tube below ostium, corpus bursae ovate.

Description

Adult (Figs 74, 75)

Wingspan: (8.5) 11.5–13 mm.

Head and thorax. Speckled with brown-tipped white scales except for upper frons and anterior half of eye cap which are entirely white; basal part of flagellum with alternating rings of white and light brown scales, remainder pale silvery grey.

Forewings. White, scattered with brown-tipped scales, less so in a mostly white longitudinal band costad to middle of wing ending on distal part of costa; with a narrow band of brown to red-brown scales along dorsum, extending to terminal cilia; longitudinal marks ill-defined or absent except for slightly oblique, short, dark brown streak just below 1/3 wing, an often large and prominent dark mark along fold in middle third of wing, frequently surrounded by red-brown scales and fused with the brown band along dorsum, and usually a brown line in wingtip extending as a narrow brown triangle onto terminal cilia; remainder of terminal cilia white with brown tips, not forming two concentric rings around apex.

Hindwings. Pale grey, cilia concolorous.

Legs. Mottled pale brownish grey, darker on more anterior legs.

Abdomen. Pale brownish grey, darker dorsally.

Male genitalia (Figs 102–104). Uncus tips short and blunt; gnathos tapering to pointed tip with apical fringe of only a few teeth; valva long, wider (1.4×) in distal half and broadly rounded; saccus long, slender, club-shaped; juxta apparently a wide band without any obvious vertical ribs, in slide preparation folded and projecting as a narrow beak; aedeagus very long, with a large crosier-shaped basal loop, broadest at base, gradually tapering to narrow apex; vesica without obvious cornuti.

Female genitalia (single female with crushed abdomen and damaged genitalia). Ovipositor lobes membranous, appressed, short and wide, with scattered bristles; posterior apophyses long, nearly twice length of sclerotised dorsal margin of ovipositor lobe. Ductus bursae apparently with a very short sclerotised tube below ostium, remainder of ductus narrow and lightly sclerotised, slightly widening near corpus bursae; corpus bursae ovate, posteriorly ending in a pointed, membranous apex leading to ductus bursae and ductus seminalis, with area of scobination in anterior 2/3.

Remarks

Among seven males of otherwise similar size there is one much smaller specimen with identical genitalia. The red-brown streak along the dorsum of the forewing and the unique gnathos tip readily characterise *O. paucidentatus*.

Etymology

The species name refers to the few teeth on the gnathos tip.

***Ogmograptis rodens* Horak, sp. nov.**

(Figs 76, 105–107)

Material examined

Holotype. ♂ [33.65S 151.28E] Church Pt., NSW, 13 Sept 1966, I.F.B. Common', 'ANIC Database No. 31-035335', 'ANIC genitalia slide No 14842 ♂' (ANIC).

Paratypes. 1 ♂, same label data as holotype but 15.ix.1966, ANIC 31-053334, ANIC GS 14753 ♂; 1 ♂, 34.23S 150.7E, CSIRO Experimental Farm Wilton, 3.x.1974, V.J. Robinson, ANIC 31-053333 (ANIC).

Diagnosis

Forewings white, speckled with dark brown scales, with five longitudinal dark grey-brown marks as obvious but ill-defined streaks or smudges, and with basal third of dorsum dark grey-brown and a grey-brown streak to apex. Male genitalia: crosier-shaped aedeagus and very long, club-shaped saccus; gnathos with broadly rounded apex with fringe of a few teeth only in centre of distal margin; valva rather short and apex tapering, narrowly rounded; juxta in slide preparation folded and projecting as a long, narrow beak.

Description

Adult male (Fig. 76)

Wingspan: 10.5–14 mm.

Head and thorax. Speckled with brown-tipped white scales except for narrow band on upper frons and along anterior margin of eye cap which are entirely white; basal part of flagellum with alternating rings of white and dark brown scales, remainder silvery grey.

Forewings. White, speckled with brown-tipped scales, particularly along costa and dorsum and in apical third; large but ill-defined longitudinal grey-brown marks, the basal one fused with a grey-brown patch reaching from dorsum to middle in basal third of wing, the second an oblique smudge just below middle of wing, the third near fold in middle of wing sometimes extending to dorsum, the fourth ill-defined beyond middle of costa, parallel to the second one, and the fifth a smudge along midline at 3/4; terminal cilia pale grey with narrow dark brown tips, whitish in middle of termen, dark tips not forming two parallel rows.

Hindwings. Pale grey-brown, cilia concolorous.

Legs. Mottled pale brownish grey, darker on more anterior legs.

Abdomen. Pale brownish grey, darker dorsally.

Male genitalia (Figs 105–107). Gnathos tip nearly parallel-sided, apex broadly rounded with fringe of few teeth only in centre of distal margin; valva rather short, wider in distal half with apex tapering, sharply rounded; saccus long, slender, club-shaped; juxta in slide preparation folded and projecting as a very long, narrow beak, apparently with two submedian vertical rods suggesting a median plate; aedeagus very long, with a large basal loop (collapsed during mounting), crosier-shaped, broadest and slightly bulbous at base, gradually tapering to narrow apex; vesica without obvious cornuti.

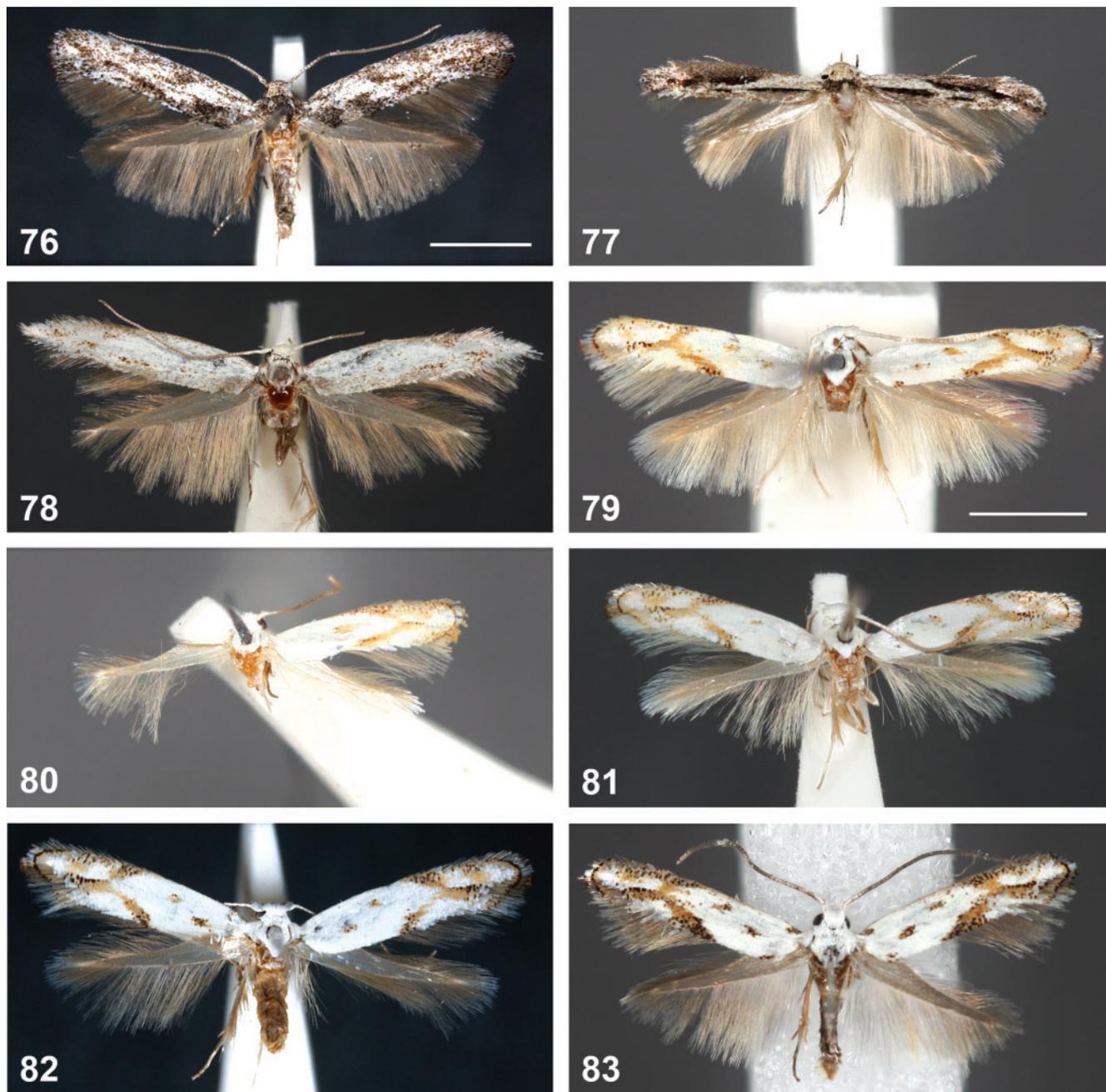
Female. Unknown.

Remarks

Superficially, *O. rodens* might be confused with other undescribed black and white mottled species, but the combination of the unique gnathos tip and the very large dorsally projecting median shield of the juxta are diagnostic.

Etymology

The species name refers to the gnathos tip which recalls a rodent's teeth.



Figs 76–83. Adults of the *Ogmograptis maxdayi* (76–78) and *O. triradiata* (79–83) groups. 76, *O. rodens*, holotype male. 77, *O. bignathifer*, holotype male. 78, *O. inornatus*, holotype male. 79, *O. triradiata*, holotype male. 80, *O. centrospila*, lectotype male. 81, 82, *O. bipunctatus*, holotype male (81), paratype female (82). 83, *O. pulcher*, holotype male. Scales = 2 mm; Figs 76–78 at same magnification, Figs 79–83 at same magnification.

***Ogmograptis bignathifer* Horak, sp. nov.**

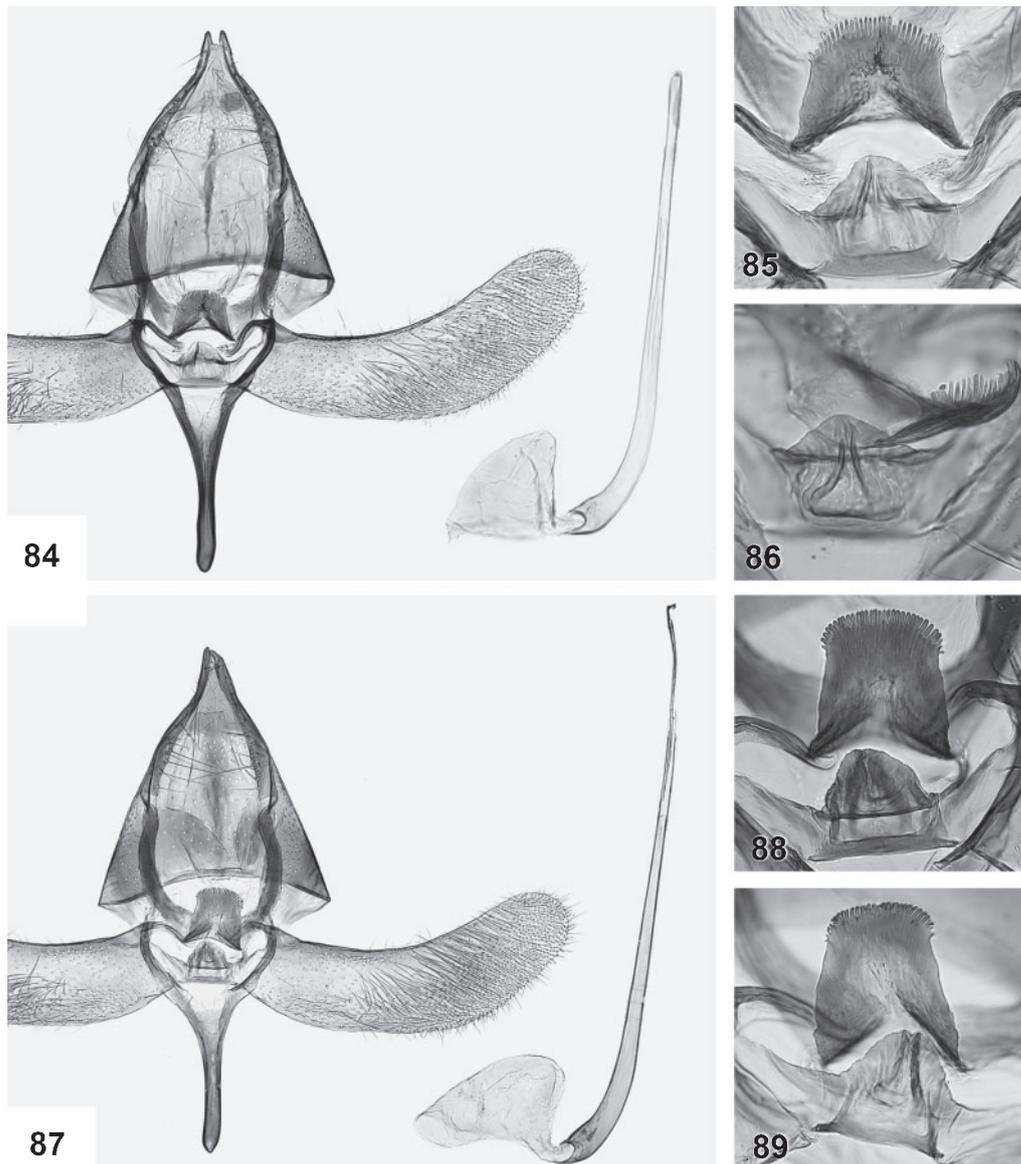
(Figs 77, 108–110)

Material examined

Holotype. ♂: '35.59S 137.11E [35.98S 137.18E], Vivonne Bay, Kangaroo Is, SA, 12 July 2007, D.A. Young', 'ANIC Database No. 31-035336', 'ANIC genitalia slide No 18600 ♂' (SAMA).

Diagnosis

Forewings with speckled white band running diagonally from base of costa to tornus, bordered by an interrupted black line on each side, outwardly followed by speckled grey. Male genitalia: crosier-shaped aedeagus with a sharply pointed apex and long, weakly club-shaped saccus; gnathos arms branched into upper paddle-shaped processes and ventral branches combining to form the twice narrowed gnathos tip with a widened and weakly curved



Figs 84–89. Male genitalia of the *Ogmograptis scribula* group. 84–86, *O. scribula*; Lee’s Spring, ACT, ANIC GS 14839 (84 genitalia, 85), H57 (84 aedeagus, 86). 87–89, *O. fraxinoides*; holotype, ANIC GS 14863 (87, 88), paratype ANIC GS 14861 (89).

apex with a fringe along its entire margin; juxta with a long and narrow central plate.

Description

Adult male (Fig. 77).

Wingspan: 11 mm.

Head. Finely speckled with narrowly brown-tipped white scales; basal part of flagellum with alternating rings of white and grey scales, remainder silvery grey.

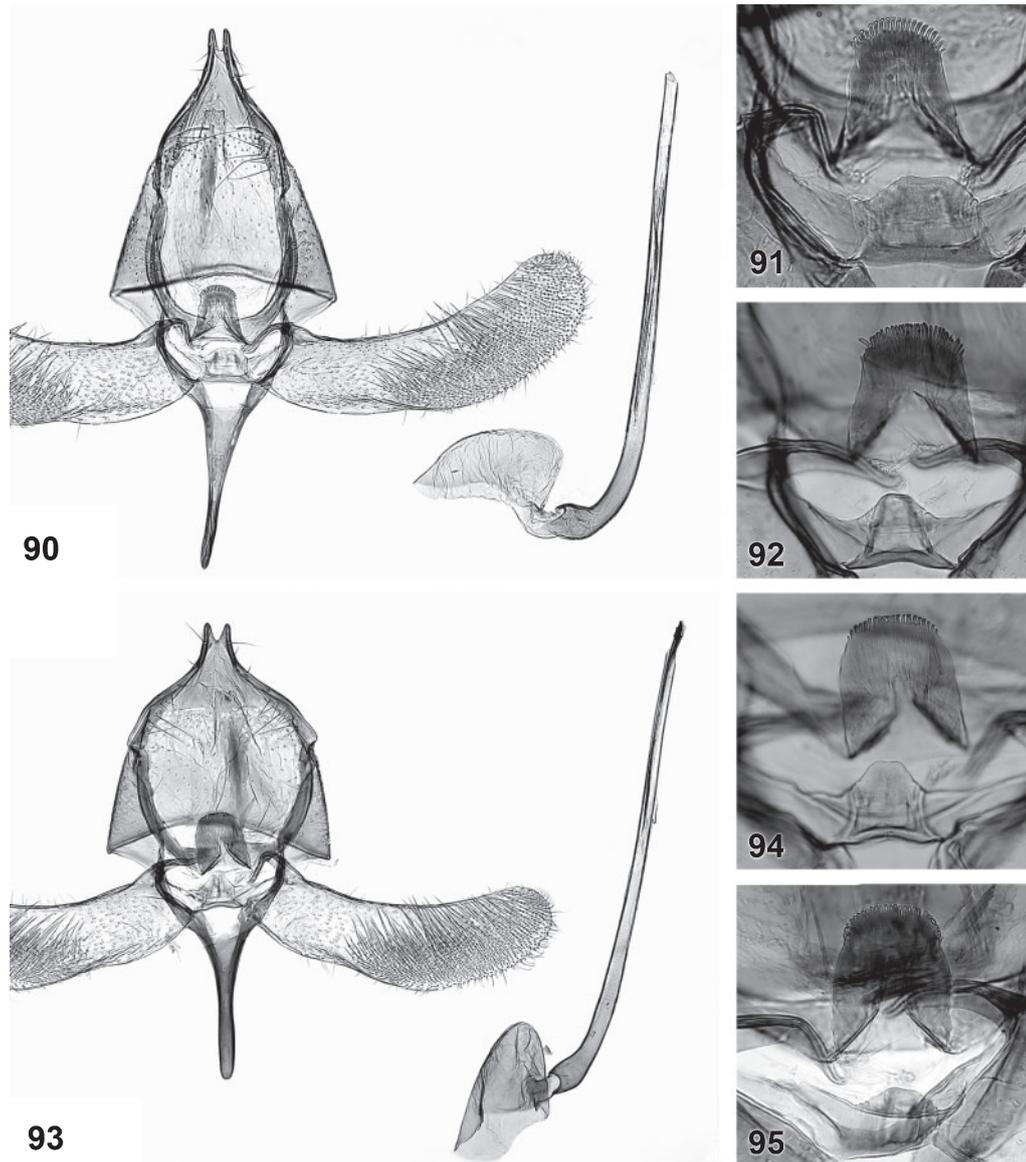
Forewings. Bold longitudinal marks of white, grey and black; an irregular white band, speckled with dark grey-tipped scales, running diagonally from base of costa to tornus, flanked dorsally by a long black streak along midline from base to nearly

middle of wing and a shorter, narrower black streak along fold just beyond middle of wing, and costad by a slightly oblique black streak along middle third of wing followed by a similar black streak in distal fourth of wing; costal and dorsal areas of wing beyond black marks are dark grey speckled with black-tipped scales; an indistinct whitish dot at base of terminal cilia; terminal cilia grey with narrow black tips, not forming two parallel rows.

Hindwings. Pale grey-brown, cilia concolorous.

Legs. Silvery grey, tarsi and tibia of anterior and median leg blackish.

Male genitalia (Figs 108–110). Gnathos highly complex, with lateral arms branching into two arms each before the ventral arms meet to form the laterally sinuate gnathos tip with a widened and weakly curved apex with a fringe along its entire margin; the



Figs 90–95. Male genitalia of the *Ogmograptis scribula* group. 90–92, *O. racemosa*; paratype, nr Gunning, NSW, ANIC GS 14780 (90, 91); Wilton, NSW, ANIC GS 14771 (92). 93–95, *O. pilularis*; holotype (93, 94), paratype, ANIC GS 14772 (95).

upper branches from each gnathos arm are expanded into long, flat, paddle-shaped processes; valva moderately long, much wider (1.6–1.7 \times) in distal half and apex broadly rounded; saccus long, slender; juxta with a well defined, long and narrow central plate with a ventral bar and lateral rods; aedeagus very long, with a large basal loop (collapsed during mounting), crosier-shaped, broadest near base, gradually tapering to pointed apex; vesica without obvious cornuti.

Female. Unknown.

Remarks

O. bignathifer is unmistakable due to its unique wing pattern and its highly modified gnathos with duplicated tips.

Etymology

The species name refers to the distally branched gnathos arms.

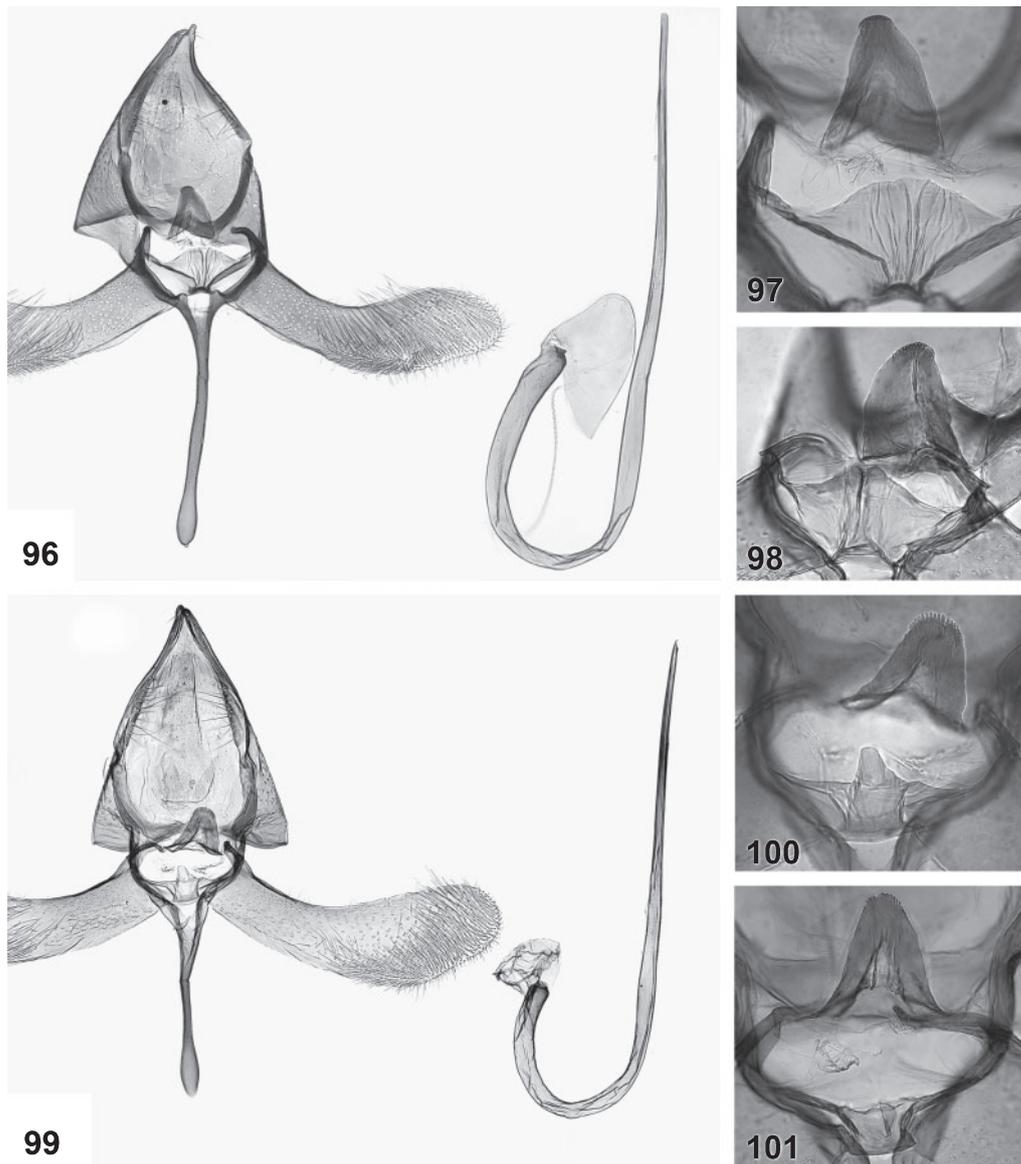
Ogmograptis inornatus Horak, sp. nov.

(Figs 78, 111–113)

Material examined

Holotype. ♂: [38.17S 141.37E] 28 miles NW Portland, Vic., 11 Nov. 1966, I.F.B. Common & M.S. Upton', 'ANIC Database No. 31-035337', 'ANIC genitalia slide No 14785 ♂' (ANIC).

Paratype. **New South Wales:** ♂: 35.58S 149.57E, 7 miles E of Captains Flat, 2.xi.1967, I.F.B. Common & A.E. May, ANIC 31-035338, ANIC GS 14869 ♂ (ANIC).



Figs 96–101. Male genitalia of the *Ogmograptis maxdayi* group. 96–98, *O. maxdayi*, holotype (96, 97), paratype, ANIC GS 14790 (98). 99–101, *O. barloworum*, paratype, GS 19331 (99, 100), holotype (101).

Diagnosis

Forewings white with scattered scales with grey-brown tips mainly in a band along costa and along dorsum, with irregular sprinklings of dark brown-tipped scales at 2/5 costa, near end of fold and in wing tip. Male genitalia: crosier-shaped aedeagus and long, club-shaped saccus, with gnathos tip complex with laterally projecting flanges and a small, inset, rounded-truncate apex with a fringe around its margin, and juxta with a long, dorsally roundly projecting median plate.

Description

Adults male (Fig. 78)

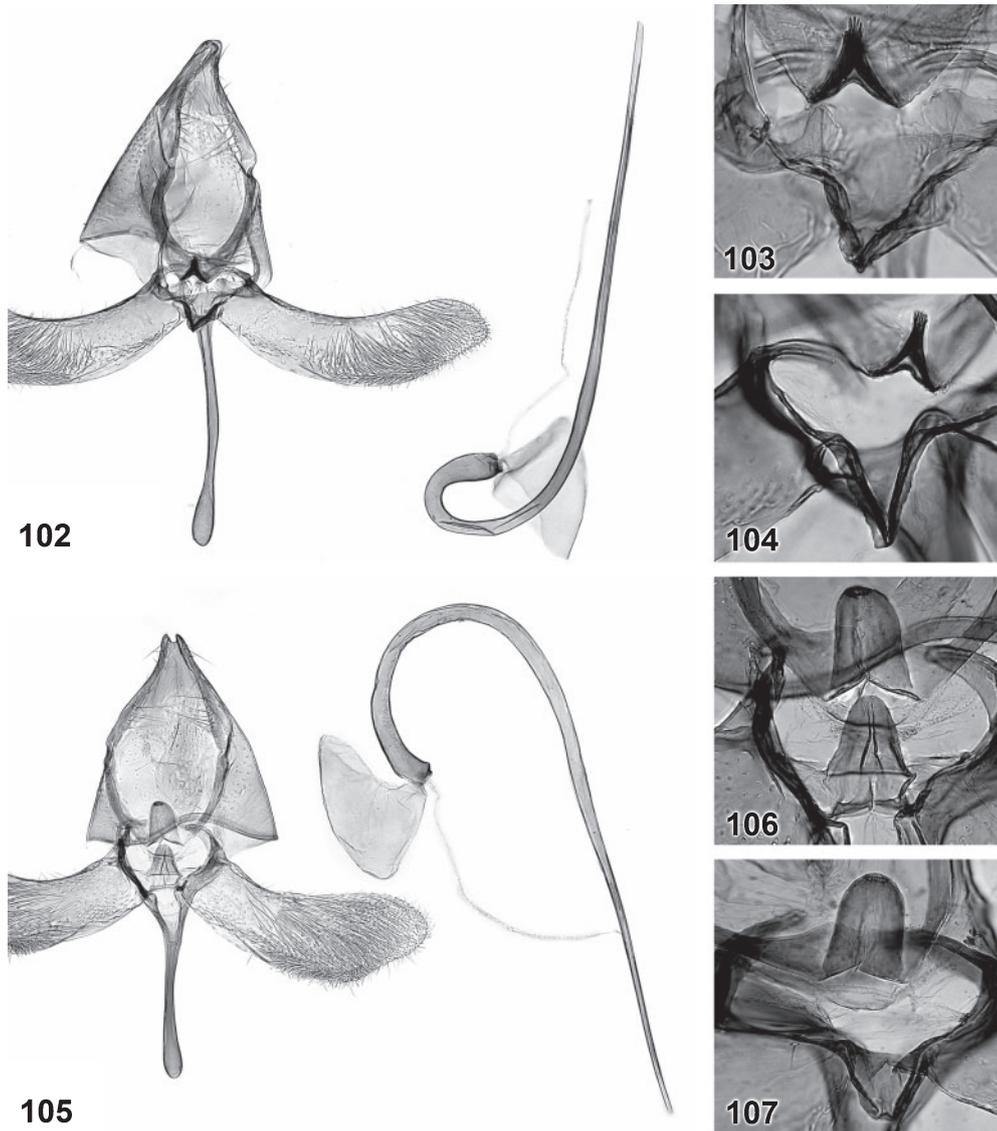
Wingspan: 11–13 mm.

Head and thorax. White except for very pale grey scales on lower part of face; a silvery grey antennal flagellum and grey-tipped scales anteriorly on tegulae and thorax.

Forewings. White, variably sprinkled with scales with grey-brown tips, especially in ill-defined band along costa and dorsum, overlaid with a series of ill-defined patches of more densely sprinkled scales with dark brown tips, including: a variably developed cluster at the centre of wing, a streak along fold beyond middle of dorsum, a dense subtriangular patch near 3/5 costa and two small indistinct groups in apical fourth; terminal cilia white with dark grey tips, at least in middle of termen; dorsal cilia pale grey.

Hindwings. Pale grey, cilia concolorous.

Legs. White faintly touched with grey, darker on more anterior legs.



Figs 102–107. Male genitalia of the *Ogmograptis maxdayi* group. 102–104, *O. paucidentatus*, holotype (102, 103), paratype ANIC GS 19335 (104). 105–107, *O. rodens*; holotype (105, 106), paratype ANIC GS 14753 (107).

Abdomen. Pale silvery grey, darker dorsally.

Male genitalia (Figs 111–113). Gnathos tip complex with sinuate lateral margins, subapical, laterally projecting flanges and a small, rounded-truncate apex with a fringe around its margin, laterally ending in two short ventral ridges; valva moderately wider in distal third; saccus moderately long, rather stout, club-shaped; juxta with a long, dorsally rounded, strongly projecting shield-shaped median plate with a prominent ventral bar and a rib on each side; aedeagus very long, with a large basal loop, crosier-shaped, broadest at base, gradually tapering to narrow apex; vesica without obvious cornuti.

Female. Unknown.

Remarks

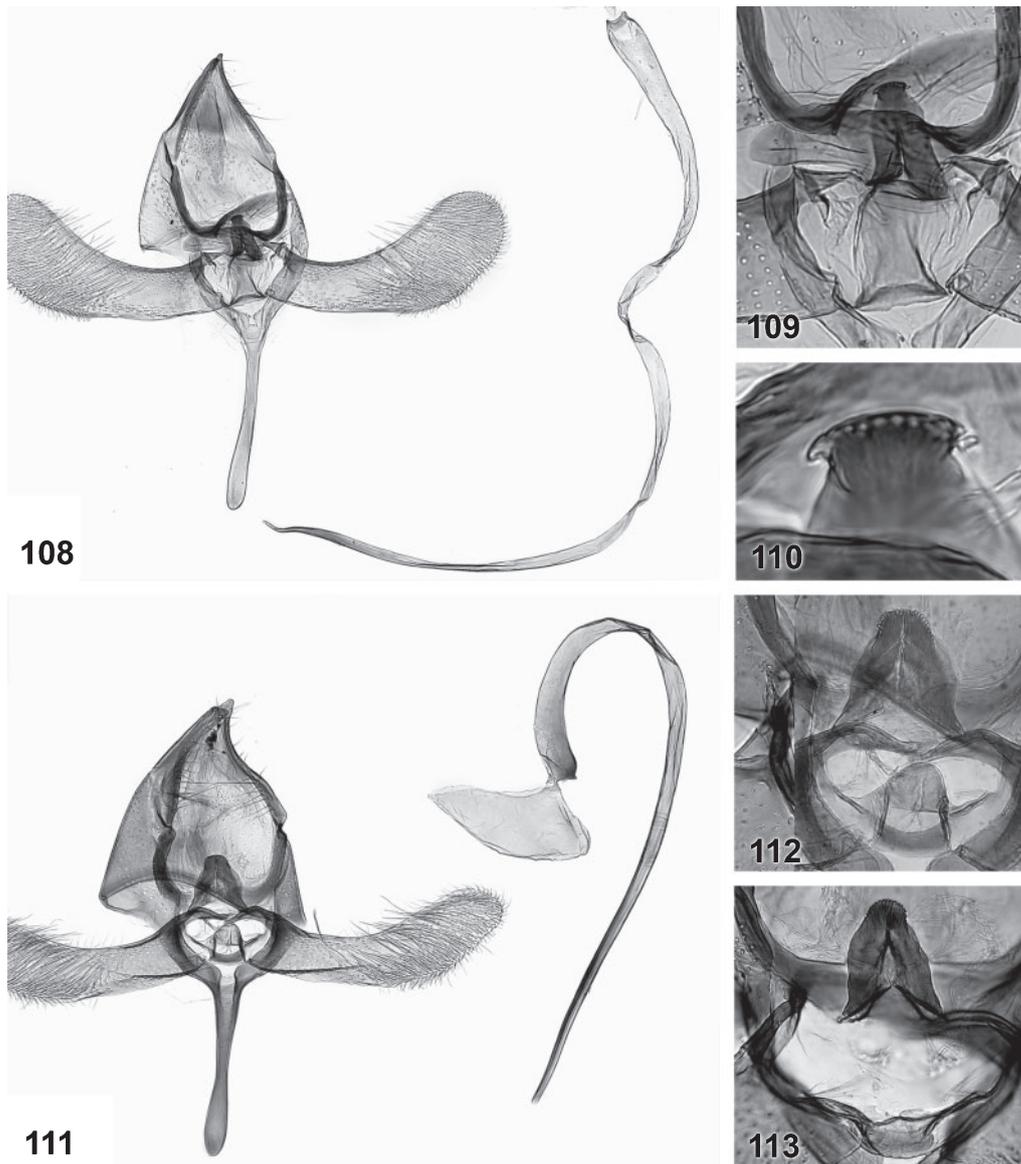
O. inornatus is the species with by far the least wing markings and is characterised by lateral flanges to the gnathos tip.

Etymology

The species name refers to the lack of a well-defined forewing pattern.

The *triradiata* group

This group is characterised by a very short saccus, a short, straight aedeagus and unmodified ovipositor lobes. The species are all very small and superficially similar, with the number of spots in the basal half of the forewing and the degree of dark speckling in its distal half providing differences between species. Interspecific genitalia differences are subtle, confined to the shapes of the uncus and gnathos tips, the juxta and possibly the aedeagus shape. A single female, of *O. bipunctatus*, is known. Specimens of this group are mostly represented as single specimens in the collection, and nothing is known about their biology.



Figs 108–113. Male genitalia of the *Ogmograptis maxdayi* group. 108–110, *O. bignathifer*, holotype. 111–113, *O. inornatus*, holotype (111, 112), paratype ANIC GP 14869 (113).

Ogmograptis triradiata (Turner) comb. nov.

(Figs 79, 114, 115)

Cateristis triradiata Turner, 1926: 150. – Nielsen, 1996: 58.

Material examined

Holotype. ♂: 'Mt Wilson [Blue Mts, 33.5S 150.38E] NSW 19.11.[19]23 [Turner]'; 'ANIC Database No. 31-035341'; 'ANIC genitalia slide No 14824 ♂' (ANIC).

Diagnosis

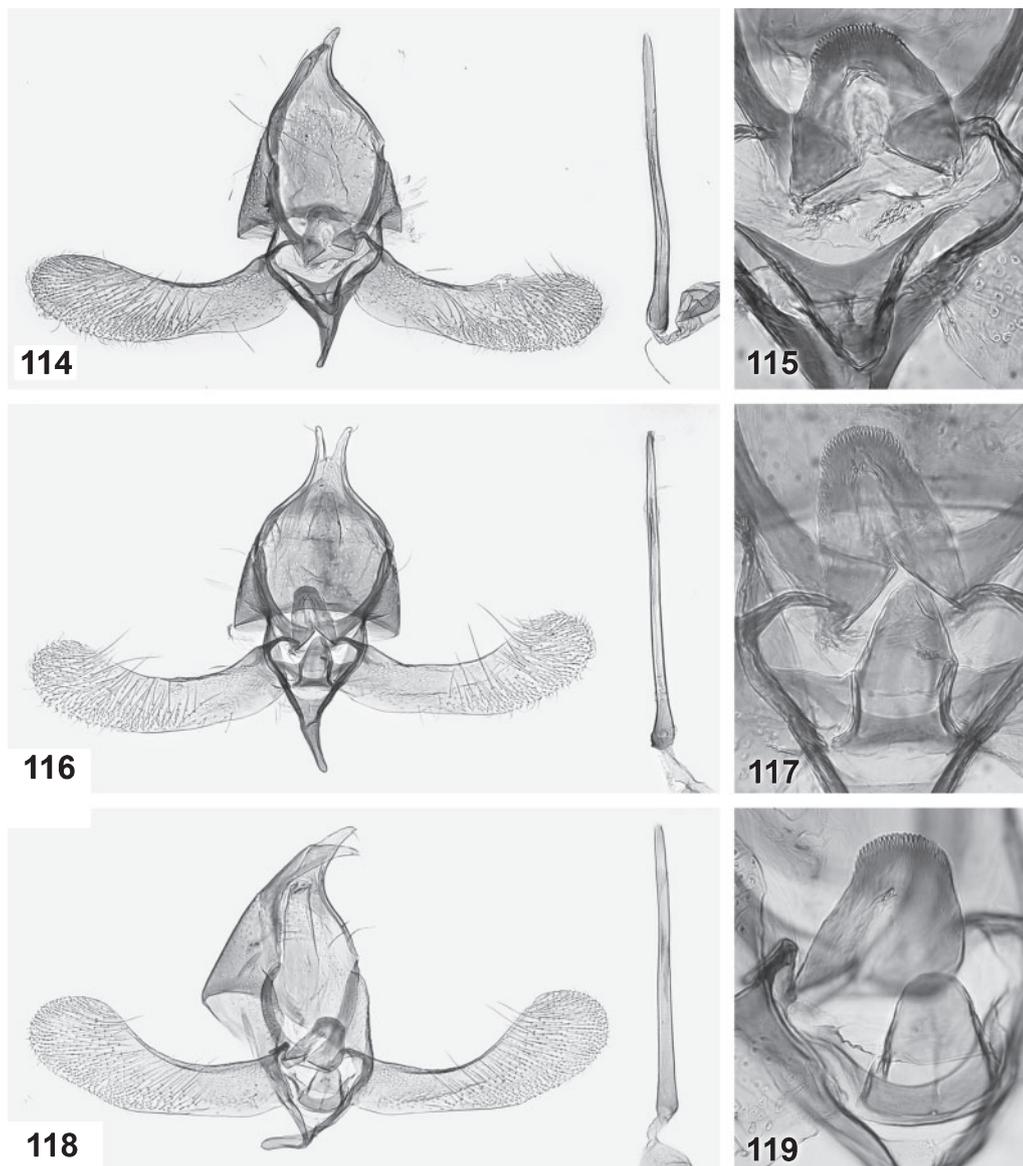
Forewings white with three small spots in line across basal half of wing and the distal markings forming a three-branched yellowish ochreous structure with black-tipped scales towards wing margin, with scattered black-tipped scales along distal 2/5

costa, a subapical yellowish mark and a conspicuous black line around termen. Hindwings pale grey. Male genitalia: faintly sinuate aedeagus with weakly bulbous base; short saccus strongly tapering to truncate apex; broad gnathos gradually tapering to weakly rounded tip and with a slight concavity in lateral margin below apical fringe; juxta (folded forward and strongly foreshortened in slide) apparently with a long, dorsally rounded-pointed strongly projecting shield-shaped median plate.

Description

Adult male (Fig. 79)

Wingspan: 9 mm.



Figs 114–119. Male genitalia of the *Ogmograptis triradiata* group. 114, 115, *O. triradiata*, lectotype. 116, 117, *O. bipunctatus*, holotype. 118, 119, *O. pulcher*, holotype.

Head and thorax. White except for a silvery grey antennal flagellum.

Forewings. White with well defined marks of yellowish ochreous and few black-tipped scales; three small spots in a line across wing in basal half; a few black-tipped scales on bend at base of dorsum, a yellowish ochreous spot with few black-tipped scales near fold at 1/5 of wing and a spot near costa below middle; the three typical *Ogmograptis* markings in distal half of wing yellowish ochreous, long and slender, confluent in middle of wing, forming a three-branched mark, sprinkled with black-tipped grey scales where the yellow streaks reach costa and dorsum and along the third streak extending towards termen; a sprinkling of black-tipped grey scales along distal 2/5 of costa; a preapical spot of yellowish ochreous scales;

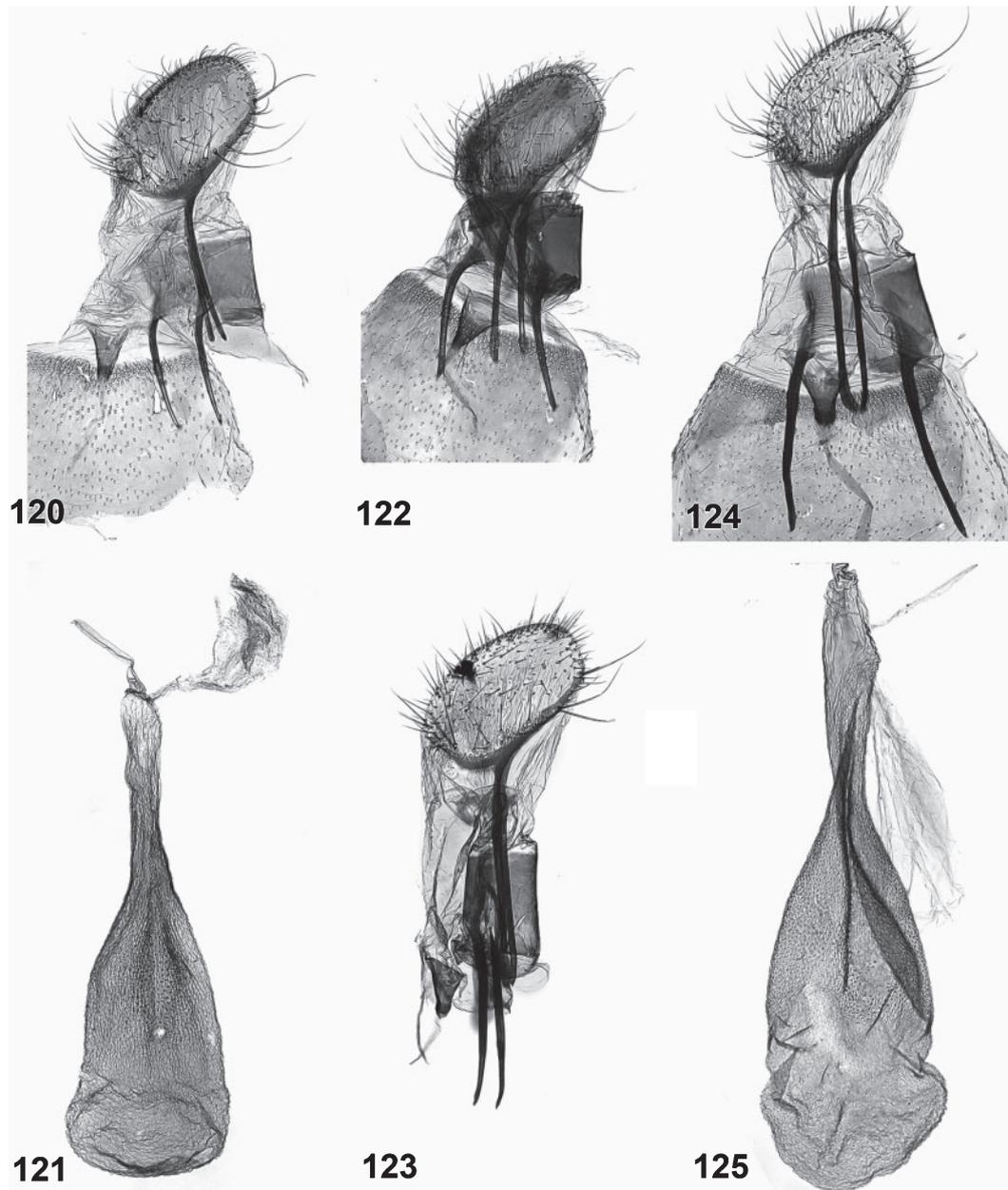
terminal cilia white, basal row black-tipped forming a black row around apex.

Hindwings. Pale grey, cilia concolorous.

Legs. White, only foreleg touched with grey.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 114, 115). Uncus tips long, slender, pointed with three or four socii bristles on each side; gnathos tip broad, gradually tapering to weakly rounded apex, with suggestion of a concavity in lateral margin below apical fringe; valva 1.5× as wide in distal third as at narrowest point at 1/3; saccus very short, subtriangular, gradually tapering to narrow, truncate tip; juxta (folded forward and strongly foreshortened as mounted on slide) apparently with a long, dorsally rounded-pointed strongly projecting shield-shaped



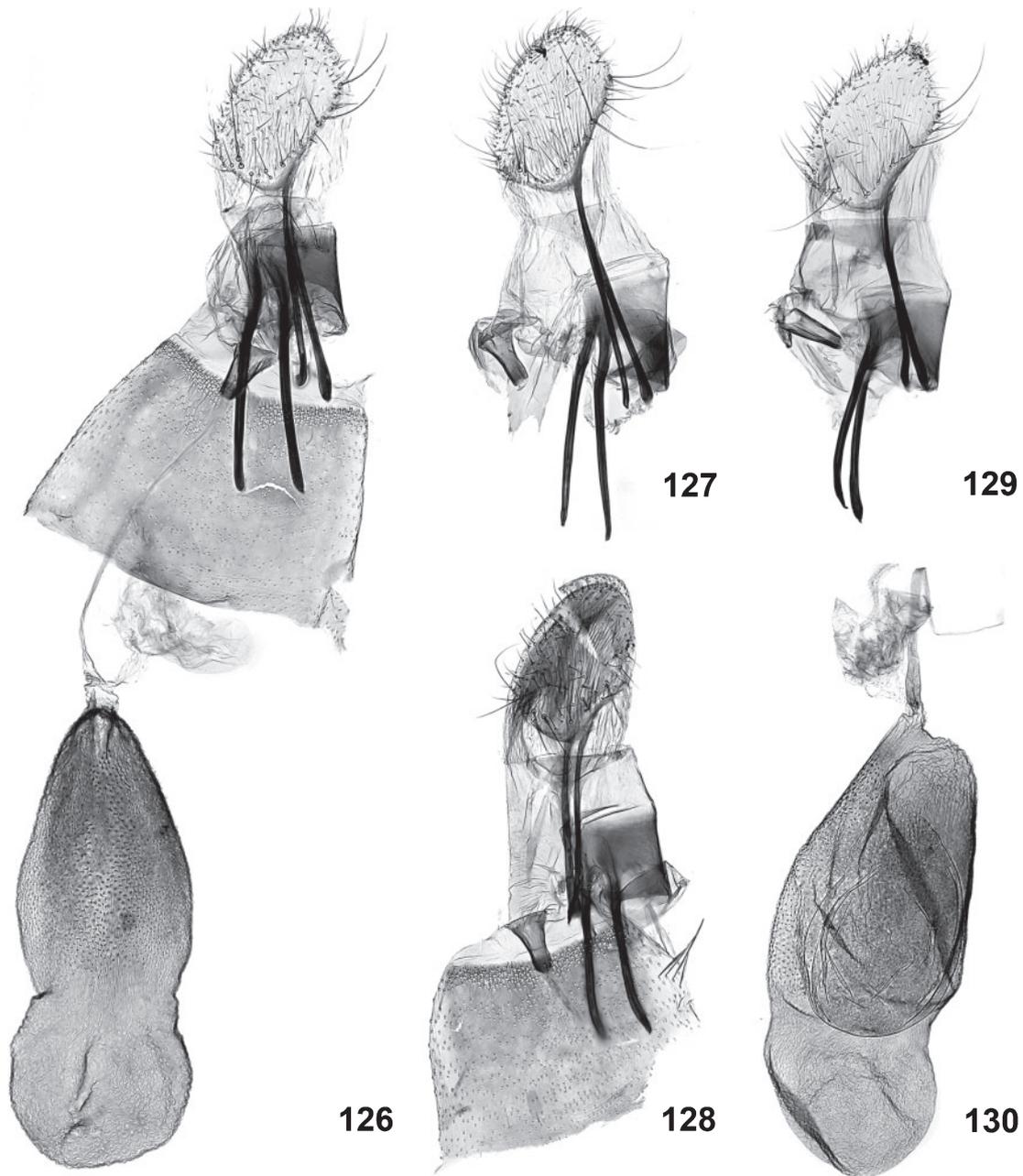
Figs 120–125. Female genitalia of the *Ogmograptis scribula* group. 120–122, *O. scribula*, Lee's Spring, ACT, ANIC GS 14791 (120, 121), ANIC GS 14776 (122). 123–125, *O. fraxinoides*, paratypes, ANIC GS 14862 (123), ANIC GS 14838 (124, 125).

median plate; aedeagus faintly sinuate, slender, with weakly bulbous base and tapering tip.

Remarks

O. triradiata was described in the New Zealand genus *Cateristis* Meyrick, 1889, in the Lyonetiidae, and listed as such in the lyonetiid part of the 'Checklist of the Lepidoptera of Australia' (Nielsen 1996a). The type species of *Cateristis*, *Cateristis eustyla* Meyrick, 1889, is known from a single male collected in the Riccarton Bush, Christchurch, New Zealand, 23 December 1882, and one specimen from Hobart, Tasmania, collected 31 January

1882, both in The Natural History Museum, London. Dugdale (1988) designated the male from New Zealand as the lectotype. *Cateristis* is quite distinct from *Ogmograptis* with a loosely scaled vertex and a pecten of long, slender scales. Neither *Cateristis eustyla* nor any congeneric material has ever been collected in New Zealand, apart from the lectotype, but the genus is clearly widely distributed in Australia with material from an unidentified species very close to, if not conspecific with, *E. eustyla* from the mountains near Canberra. The taxonomic position of *Cateristis* is unresolved, but it is clearly not a bucculatricid.



Figs 126–130. Female genitalia of the *Ogmograptis scribula* group. 126, 127, *O. racemosa*, paratype, Botanical Gardens, ACT, ANIC GS 14784 (126), paratype, nr Gunning, NSW, ACT GS 14773 (127). 128–130, *O. pilularis*, paratypes, ANIC GS 14840 (128), ANIC GS 14752 (129, 130).

Ogmograptis centropila (Turner) comb. nov.

(Fig. 80)

Opostega centropila Turner, 1923: 179

Cateristis centropila. – Nielsen, 1996 (comb.)

Material examined

Lectotype. ♂: 'Mt. Tambourine Q. [27.92S 153.15E] 4–11-[19]11 [Turner] [without abdomen]'; 'ANIC Database No. 31-035339' (ANIC). Lectotype here designated.

Paralectotype. **Queensland:** ♂ 'Brisbane [27.47S 153.03E] Aug.' [without abdomen]; 'ANIC 31-035340' (ANIC) [identity uncertain].

Diagnosis

Forewings white with a small yellowish ochreous mark near centre of wing and the distal markings forming a pale, three-branched yellowish ochreous structure with few black-tipped scales, with scattered black-tipped scales along distal 2/5 costa, an indistinct subapical yellowish mark and a narrow black line around termen. Hindwings very pale grey.

Description

Adult male (Fig. 80)

Wingspan: 7–8 mm.

Head and thorax. White except for a silvery grey antennal flagellum.

Forewings. White with markings of yellowish ochreous and dark grey-tipped scales in distal 2/3 of wing; a small, yellowish ochreous longitudinal streak near centre of wing and the three typical *Ogmograptis* markings in distal half yellowish ochreous, long and very slender, confluent in middle of wing, forming a three-branched mark, sprinkled with few dark-grey-tipped grey scales on branch near dorsum and along third streak extending towards termen; an indistinct broad streak sprinkled with dark-grey-tipped scales along distal half of costa, connected with a preapical spot of yellowish ochreous scales; terminal cilia white around apex, yellowish in tornus, basal row black-tipped forming a narrow black line around apex.

Hindwings. Very pale grey, cilia concolorous.

Legs. White, only foreleg touched with grey.

Female. Unknown.

Remarks

Both male syntypes in the ANIC lack the abdomen. The specimen labelled 'type' by Turner is here designated as the lectotype for taxonomic stability. The paralectotype from Brisbane has much darker scaling on the underside of the forewing, similar to *O. triradiata*, and is probably not conspecific with the lectotype.

***Ogmograptis bipunctatus* Horak, sp. nov.**

(Figs 81, 82, 116, 117, 133)

Material examined

Holotype. ♂ [35.12S 150.083E] 5 mls NE Nerriga, NSW, 27 Nov. 1962, I.F.B. Common & M.S. Upton', 'ANIC Database No. 31-035342', 'ANIC genitalia slide No 14783 ♂' (ANIC).

Paratype. ♀, same label data as holotype but ANIC 31-035343, ANIC GS 14786 ♀ (ANIC).

Diagnosis

Forewings white with two small spots in basal half of wing and distal markings forming a three-branched yellowish ochreous structure with conspicuous black-tipped scales towards wing margin, with scattered black-tipped scales along distal 2/5 costa; a subapical yellowish mark and a conspicuous black line around termen. Hindwings pale grey. Male genitalia: straight slender aedeagus with bulbous base; short saccus strongly tapering to rounded apex; a rather narrow gnathos tapering to rounded-truncate tip with fringe extending onto lateral margin; juxta with a very long, dorsally rounded-triangular and strongly projecting shield-shaped median plate with prominent lateral ribs. Female genitalia: unmodified, spinulose, posteriorly directed ovipositor lobes, ductus bursae membranous, short, with sclerotised funnel below ostium, corpus bursae bottle-shaped, membranous.

Description

Adult (Figs 81, 82)

Wingspan: 8–9 mm.

Head and thorax. White except for a silvery grey antennal flagellum and a touch of yellowish ochreous on tips of eye cap scales.

Forewings. White with well defined marks of yellowish ochreous and black-tipped grey scales; two small spots in basal half: one of black-tipped scales in middle of wing at 1/5 and one with additional yellowish scales closer to costa beyond 1/3 wing length; the three typical *Ogmograptis* markings in distal half of wing connected in middle of wing, forming a yellowish ochreous three-branched mark with all three branches extended, overlaid or bordered by black-tipped grey scales towards the wing margin; irregular band of scattered black-tipped grey scales along distal 2/5 of costa, connected by a yellowish ochreous patch with distal branch of triradiate mark; terminal cilia ochreous to grey except for white scales in apex and tornus, basal row black-tipped forming a conspicuous black line around apex.

Hindwings. Pale grey, cilia concolorous.

Legs. White, two anterior pairs touched with grey.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 116, 117). Uncus tips long, slender, digitate, only two socii bristles on each side; gnathos tip simple, rather narrow, gradually tapering to rounded-truncate tip, fringe extending onto lateral margins; valva 1.4× as wide in distal third as at narrowest point at 1/3; saccus short, subtriangular, gradually tapering to narrow, rounded tip; juxta with a very long, dorsally rounded-triangular and strongly projecting shield-shaped median plate with a ventral bar and prominent lateral, vertical ribs; aedeagus straight, very slender with strongly bulbous base.

Female genitalia (Fig. 133). Ovipositor with apophyses slender and rather short, posterior pair shorter; ovipositor lobes unmodified, posteriorly oriented, densely spinulose and sclerotised with few large bristles, not leaf-like; ostium on S8, without sclerotised sterigma; ductus bursae shorter than length of corpus bursae, with a sclerotised funnel below ostium, remainder of ductus narrow and membranous; corpus bursae bottle-shaped with a long, slender, membranous neck leading to ductus bursae and ductus seminalis, without spinules.

Etymology

The species name refers to the two dots in the basal half of the forewing.

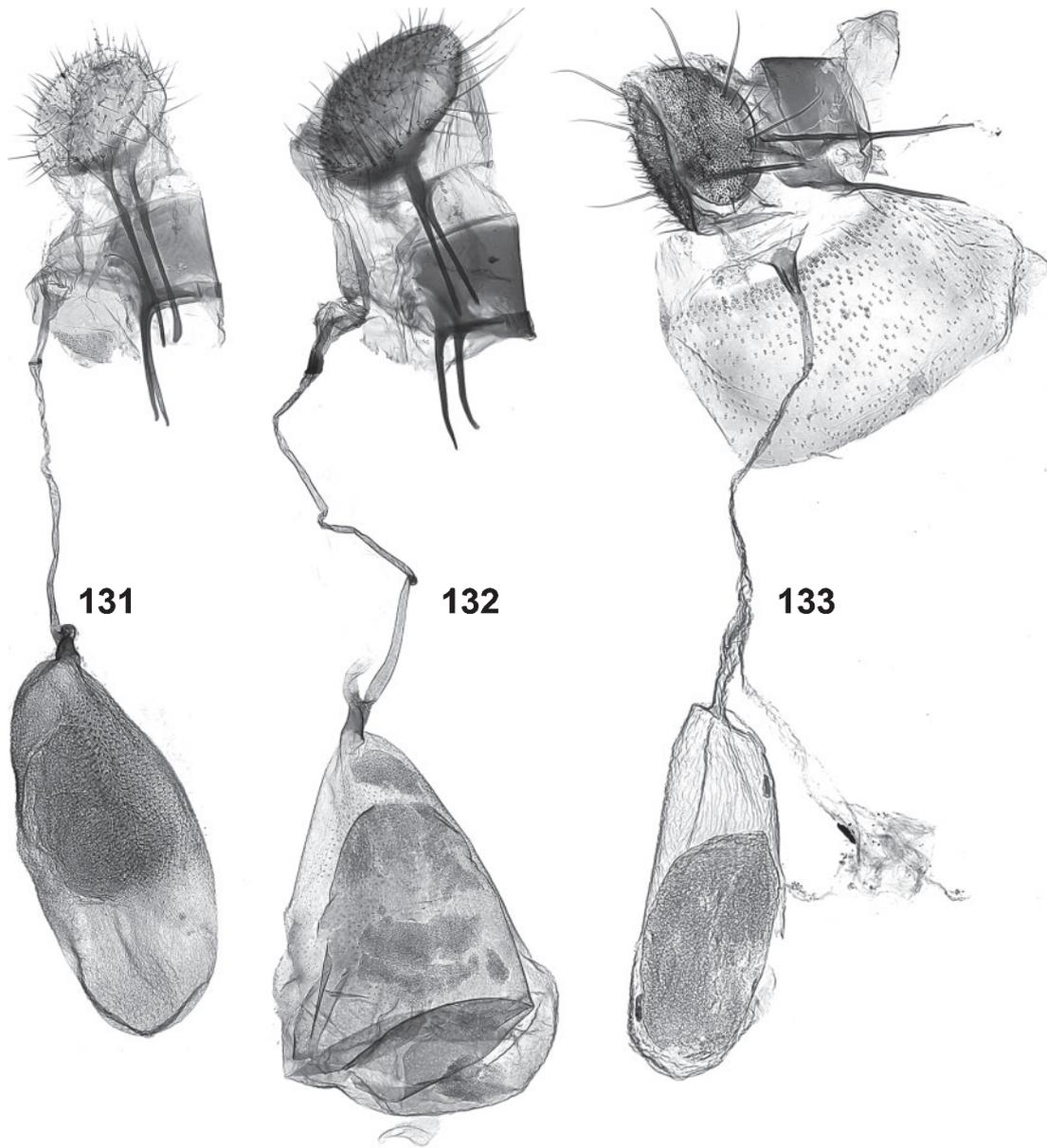
***Ogmograptis pulcher* Horak, sp. nov.**

(Figs 83, 118, 119)

Material examined

Holotype. ♂: 'Australia, Victoria, E of Melbourne, Gembrook Gilwell Pk., 37°26'S 145°39'E [37.43S 145.64E], 30 Oct. 2009, lux, leg Kallies, Marriott & Hilton', 'ANIC Database No. 31-035344', 'ANIC genitalia slide No 14877 ♂' (DEM).

Paratypes. 2 ♂, same label data as holotype but ANIC 31-035345 & 31-035346, ANIC GS 14870 ♂ (ANIC).



Figs 131–133. Female genitalia of the *Ogmograptis maxdayi* (131, 132) and *triradiata* (133) groups. 131, *O. maxdayi*, paratype, ANIC GS 19328. 132, *O. barloworum*, Gembrook, Vic. 133, *O. bipunctatus*, paratype, ANIC GP 14786.

Diagnosis

Forewings white with four small spots in basal half of wing and the distal markings forming a three-branched yellowish ochreous structure with patches of black-tipped scales towards wing margin, with scattered black-tipped scales along distal 2/5 costa, an indistinct subapical yellowish mark and a conspicuous black line around termen. Hindwings leaden grey. Male genitalia: straight gradually tapering aedeagus; very short saccus with distal half not tapering; broad gnathos gradually tapering to rounded-truncate apex with fringe along entire apex; juxta (folded forward and strongly foreshortened in slide) apparently with a long, dorsally rounded-truncate shield-shaped median plate.

Description

Adult male (Fig. 83)

Wingspan: 8–8.5 mm.

Head and thorax. White except for a silvery grey antennal flagellum.

Forewings. White with well defined marks of yellowish ochreous and black-tipped grey scales; four small marks of black-tipped scales in basal half: a spot each at base of costa and on bend at base of dorsum, an oblique dash across fold at 1/5 of wing and a spot near costa below middle; a distally increasing line of grey scales along edge of costa; the three typical *Ogmograptis* markings in distal half of wing confluent in

middle of wing, forming a yellowish ochreous three-branched mark, bordered and overlaid by patches of black-tipped grey scales where the yellow streaks reach costa and dorsum and along the third streak extending to termen; band of black-tipped grey scales along distal 2/5 of costa; few scattered black-tipped scales below middle of costa and often a preapical patch of yellowish ochreous scales; terminal cilia grey except for a few white scales in apex, basal row black-tipped forming a conspicuous black line around apex, distal row dark grey-tipped.

Hindwings. Leaden grey, cilia concolorous.

Legs. White variably touched with grey, darker on more anterior legs.

Abdomen. Silvery grey, darker dorsally.

Male genitalia (Figs 118, 119). Uncus tips long, triangular, pointed; only two socii bristles on each side; gnathos tip simple, broad, weakly tapering, distally rounded-truncate, fringe along entire apical margin; valva 1.5× as wide in distal third as at narrowest point at 1/3; saccus very short, stout, distal half nearly parallel-sided, tip rounded; juxta (folded forward and strongly foreshortened as mounted on slide) apparently with a long, dorsally rounded-truncate and strongly projecting shield-shaped median plate with a prominent ventral bar; aedeagus straight, gradually tapering (tip broken in holotype).

Female. Unknown.

Etymology

The species name refers to the beautiful forewing pattern.

Unassigned to species group

Ogmograptis notosema (Meyrick, 1922)

Cryphioxena notosema Meyrick, 1922: 507. – Nielsen, 1996b: 45, 341.

Ogmograptis notosema. – Meyrick, 1935: 600 (comb.)

Original description

‘♂. 13 mm. Head, thorax white, tongue obsolete. Palpi porrected, grey-whitish. Forewings elongate-lanceolate, acute; white; an oblique-triangular dark fuscous blotch on dorsum near base, a trapezoidal spot beyond middle, and an erect-triangular spot of irroration at tornus, these connected by an irregular dorsal line; two or three scattered dark fuscous scales towards costa, and a small group towards apex; cilia light grey, on costa white, on upper part of termen mixed white, at apex with a patch of black irroration. Hindwings 3 absent; grey; cilia light ochreous-grey. VICTORIA, Gisborne; 1 ex. (Coll. Lower).’

Remarks

The holotype of *O. notosema* has not been found. The species was based on material sent by Lower to Meyrick for description. Meyrick eventually returned the material to Lower with a numbered list of his identifications, including species he described in 1922 from the material. The specimens bore corresponding numbers but were otherwise unlabelled, and the types were not labelled. It is possible that the holotype is still unrecognised in the SAMA.

Nielsen (1996b) included *Cryphioxena notosema* in its original combination in the Bucculatricidae, a decision in line with Meyrick’s remark that *Cryphioxena* Meyrick ‘is possibly

allied to the Australian *Paraphyllis*’, which is a junior synonym of the bucculatricid *Tritymba* Lower. Meyrick’s (1935) decision to include the species in *Ogmograptis* is here followed though the description of the wing pattern does not tally with any of the known species of *Ogmograptis*. The type species of *Cryphioxena* is *C. haplomorpha* Meyrick from Mozambique.

Discussion

Insect–plant interactions between Ogmograptis and Eucalyptus

Ogmograptis comprises three species groups; however, in the present study detailed biological information was obtained only for members of the *O. scribula* group, the classical ‘scribbly moths’ that produce the well known bark scribbles on smooth-barked *Eucalyptus* species (Figs 1–6). Immature stages of the closely related genus *Tritymba* also have been collected from *Eucalyptus*, with several larvae extracted from tracks in the vascular cambium of *E. racemosa* spp. *rossii* (Fig. 11). Such tracks in the cambium are known not only from smooth-barked species like *E. racemosa* spp. *rossii* where their scars appear on the surface as ‘ghost scribbles’ (Fig. 10), but also from rough-barked eucalypt species where their scars appear on the sapwood of bark-stripped logs. Ghost scribbles have not been observed on other tree genera except for *Angophora floribunda* (Sm.) Sweet (Moore 1972), suggesting that *Tritymba* is restricted to *Eucalyptus* and possibly close relatives. Hence, we suspect that the larvae of the other two species groups of *Ogmograptis* also feed on *Eucalyptus* or at least on members of the Myrtaceae. Females of the *O. maxdayi* group share modified leaf-like ovipositor lobes with the *scribula* group whilst those of the *triradiata* group are less derived, similar to those of *Tritymba*. These differences in ovipositor morphology suggest different egg-laying behaviour. Two species of the *maxdayi* group have been collected at Warrandyte in Victoria, a locality with eucalypts but without any bark scribbles. Further investigations of the associations between larvae of these other *Ogmograptis* species groups and their host trees will likely greatly expand our knowledge of this mutualism.

The tracks of the *O. scribula* group are characterised by three very unusual traits: (1) the entire track is positioned at the level of the phellogen layer (cork cambium) and becomes exposed when the outer bark is shed (Figs 1–6), (2) the later part of the track becomes filled with callus tissue that is contiguous with the phellogen (Fig. 22), and (3) the last-instar larva re-enters the callus-filled track and feeds exclusively on callus. This obligate behavioural switch, from a legless borer feeding on bark tissue to a last-instar larva with legs feeding on callus tissue, is reliant on the appropriate reaction of the host tree to the larval activity to produce the necessary callus tissue. The formation of these distinctive tracks therefore depends on an intimate interaction between the *Ogmograptis* larva and its eucalypt host tree. Development of the larva and the associated track is synchronised, within a narrow window, for each species. It seems to be correlated with host phenology, in particular with the cycle of bark shedding, though this may be an epiphenomenon. *Ogmograptis* track formation here is primarily considered from an entomological angle, in relationship to the life history of *Ogmograptis*. A companion paper addressing the

tissue reaction of the eucalypt host to the larval activity of *Ogmograptis*, in conjunction with bark phenology, is currently in preparation.

At present we can only point to the synchronicity of *Ogmograptis* larval activities with eucalypt phenology and tissue developments without providing any causal explanations. The close fit between host tree physiology and *Ogmograptis* life history suggests, however, a finely tuned system of host/herbivore interactions. The main questions to be addressed are (1) the role of the phellogen with regard to the location of the larval track, and (2) the mechanism leading to the callus production within the section of doubled tracks. Mining close to or within a cambial layer is a highly unusual biology for a lepidopteran larva, confirmed only for three species of Opostegidae (Davis 1989). Opostegid biology is known for only a few species, which are either leaf miners, stem miners or produce very long mines within the vascular cambium (Grossenbacher 1910; Kumata 1984; Davis 1989; Davis and Stonis 2007). In one Hawaiian leaf-mining species the mine terminates in a circular callus-like structure that is formed by the larva feeding in a spiral pattern and the upper epidermis of this area proliferating. According to Davis and Stonis (2007), 'the larva [then] feeds beneath it until maturity'. In the *O. scribula* group, this behaviour is obligate and highly refined, with the eucalypt host usually shedding only part of its outer bark in any given year, and the areas shed from year to year not congruent. Active *Ogmograptis* tracks are restricted to bark due to be shed at the next bark dehiscence, and the larvae consistently turn back just before they reach the edge of the bark that will slough off (Fig. 9). According to our cursory observations the phellogen layer in *Eucalyptus* bark is morphologically not discernible when the *Ogmograptis* larva bores its early mine, yet the larva bores at the correct level. Once the outer bark falls off the entire track is revealed at exactly this level (Figs 1–6). We have not investigated whether the female oviposits randomly, resulting in death of all larvae from eggs laid on bark that will not be shed in the next season, whether the female moth lays her eggs only on areas of bark that will be shed in the next summer, or if the first-instar larvae can orient on the tree to such areas. The latter is unlikely as we have never found an early track crossing the boundary between patches of bark shed in different years. If the second option applies, then the adult can determine, at a time when we were not able to morphologically locate the phellogen, where it will develop.

The synchronicity of larval development and tree phenology is very obvious when the larva switches from being a borer to a callus feeder. As described in the Biology section, the final moult to the last-instar larva and the growth of callus in the second part of the track coincide, with a few weeks' delay on the cooler southern side of the tree trunk. The second turning point is the location of the final moult, and examination of old scribbles shows that its position varies, from along the zig-zag track (Fig. 4) to well beyond it (Fig. 9), suggesting that external factors provide the cue for the final moult. The final moult also coincides with the moment when it becomes possible to easily remove the outer bark layer, along the friable abscission layer of cork starting to be produced by the phellogen. The timing of the final moult at the moment when the track becomes filled with callus tissue ensures that the necessary food is available for the last-instar larva.

The most remarkable and unique aspect of the life history of the *O. scribula* group is that the final-instar larva returns to feeding on the callus filling the mine it has previously excavated. At this point the larva exclusively consumes callus tissue, together with the embedded droppings from the earlier boring phase, and it grows very quickly. While feeding on callus forming around the entrance to the larval tunnel is widespread among lepidopteran larvae, especially in xyloxyctids, cossids and hepialids, there are very few examples where a mining insect returns to feed on the callus growing within its mine (Hering 1951). Examples include *Liriomyza strigata* Meigen (Diptera: Agromyzidae), which produces a forked track along the mid-rib of the leaf, and species of the *Nepticula argyropeza* group (Lepidoptera: Nepticulidae), which produce a thickening of the leaf petiole. In both cases, however, the larvae feed as conventional leaf miners in the leaf blade between consuming callus tissue in their central mine channel. Two *Phytomyza* (Diptera: Agromyzidae) species on thistles also mine in the mid-rib of leaves, which becomes considerably swollen and appears like a gall, but both species also mine lateral tracks outside the thickened area (Hering 1951). The Hawaiian opostegid *Paralopostega callosa* Swezey, with its larva feeding under a callus-like structure (Davis 1989), is the only known case of obligate callus-feeding within a mine by a lepidopteran. Among all these examples none have the obligatory switch of feeding mode observed in the *O. scribula* group, or the significant morphological changes between relevant larval instars.

The obvious question is what triggers callus growth in the second half of the mine. Callus growth is a common wound reaction and is known to occur within insect mines, particularly in association with vascular bundles, and is often more pronounced around the excrements of the miner (Hering 1951). In the *Ogmograptis* track, however, callus growth is restricted to the final, doubled-up zig-zags, usually within an area of stained bark, suggesting physiological change (Figs 12, 13). Narrow early tracks may become filled with callus only if they are close to a doubled-up zig-zag track, and then only in the portion close to the double track. Interestingly, in the drought summer of 2006–07 the *E. racemosa* ssp. *rossii* at Gunning produced hardly any callus and most larvae died in their track before reaching maturity. Given that the last-instar larva relies, for its survival, on the presence of callus, the question arises whether callus growth is a by-product of a wound reaction, or whether larval activity induces callus growth. Two aspects of its behaviour indicate that the *Ogmograptis* larva may maximise production of callus in the latter part of its mine. First, the double track means a concentration of larval activity, which could enhance any effect on the host, whether through simple mechanical damage alone or also through chemical stimuli from droppings or feeding activity. The physiology of the tissue including and surrounding these double-tracked zig-zags appears modified, as suggested by discolouration (Figs 4, 12, 13). This discolouration is not yet visible when the penultimate instar is ready to moult (Fig. 9). Second, the life history of the larva is timed so that completion of the double track coincides with the activity of the cork cambium.

The obligatory switch by the last-instar larva of the *O. scribula* group from feeding as a borer in the bark at the phellogen layer to

feeding on callus growing within its own mine represents a unique and highly adapted life history. In the nutritionally poor substrate of the outer bark the penultimate instar larva sets up a system that produces highly nutritious food for the last-instar larva. A planned study on host tissue reaction to larval activity will hopefully shed some light on the stimuli needed for callus growth, and to answer the question of whether it is induced by larval activity beyond simple wounding and the presence of frass.

Host specificity of the Ogmograptis scribula group

Both *Ogmograptis* and *Tritymba* are probably confined to the genus *Eucalyptus* and possibly close relatives within the Myrtaceae. *Ogmograptis* has been observed only on smooth-barked eucalypts of the subgenus *E. (Eucalyptus)*, and then only on the smooth-barked parts of the tree; however, we have not tried to investigate whether *Ogmograptis* tracks are present within rough eucalypt bark where they never become exposed. The life history of both the *O. maxdayi* and *triradiata* groups are unknown and their larvae could possibly mine in rough-barked eucalypts. *Tritymba* definitely feeds also on rough-barked eucalypt species where the scars of the tracks made in the vascular cambium do not become visible on the surface but may be seen when the bark is stripped. Moore (1972) described and figured tracks of an unidentified insect, likely to be *Tritymba*, from many species of *Eucalyptus* and also from *Angophora floribunda* (Sm.) Sweet in New South Wales. On the basis of molecular data (Fig. 30), possibly two *Tritymba* species have been found together on *E. racemosa* ssp. *rossii*, and the very diverse tracks suggest that there may be even more species on this eucalypt species. The question whether each *Tritymba* species is restricted to a single host while eucalypt species can host several *Tritymba* species has to be left to a future study of this large genus.

Eucalypts and *Ogmograptis* species of the *scribula* group, on the other hand, seem to have a more exclusive host relationship. Cooke and Edwards (2007) surveyed bark scribbles from the *scribula* group on three eucalypt species (*E. pauciflora*, *E. racemosa* ssp. *rossii* and *E. delegatensis* R.T. Baker) in the Australian Capital Territory, and demonstrated that ‘scribble measurements differed significantly between all three host species’. Whilst the initial mining direction of the larva, i.e. burrowing left versus right or up versus down, appeared random, there were clear differences in the density of scribbles depending on trunk aspect, with the southern face favoured in *E. racemosa* ssp. *rossii* and both the eastern and southern faces in *E. pauciflora*. Scribble shape was analysed on the basis of 10 parameters, including various measurements and directional changes of the two track parts, and found to differ significantly between all three host species. Our morphological studies of four species of the *scribula* group revealed diagnostic differences in the genitalia among the four species and, more surprisingly, differences also in larval morphology among the three species examined.

Ogmograptis bark scribbles have been reported from 26 species of *Eucalyptus* (Brooker *et al.* 2002), listed in Table 3 according to the classification by Brooker (2000). All 26 species belong to the monophyletic subgenus *E. (Eucalyptus)* which is endemic to eastern and south-western Australia (Ladiges

et al. 2010). However, bark scribbles are present only in part of the range of the subgenus *Eucalyptus*, namely in the south-eastern corner of Australia from Fraser Island to Tasmania, as far west as the Pilliga scrub in New South Wales and the Grampians in Victoria. Scribble tree species range from mallees to tall trees, some on good soils, but most on skeletal and poor soils. Scribble density may vary greatly, from extremely crowded to sparse, even between neighbouring trees. In some species they seem to be generally infrequent. In species such as *E. pilularis* and *E. delegatensis* with a rough-barked trunk, scribbles are apparent only on the smooth-barked upper branches, though the rough bark has not been investigated. Fourteen of the 26 eucalypt species reported to have scribbles in their normal habitat are cultivated in the Australian National Botanic Gardens in Canberra, but there scribbles are found only on the two subspecies of *E. racemosa*. The resident population of *O. racemosa* on the local *E. racemosa* ssp. *rossii* uses ssp. *racemosa* as a host but does not colonise any of the other 13 species. This strengthens the hypothesis that species of the *scribula* group are restricted largely to a single eucalypt species; however, this is not an exclusive association. Of the four species studied, *O. racemosa* is found on both subspecies of *E. racemosa*, with the closely related *E. haemastoma* a possible second host species. *O. fraxinoides* has been reared from both *E. fraxinoides* and *E. pauciflora*. On the latter it may coexist with *O. scribula* on the same tree, albeit in a differently shaped track predominantly on the southern face of the trunk. Very rarely, oviposition occurs on the ‘wrong’ tree, and larval development apparently can take place. On Fraser Island, in the close vicinity of large and densely scribbled specimens of *E. racemosa* ssp. *racemosa*, a few isolated scribbles were found on adjacent *Angophora costata* (Gaertn.) Britten. However, their rather irregular shape suggests that conditions on *Angophora* were maybe suboptimal for the larva, and such scribbles were never found at any distance from stands of *E. racemosa*.

Taxonomic position of Ogmograptis

The four previously named *Ogmograptis* species were described in four different genera assigned to three different families: *Opostega centrospila* Turner as a Lyonetiid (Turner 1923), *Cateristis triradiata* Turner as a tineid (Turner 1926), and *Cryphioxena notosema* Meyrick (Meyrick 1922) and *O. scribula* Meyrick (Meyrick 1935) as elachistids. Nielsen and Common (1991) tentatively included *Ogmograptis* in the Bucculatricidae on the strength of its ribbed cocoon, as foreshadowed by Meyrick in his description. Both *O. centrospila* and *O. triradiata* were referred to the Lyonetiidae as species of *Cateristis* in the ‘Checklist of the Lepidoptera of Australia’ (Nielsen 1996a). The identity of *Cryphioxena notosema* Meyrick cannot be conclusively resolved as the holotype has not been located in the South Australian Museum. Meyrick (1922) initially described it as an elachistid in the genus *Cryphioxena* Meyrick, which is based on a type species from Mozambique (Meyrick 1921), but later transferred it to *Ogmograptis* (Meyrick 1935). Nielsen (1996b) restored its original combination but transferred the genus *Cryphioxena* to the Bucculatricidae, and considered it closely related to *Ogmograptis*. However, the fact that Meyrick (1935) had referred this species to *Ogmograptis* when describing that

Table 3. Species of *Eucalyptus* subgenus *Eucalyptus* on which scribbles have been recorded (following system of Brooker 2000)

Section	Series	Subseries	Species	Scribbles photographed?
Pseudophloius			<i>pilularis</i> Smith	Yes
Aromatica	Radiatae		<i>elata</i> Dehnhardt	Yes
	Radiatae		<i>croajingolensis</i> Johnson & Hill	No
	Radiatae		<i>willisii</i> ssp. <i>falciformis</i> Newman, Ladiges & Whiffin	Yes
	Insulanae		<i>nitida</i> Hooker	Yes
Capillulus	Limitares		<i>deuaensis</i> Boland & Gilmour	No
Nebulosa			<i>olsenii</i> Johnson & Blaxell	No
Eucalyptus	Regnantes		<i>fastigata</i> Deane & Maiden	Yes
	Strictae	Irregulares	<i>stricta</i> Sieber & Springer	Yes
	Strictae	Irregulares	<i>triflora</i> Maiden	Yes
	Strictae	Irregulares	<i>dendromorpha</i> Johnson & Blaxell	Yes
	Strictae	Irregulares	<i>burgessiana</i> Johnson & Hill	Yes
	Strictae	Regulares	<i>cunninghamii</i> Sweet	No
	Contiguuae		<i>kybeanensis</i> Maiden & Cabbage	No
Longitudinales			<i>stellulata</i> Sieber ex DC.	Yes
Cineraceae	Fraxinales		<i>fraxinoides</i> Deane & Maiden	Yes
	Fraxinales		<i>delegatensis</i> Baker	Yes
	Pauciflorae		<i>pauciflora</i> Sieber & Springel	Yes
	Psathyroxyla	Considenianae	<i>multicaulis</i> Blakely	No
	Psathyroxyla	Considenianae	<i>andrewsii</i> Maiden	No
	Psathyroxyla	Considenianae	? <i>remota</i> Blakely	No
	Psathyroxyla	Haemastomae	<i>haemastoma</i> Smith	Yes
	Psathyroxyla	Haemastomae	<i>racemosa</i> ssp. <i>racemosa</i> Cavanilles	Yes
	Psathyroxyla	Haemastomae	<i>racemosa</i> ssp. <i>rossii</i> (Baker & Smith) Pfeil & Henwood	Yes
	Stenostomae		<i>stenostoma</i> Johnson & Blaxell	No
	Piperitales		<i>piperita</i> Smith	Yes

genus justifies including it in *Ogmograptis*, in the absence of further information.

The initially diverse family assignments of *Ogmograptis* species were prompted by the greatly enlarged antennal scape, the common denominator of all the groups concerned. An antennal scape with a strong pecten or an eye cap is found in several lepidopteran superfamilies, invariably in groups of very small body size, probably to cover the eyes. A particularly large version, a so-called eye cap, occurs in the monotrysian Nepticuloidea and somewhat less prominent developments are found in two lower ditrysian groups, the gracillarioid Bucculatricidae and the yponomeutoid Lyonetiidae, as well as in several gelechioid groups. Independent developments of such an obvious trait has long caused taxonomic confusion, and species of *Ogmograptis* have been described in, or assigned to, all the above groups. For similar reasons, the Bucculatricidae have long been incorrectly associated with the Lyonetiidae.

The large, widely distributed and highly derived genus *Bucculatrix* Zeller was an isolated taxon of uncertain affinity. Description of a second bucculatricine genus, the monotypic *Leucoedemia* Scoble & Scholtz from southern Africa, rich in plesiomorphies, did not provide any obvious apomorphies for the group beyond the longitudinally ribbed cocoon (Scoble and Scholtz 1984). Nielsen and Common (1991) tentatively included *Ogmograptis* in the Bucculatricidae on the strength of such a cocoon. With its life history better known it is now evident that *Ogmograptis* also shares the other three attributes that Scoble and Scholtz (1984) listed as relating *Leucoedemia* and *Bucculatrix*,

namely a larval character and two life-history traits. Setae L1 and L2 on the abdominal larval segments are widely separated in all three taxa, a configuration Mackay (1972) listed as a possible bucculatricid family character, in contrast to the lyonetiid condition with L1 and L2 closer on the abdominal segments. The three groups share the same type of heteromorphosis between the penultimate and the final larval instar, from a legless larva to one with well developed thoracic legs, abdominal prolegs and a spinneret. Detailed study of the larva of *Ogmograptis* has identified two additional unique synapomorphies also shared with *Bucculatrix*. The first is a modified, slender tarsal claw on the prothoracic leg (Fig. 40) together with a pair of hugely enlarged, spatulate, dorso-distal setae on the meso- and metathoracic legs (Figs 42, 43); the second is a highly modified last abdominal segment (Figs 55–57). None of these modifications are mentioned in the description of the larva of *Leucoedemia*, but the internal skeleton of the last abdominal segment is figured (Scoble and Scholtz 1984: fig. 16). The tarsal modifications are apparent only if investigated at very high magnification and without a SEM could well have escaped attention. Significantly, the dorsal pair of tarsal setae is missing in the drawing of the metathoracic larval leg of *Leucoedemia* (Scoble and Scholtz 1984: fig. 13). Davis *et al.* (2002) provided excellent figures of these tarsal modifications for *Bucculatrix caribbea* Davis & Landry, and suggested that the slender prothoracic claw might assist in cocoon construction. Our observation of the initial construction of a loose outer cocoon layer in *Ogmograptis*, longitudinal folds of which are then pulled inward and spun together with the inner layer to form

the characteristic ribs, would support such an hypothesis. Absence of the paddle-shaped modified setae could be important to the function of the hook-like slender prothoracic claw.

In parallel to the present study, a recent phylogenetic analysis of lepidopteran relationships based on molecular evidence (Mutanen *et al.* 2010) indicated that *Ogmograptis* and *Tritymba* are closely related and linked to *Bucculatrix* Zeller. This finding came as a surprise as *Tritymba* had been included in the Plutellidae because the antennae are held forward when the moth is at rest, unlike *Ogmograptis*, in which the antennae rest along the costa (Zborowski and Edwards 2007). Morphology of adults and immatures of *Tritymba* confirm that it is a rather generalised taxon within the Bucculatricidae, and possesses the newly identified synapomorphies of this family – the leg structures and modified last abdominal segment, described above. The similarity of the larval biology of *Tritymba* and *Ogmograptis* further reinforces their close relationship.

With the Bucculatricidae now comprising four genera it is timely to re-evaluate this family. Adult morphology of these genera reveals a deep split between *Bucculatrix*, present on all continents, and the other three genera which are restricted to southern Africa and Australia. The adults of *Ogmograptis*, *Tritymba* and *Leucoedemia* are structurally much more generalised than the highly derived *Bucculatrix*. All three share a short frons not extending below the eye, appressed vertex scaling and well developed, 3-segmented labial palpi, in contrast to the strongly lengthened frons, the tufted vertex scaling and the reduced, 1-segmented labial palpi of *Bucculatrix*. Unlike *Bucculatrix*, *Ogmograptis* has a metafurca with elongate, slender posterior apophyses and shares rather plesiomorphic male genitalia with well developed uncus and gnathos with *Tritymba* and *Leucoedemia*, but the socii are present only as a line of setae in *Ogmograptis* and are apparently absent in *Leucoedemia*. The gnathos of *Tritymba* shares unique and conspicuous apomorphies with both *Leucoedemia* and *Ogmograptis*, a hairy medial plate with the former and a fringe along its apical margin with the latter. This strongly suggests that the three genera are monophyletic. They also share several plesiomorphies such as a well developed juxta and a pronounced saccus. The valva is simple in *Ogmograptis* but has a hairy ventral ridge in *Tritymba* and a free ventral lobe covered with modified, hand-shaped setae in *Leucoedemia*, structures that could be interpreted as a sacculus. The female genitalia of all three genera have the apophyses anteriores present and, except for one subordinate species group within *Ogmograptis*, they all have the distal end of the ductus bursae forming a sclerotised funnel below the ostium. Only *Leucoedemia* has a signum, a spinulose plate. The genitalia of *Bucculatrix* are very different and highly derived in both sexes. Those of the male are especially varied and indicate a long period of diversification, corroborated by the wide distribution of the genus, which is found on all continents (Braun 1963). Prominent, usually dorsally projecting setose socii are characteristic for *Bucculatrix*, with the uncus and gnathos nearly always absent. Discussing evolutionary trends of the male genitalia within *Bucculatrix*, Braun (1963) states that ‘the most complex are considered the most specialised’; however, the description by Puplesis *et al.* (1992) of a species with a well developed gnathos and a large saccus disproves this assessment.

In this case complexity represents an ancestral, not yet reduced, configuration. Seksjaeva (1995) acknowledges this and suggests that a valva differentiated into a sacculus and cucullus also represents an ancestral state, preceding the simple digit-shaped valva of most *Bucculatrix* species. The female genitalia are characterised by a unique signum, a ring of spined longitudinal ribs, and by the loss of the anterior apophyses except in one species with mostly generalised male genitalia (Puplesis *et al.* 1992).

Immature morphology of the four bucculatricid genera also reflects the deep split between *Bucculatrix* and the three southern hemisphere genera. *Leucoedemia*, *Ogmograptis* and *Tritymba* share a strongly modified last abdominal segment with an internal skeleton and reduced anal prolegs whilst *Bucculatrix* has highly developed, long and slender abdominal prolegs. However, whilst the last abdominal segment is unmodified in the last-instar *Bucculatrix* larva, two sclerotised rods are present in the penultimate instar of an Australian *Bucculatrix* species (Fig. 57), presumably remnants of the synapomorphic bucculatricid interior skeleton. Immatures of *Tritymba* have not been studied in detail, but larval and pupal morphology of *Ogmograptis* agree very well with that of *Leucoedemia* (Scoble and Scholtz 1984), apart from the following differences. The larva of *Leucoedemia* lacks the puncture on the prothoracic shield, V on T2+3 and some setae on A7–9, presumably of the L and/or SV series. The pupa of *Leucoedemia* has a band of spinules also on the second abdominal segment and its wings reach to the tip of the abdomen. The relevant figure (Scoble and Scholtz 1984: fig. 17) suggests that labial palpi are present, as in *Ogmograptis*. In contrast, the pupa of *Bucculatrix* has no visible labial palpi and only a single row of small abdominal spines (Mosher 1969; Davis *et al.* 2002).

The molecular phylogeny (Fig. 30, Table 2), based on *Cox1* and 18S, confirms and refines the bucculatricid relationships derived from morphology as outlined above. Within *Ogmograptis* there is a deep split between the *scribula* and the *maxdayi* groups, with the species of the latter group much more deeply divided than those of the *scribula* group. In our samples, *O. scribula* and *O. fraxinoides*, while monophyletic, are poorly supported, which might indicate comparatively recent speciation between the two, further supported by their sharing of *E. pauciflora* as a host. The *Tritymba* cluster comprises three deeply divided taxa, one a single adult and two based on five larvae extracted from *E. racemosa* ssp. *rossii*. The very deep splits within *Tritymba* indicate that more than one genus may be involved, suggesting that a revision of the group may reinstate *Paraphyllis* Meyrick, which was synonymised in the Checklist of the Lepidoptera of Australia (Edwards 1996).

In summary, the molecular data and the morphology of larva, pupa and adults all indicate that *Bucculatrix* is the sister group of *Ogmograptis*, *Tritymba* and *Leucoedemia*. A bucculatricid phylogeny based on such a basal split makes sense in every respect. The *Leucoedemia* group has, at best, vestigial socii but retains a well developed uncus and gnathos, while in *Bucculatrix* the socii have become prominent and the uncus and gnathos have been lost except in the most generalised genitalia. Seksjaeva’s (1995) assessment that a valva differentiated into sacculus and cucullus is an early stage in the evolution of *Bucculatrix* could well be paralleled within

the *Leucoedemia* group, with the simple, reduced valva of *Ogmograptis* being the derived condition. In the female, the apophyses anteriores are retained in the *Leucoedemia* group but present in *Bucculatrix* only in *B. formosa* Puplesis, Seksjaeva & Puplesiene, the species with the least derived male genitalia (Puplesis *et al.* 1992). The hairy gnathos shared by the African *Leucoedemia* and the Australian *Tritymba* is such an astonishing and unique synapomorphy that it can only be explained by a sister group relationship between the two genera, pointing to a shared Gondwanan ancestry. Gentry (1982) suggested a Gondwanan origin for the family Anacardiaceae, which includes the host of *Leucoedemia*, *Ozara paniculosa* (Sond.). *Eucalyptus*, the host of *Tritymba* and *Ogmograptis*, has a long history on parts of Gondwana including Patagonia and Australia (Ladiges *et al.* 2003; Gandolfo *et al.* 2011).

Evolution of feeding modes within the Bucculatricidae can only be assessed once the insect–plant interactions between *Ogmograptis* and its eucalypt host are fully understood. The feeding mode of the larvae of *Tritymba* and the *Ogmograptis scribula* group is, as far as known, unique: boring a tunnel along a cambium layer which then becomes filled with callus tissue on which the last-instar larva feeds. *Leucoedemia* and several species of *Bucculatrix* produce stem galls, but most *Bucculatrix* species feed externally after an initial mining phase. Nearly all gall-producing *Bucculatrix* species feed on Asteraceae and their genitalia are much more derived than those of some externally feeding species (Braun 1963).

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