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The Australian scribbly gum moths *Ogmograptis* Meyrick (Bucculatricidae) and their unique insect-plant interaction.

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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)

## **Abstract**

The formerly monotypic genus *Ogmograptis* Meyrick is revised and divided into three species groups. Eleven new species are described and figured: Ogmograptis fraxinoides Horak **sp. nov.**, Ogmograptis racemosa Horak **sp. nov.** and Ogmograptis pilularis Horak **sp. nov.** forming the *scribula* group together 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. and Ogmograptis pulcher Horak sp. nov. as the triradiata group together with Ogmograptis triradiata (Turner) comb. nov. and Ogmograptis centrospila (Turner) comb. nov. Ogmograptis notosema (Meyrick) cannot be assigned to any of the species groups as the holotype has not been located. The biology of the scribula group, the 'scribbly moths' on certain smooth-barked species of Eucalyptus, is described and figured. Whilst the legless early instar larva feeds as a true borer within the bark at the level of the cork cambium, the final instar larva returns to the terminal part of its mine now filled with callus on which it feeds until fully grown, exiting the mine and pupating at the base of the tree. Three unique synapomorphies, a longitudinally ribbed cocoon and in the larva modified tarsal claws and setae and an

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internal skeleton in its last abdominal segment, join *Ogmograptis*, the Australian *Tritymba* Meyrick, the South African *Leucoedemia* Scoble & Scholtz with *Bucculatrix* Zeller, redefining the family Bucculatricidae. The three southern hemisphere genera are the sister group of *Bucculatrix*.

#### Introduction

The 'scribbles' on the bark of some smooth-barked *Eucalyptus* species in south-eastern Australia have iconic status as a quintessentially Australian emblem, largely as a result of the classic children's books by May Gibbs (1918 and later). The poem 'Scribbly-Gum' by Judith Wright (1955) contains the evocative phrase '[I] found the written track of a life I could not read' which provided inspiration for our study. These scribbles were first thought to be caused by beetle larvae, a misconception still alive (Flannery 2010). Upton (1997) detailed the discovery by T. Greaves in 1934 that a very small moth is responsible. Meyrick (1935) described the moths, 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 the tracking occurs beneath the bark and therefore is not observable while the larva is present. Guided by E. D. Edwards, J. Cooke as a high school project analysed the pattern of scribbles on three species of *Eucalyptus* in the Australian Capital Territory. The results, subsequently reanalysed and published (Cooke and Edwards 2007), emphasized that more than one species of *Ogmograptis* occur. 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 a fortuitous collaboration between entomologists and botanists, initiated and patiently guided over several years by M. F. Day, an ecologist familiar with insects and tree physiology. It has finally resolved the intricate life history of those *Ogmograptis* species which produce the bark scribbles. It has also revealed a unique interaction between the moth larva and the tree producing the scribbly tracks and has

shown that *Ogmograptis* comprises many species in three different species groups. The biology has so far been resolved only for the *scribula* group, the 'scribbly moths' which produce the surface scribbles in the bark. No species of the *maxdayi* and *triradiata* groups have so far been reared. But we have established that the 'ghost scribbles', formed in the vascular cambium and eventually reaching the surface as raised scars, are not made by *Ogmograptis* but by species of *Tritymba* Meyrick. 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 because *Tritymba* had been included in the Plutellidae until now because the antennae are held forward when the moth is at rest, unlike Ogmograptis where the antennae rest along the costa (Zborowski and Edwards 2007). Morphology of adults and immatures of *Ogmograptis* and *Tritymba* confirm that both are rather generalised genera of the Bucculatricidae, and larval structure provides unique additional characters to define this family.

### **Material and Methods**

#### Material studied

*Ogmograptis* species are so small and difficult to handle that they are only collected by very dedicated lepidopterists. Hence the revision was largely based on specimens either stored in the ANIC or reared during the present study. However, some crucial material was contributed by a few committed collectors. Because differences among species are often subtle, type series were usually restricted to a single population.

# Preparatory techniques

Genitalia preparations were made following Robinson (1976) and Common (1990), and wing preparations followed the method developed by Common (1990).

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 and placed as quickly and gently as possible into a cryo-vial and then into a dry shipper previously cooled with liquid N<sub>2</sub> to -196°C. Samples were transferred to a -196°C cryo-store until required. The samples were examined in a Cambridge 360 SEM equipped with a cryo-stage and cryo-transfer unit. Samples were removed from the vials and, with minimal time spent out of liquid nitrogen, 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. Samples were returned to the preparation chamber of the cryo-transfer unit and sputter coated with gold then placed back into the SEM column for observation. Images were captured digitally.

Scanning electron micrographs of larval legs and abdominal structures were done by Eric Hines. Larvae were fixed in 70% ethanol, dehydrated through a graded ethanol series, critical point dried and then mounted on stubs and gold sputter coated. Images were captured with a JEOL 6400 scanning electron microscope at an accelerating voltage of 15KV.

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

### Molecular methods

Whole genomic DNA was extracted from thoracic muscle tissue with the DNeasy Blood & Tissue kit (QIAGEN). Two genes were amplified, a portion of the mitochondrial cytochrome c oxidase subunit 1 (= cox1) and the nuclear small subunit ribosomal RNA 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 papers (Cameron et~al.~2008;~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 done in Sequencher ver 4.9 by eye using *Buccalatrix* 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 & 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 using MrBayes (BA) 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 three (BA) data partitions based on each gene region. All Bayesian analyses were run with unlinked partitions using 2 independent runs, each run consisting of 4 chains (3 hot and 1 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 behavior of each parameter and of total tree likelihood; trees collected prior to this asymptotic point were treated as burn-in and discarded (generally the first 30-60,000 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

DEMV Department of Entomology, Museum of Victoria, Melbourne

GS genitalia slide NP National Park

SAMA South Australian Museum, Adelaide

SEM scanning electron micrograph

# **Taxonomy**

Ogmograptis Meyrick, 1935

Type species: Ogmograptis scribula Meyrick, 1935

# **Diagnosis**

Head scaling smoothly appressed, from short, antennal scape anteriorly strongly extended by broad scales to form a partial 'eye cap', labial palpus 3-segmented, straight, maxillary palpus 1-segmented. Wing 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 Mbranches on weakly developed vein along middle of wing, cell open, CuA well-developed, unbranched. Sternal apodemes long, slender. Tegumen hood-shaped, fused with bandshaped 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 sclerotized 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. 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 posteriolaterally 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 adecticous, protruded from longitudinally ribbed cocoon on emergence.

# **Description**

Adults (Figs 19, 57-82)

Head (Figs 57-60). Head scaling smoothly appressed, from short, ventrally narrowing, triangular, frontal 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, 0.75-0.95x 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 x length of labial palpus, naked, with small, one-segmented, knob-shaped maxillary palpus with few large scales.

Thorax scaling smooth. Metafurca with posterior apophyses elongate, straight, slender, free. Wingspan 8-13 mm. Forewing 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; radius 4-branched, weak up to R1, R1 from below middle, R2 from 3/5, R3, R(4+5) fused into single vein (stalked in *Tritymba* Meyrick) and stalked with M1 from end of cell, R(4+5) to before 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 lanceolate, widest just before middle, ca 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. 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 83-118). Tegumen well-sclerotised, broad, hood-shaped, fused with band-shaped vinculum. Uncus well-developed, two adjacent, parallel points. 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 119-132). 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.

Eggs (Figs 8, 9).

Length 0.41-0.50 mm, width 0.17-0.25 mm; elongate-ovate, more slender and rounded-pointed towards 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, 30, 31, 36-55)

Penultimate larval instar (Figs 7, 8, 24-27, 55). Maximum length 4.5 mm. Extremely long and slender, without legs; head prognathous, dorso-ventrally 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 (26), with internal skeleton (Fig. 55).

Final instar larva (Figs 12, 14-16, 28, 30, 31, 36-54). Maximum length 11 mm. Head prognathous, dorso-ventrally flattened, reddish ochreous to reddish brown; epicranial notch extending 1/3 length of head; frontoclypeus subtriangular, point not quite reaching epicranial notch; 6 stemmata on each side, with the 6<sup>th</sup> not visible except in macerated head capsule: 1 and 2 close to touching each other, 3 close to usually partially fused 4 and 5, and 6 strongly reduced, not protruding, narrow and posteriorly attenuated (Figs 36, 48, 49); 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. 31). Thoracic legs well developed, with polymorphic tarsus, prothoracic tarsus with two distal setae unmodified and a long, slender claw (base obliterated by fluid in all SEM preparations) (Fig. 39), meso- and metathoracic tarsus with the two distal setae strongly modified, spatulate to cone-shaped, with a strong,

distally curved claw (Figs 41, 42, 44, 45, 52, 53). 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 four to six setae on each side, with position even of the two dorsal ones very variable (Fig. 30). Prolegs present on A3-6, 10; ventral prolegs rather short, with a semicircle of 5-6 crochets along the inner side of each proleg (Fig. 40); anal prolegs reduced, without crochets (Figs 38, 46, 47 51). A10 modified (Figs 38, 46, 47, 50, 51), 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 (Figs 54).

Pupa (Figs 17, 32-34). Length: 3.8-4.4 mm. Adecticous, with appendages free. Frontal process a pointed, blade-shaped process (Figs 33, 34). 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.

### **Biology**

Ogmograptis comprises three clearly defined species groups described below, and so far detailed biological information is available only for the *Ogmograptis scribula* group, the classical 'scribbly moths' which produce the well known bark scribbles on some *Eucalyptus* species with smooth bark (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 trees genera except on *Angophora floribunda* (Sm.) Sweet (Moore 1972) and we assume 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 the genus *Eucalyptus*. Females of the *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.

The life history of the scribula group is based mainly on our study of O. racemosa and, in lesser detail, of O. scribula and O. fraxinoides. The layout of larval tracks in the scribula group follows a general pattern which is summarized in Table 1, with crucial points in the track marked from A to D as explained in Table 1 and indicated in the relevant illustration (Figs 4, 9). However, there are differences in the spatial arrangement of the various track components between some 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 track reaches the depth where next year's cork cambium (phellogen) will be formed it makes a 90° turn (A), usually associated with a small 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, and, together with the small widening, this suggests that the larva may be moulting into the second instar at this point. However, no head capsule has been found among the droppings in this section of the track in about 10 samples examined. The tangential track (A-B) is typically at an angle between 90° and 120° to the axis of the trunk, usually forming a few loose long zig-zags, always beneath bark that will be shed in the following year. Each time the track reaches the margin of the bark portion to be shed in the next year it turns back and remains within the confines of the bark patch 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 its probably fourth, 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. This set of shorter and more regular zig-zags varies in two ways between taxa. The first variable is whether this final set of zig-zags follows as a continuation in the same direction either downward or upward on the surface of the trunk as the narrow, initial zigzags (Figs 1-3, 5), or whether, as in O. pilularis, it changes direction and is superimposed over the second half of the earlier track (Figs 4, 6). The second variable concerns two different patterns with regard to the return track from the turning loop. In O. scribula, O. fraxinoides, O. pilularis and tracks of 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). Casual observations of scribbles on various eucalypt species suggest that the track of O. racemosa is the exception, with the majority of 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 extremely long and slender, lacks legs, has a differently 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 (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 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 (Fig. 12, 14-16, 28) which includes the frass left by the larva while boring the track. 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). 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 bores to the outside of the bark, producing a narrow, slit-like exit hole. 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 for all 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.

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. We have direct observations that this life history with two morphologically different larval forms applies also to 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 an analogous life history applies to all *Ogmograptis* species feeding in the cork cambium layer. Ogmograptis racemosa is the only species for which we have sufficient data to roughly time the life history. Adults emerged from collected larvae or pupae and were attracted to light from 28 March to 15 May in the wider Canberra region, Jervis Bay and Wedderburn, NSW, with the large majority on the wing during April. The next fixed point was 1 December (2008), when on E. racemosa spp. rossii on the Barlow property near Gunning, NSW, we found legless larvae of the penultimate instar on the southern, cooler side of the trees. On the northern side of the same trees the larvae were already in their final instar with well-developed 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), moulting into the final instar with legs which were clearly

visible beneath the soon-to-be-shed larval skin of the last legless instar. 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 hours 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.

### **Remarks**

Genitalia morphology in both sexes suggests three discrete species groups within the genus Ogmograptis, for two of which we have supporting DNA data. The scribula group, O. scribula and all other species reared from bark scribbles, ie. with tracks in the cork cambium layer, have the base of the aedeagus bent at up to 90°, a moderately long saccus, a sclerotized 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 biology and diverse wing pattern, 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. Ogmograptis 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 termen, form the apparently more plesiomorphic triradiata group, also with unknown biology, with 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 bark scribblers (*scribula* group) and the single analysed species with a looped aedeagus (*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

scribula group

Ogmograptis scribula Meyrick

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) (Cateristis) comb. nov.

Ogmograptis centrospila (Turner) (Opostega) comb. nov.

Ogmograptis bipunctatus Horak sp. nov.

*Ogmograptis pulcher* Horak sp. nov.

Unassigned to species group

Ogmograptis notosema (Meyrick) (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. The biology is discussed in detail above.

# Ogmograptis scribula Meyrick

(Figs. 1, 2, 12, 15, 20, 21, 36-42, 61, 62, 89-91, 119-121) *Ogmograptis scribula* Meyrick, 1935: 600.

### Material examined.

Holotype \$m: 'Scribble Insect, larvae on *Eucalyptus coriacea* [= *E. pauciflora*], Pupated 8-12 Feb[ruar]y [19]35, Emerged 11 March [19]35, Lee's Spring, Brindabella Range [35.23S 149.13E], FCT [Federal Capital Territory], Australia, coll. T. Greaves.'; 'ANIC 31-035161' (ANIC).

Other material examined. Australian Capital Territory: 4 \$m, same label data as holotype, ANIC 31-035162 to 31-035165, ANIC GS 14775\$m, 14839\$m; 1 \$f, 35.55S 148.77E, Lees Springs, 1 Feb.1933, W. Bruce & F.G. Holdaway, ANIC 31-035170; 4 \$f, Canberra [Brindabella Range, coll. T. Greaves], em. Brisbane, 13-18 March 1934 [Turner's handwriting], ANIC 31-035181 to 31-035184, ANIC GS 14776\$f, 14791\$f; 2 \$m, 2 \$f, 35.55S 148.77E, Lee's Springs, 4000 ft, em. 18 Feb. 1958, I.F.B. Common, ANIC 31-035166 to 31-035169, ANIC GS H57\$m, H58\$f; 2 \$m, 6 \$f, 35.38S 148.8E, Brindabella, Bull's Head, larvae coll. 10 & 12 Feb. 2010 on *E. pauciflora*, em. 8-20 Mar. 2010, Horak & Su, Horak & Su & Macnicol, ANIC 31-035171 to 31-035178, ANIC GS 14864\$f.

Diagnosis. Forewings evenly speckled, somewhat darker along dorsum, with five well-defined longitudinal dark streaks, the two distal ones usually connected. Male genitalia with base of aedeagus lightly curved and saccus rather short and stout, with broadly rounded gnathos tip with long, slender fringe, and with central juxta plate dorsally triangularly projecting, with dorsally converging ribs. Female genitalia with appressed, leaf-like, elongate-ovate ovipositor lobes, with short posterior apophyses and with

sclerotised funnel below ostium narrow, less wide than long, and with bottle-shaped corpus bursae.

# Description

Adult (Figs 61, 62). Wingspan: (7.5) 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 ¼ 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 83-85). Gnathos tip broadly rounded, with full apical fringe of long, slender teeth, 4-5 times as long as wide; valva long and nearly parallel-sided, widest near apex, saccus rather short, juxta a dorsally deeply sinuate band with a dorsally triangularly projecting 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 evenly curved, short, lightly bulbous base; vesica with an indistinct needle-shaped cornutus.

Female genitalia (Figs 119-121). Ovipositor lobes membranous, appressed; elongate-ovate, posterior apophyses short, 1.2-1.3 x length of sclerotised dorsal margin of ovipositor lobe. Ductus bursae membranous, with narrow sclerotised funnel below ostium; corpus bursae bottle-shaped, with posterior 2/3 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, often the terminal ones 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, such as the slope above 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.

## Remarks

According to Meyrick's description there are 3 paratypes with the same data as the holotype in the BMNH. There are also 5 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*.

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.

O. 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, 34,43-47, 57, 78, 63, 64, 86-88, 122-124)

### Material examined.

Holotype \$m: '36.36S 149,27E [36.6S 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\$m' (ANIC).

Paratypes: New South Wales: 3 \$m, 3\$f, same label data as holotype, but em. 21-26 Mar. 2010, ANIC 31-053186, 053188 to 31-053192, ANIC GS 14861\$m, 14862\$f; 1 \$m, 36.6\$ 149.45E, Brown Mt., pupa coll. 2 Mar. 2009, em. 24 Mar. 2009, M. Horak & Y.N. Su, ANIC 31-035199, ANIC GS 14823\$m; 2 \$f, 36.6\$ 149.45E, Brown Mt., pupa coll. 14

Mar. 2010, em. 2 & 5 April 2010, ANIC 31-035197 & 31-035198, ANIC GS 14838\$f; 2\$f, Piper's Lookout 18 km ESE of Nimmitabel [Brown Mt.], em. 15 & 19 Mar. 2007, E.D. Edwards & M.F. Day, ANIC 31-035195 & 31-035196, ANIC GS 14750\$f; (ANIC, AMSA).

### Other material

New South Wales: 2 \$f, 36.1S 148.2E, Kosciuszko National Park, Sawpit Creek, larvae coll. 6 Feb. 2010 on *E. pauciflora*, em. 11 Mar. 2010, Horak, Hines, Corbett & Mackenzie, ANIC 31-035179 & 31-035180, ANIC GS 14872\$f. (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 57, 58, 63, 64). 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, with 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 86-88). 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 (xx length of valva), 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, (xx length of valva),

straight except for short, slightly rounded-angled, lightly bulbous base; vesica with a needle-shaped cornutus.

Female genitalia (Figs 122-124). Ovipositor lobes elongate-ovate, membranous, appressed; posterior apophyses long, 1.6-1.9 x length of sclerotised dorsal margin of ovipositor lobe. Ductus bursae membranous, with wide sclerotised funnel below ostium (as wide as long); corpus bursae bottle-shaped, with posterior 2/3 much narrower and parallel-sided, with large central area of scobination.

# **Biology**

White Ash, *Eucalyptus fraxionoides* 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 so that the distance between the parallel 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* on the slope above Sawpit Creek, Kosciuszko NP, 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 were found boring out of their tracks on *E. pauciflora* to pupate on 7 February 2010. The first cocoon was found 6 hours after the larva was collected, several more formed their cocoon in the next 48 hours, and two adults emerged after 33 days.

### Remarks

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.

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. The two larvae from snow gum analysed for the molecular phylogeny are on the edge of the *fraxinoides* cluster, prompting the question whether *O. fraxinoides* interbreeds with the closely related *O. scribula* if the two occur at the same locality on the same host.

# Ogmograptis racemosa Horak sp. nov.

(Figs 4, 7, 8, 9, 13, 14, 16-19, 22, 24-28, 30-33, 35,48-55, 65, 66, 89-91, 125, 126)

### Material examined.

Holotype \$m: '35.17S 149.06E [35.28S 149.1E], Botanical Gardens, Canberra, ACT, Emg. 30 Apr 2007, Day, Horak & Edwards'; 'Cocoon in litter beneath Eucalyptus maculosa', 'ANIC Database No. 31-035200', 'ANIC Genitalia slide No 14873\$m' (ANIC). Paratypes: Australian Capital Territory: 4\$m, 3\$f, same label data as holotype but em. 2-30 Apr. 2007, ANIC 31-0352001 to 31-0352007, ANIC GS 14878\$m; 1\$m, 2 \$f, 35.28\$ 149.1E, Botanical Gardens, Canberra, Apr. 2006, M. Day, ANIC 31-035212 to 31-035214, ANIC GS 19315\$f; 2\$m, 35.28S 149.1E, Botanical Gardens, Canberra, 14 Apr. 2006, M. Day (AMSA); 3\$m, 8\$f, 35.28S 149.1E, Botanical Gardens, Canberra, 28 Mar. to 19 Apr. 2007, Day & Edwards, ANIC 31-035215 to ANIC 31-035225, ANIC GS 14784\$f; 1\$m, 35.28\$ 149.1E, Botanical Gardens, Canberra, pupa on E. racemosa ssp. rossii, em. 4 Apr. 2007, Macnicol & Horak, ANIC 31-035209, ANIC GS 14751\$m; 1\$m, 2\$f, 35.27\$ 149.1E, Black Mt., Canberra, 2 & 9 Apr. 1963, 15 May, 1964, I.F.B. Common, ANIC 31-035208, 31-035210 & 31-035211, ANIC GS H59. New South Wales: 5\$m, 5\$f, 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 Apr. 2009, ANIC 31-035226 to 31-035235, ANIC GS 14773\$f, 14780\$m, 14788\$f, 19316\$m; (ANIC, AMSA, BMNH).

Other material: New South Wales: 5\$m, 6\$f, 34.13S 150.82E, 3 km E Wedderburn, at MV light, 15 &21 Apr. 2007, em. 18-28 Apr. 2007, D. Britton, ANIC, 31-035271 to 31-035281, ANIC GS 14782\$m, 19357\$m, 19358\$f; **1\$m, 1\$f, 33.97S 150.03E, Boyd River, 6 Mar. 1976, V.J. Robinson, ANIC 31-035269 & 31-035270;** 1 \$, 34.7S 150.72E, Barren Grounds Fauna Res., 5 Apr. 1975, V.J. Robinson, ANIC 31-035268; 16\$m, 16\$f, 34.23S 150.7E, CSIRO Exp. Farm, Wilton, 18 Apr. 1974, 28 Apr. 1974, 8 May 1974, 11 Apr.

1975, 19 May 1975, 15 May 1977, V. J. Robinson, ANIC 31-035236 to 31-035267, ANIC GS 14754\$m, 14771\$m, 14774\$m, 19329\$m, 19330\$f, 19336\$f; 4\$m, 35.15S 150.65E, Jervis Bay Nat. Res., 3 Apr. 1999, L. Kaila, black light, ANIC 31-035282 to 31-035285, ANIC GS 19400\$m; 2\$f, 35.15S 150.67E, Jervis Bay Botanical Gardens, cocoon beneath *E. racemosa*, em. 24 & 25 Apr. 2007, E.D. Edwards & M.F.Day, ANIC 31-035286 & 31-035287, ANIC GS 14748\$f.

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 with 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 with appressed, leaf-like, elongate-ovate ovipositor lobes, with long posterior apophyses and with sclerotised funnel below ostium narrow, less wide than long, and with ovate to slightly hourglass-shaped corpus bursae.

# Description

Adult (Figs 19, 65, 66). 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 distally slightly converging 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 89-91). 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 125, 126). Ovipositor lobes elongate-ovate, membranous, appressed; posterior apophyses long, 1.7-2.0 x 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**

Ogmograptis 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* spp. racemosa Cav., confirming 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 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 zigzags followed by a final set of much thicker, shorter, single zigzags 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,

# Ogmograptis pilularis Horak sp. nov.

(Figs 5, 6, 67, 68, 92-94, 127-129)

### Material examined.

Holotype \$m: '[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\$m' (ANIC).

Paratypes: New South Wales: 2 \$m, same label data as holotype but ANIC 31-035289 & 31-035290; 6 \$m, 6 \$f, 35.63S 150.32E, Ryans Ck Rd, Depot Beach, 16km NE of

Batemans Bay, 11 Apr. 1975, I.F.B. Common, ANIC 31-035291 to 031302, ANIC GS 14752\$f, 14772\$m, 14840\$f, 14868\$f, 19337\$m (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 with 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 with appressed, leaf-like, elongate-ovate ovipositor lobes, with long posterior apophyses and with sclerotised funnel below ostium narrow, less wide than long, and with ovate to hourglass-shaped corpus bursae.

# Description

Adult (67, 68). 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 greybrown 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 (92-94). 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, (xx length of valva), straight to faintly sinuate with a curved to weakly angled, lightly bulbous base; vesica with one needle-shaped cornutus.

Female genitalia (127-129). 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 high on the larger smooth branches above the entirely rough-barked trunk. The track of *O. pilularis* (5, 6) is unlike other scribbles examined, having the terminal set of thick zigzags produced in the reverse direction, superimposed over the initial, slender zigzags. The initial, widely spaced zigzag 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 zigzags across the zigzags 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.

### 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 biology of this group.

### Ogmograptis maxdayi Horak sp. nov.

(Figs 59, 60, 69, 70, 95-97, 130)

#### Material examined

Holotype \$m: '[35.27S 149.1E] Black Mt., A.C.T., Light Trap, 15 Oct. 1963, I.F.B. Common', 'ANIC Database No. 31-035303', 'ANIC genitalia slide No 14879\$m' (ANIC). Paratypes: Australian Capital Territory: 13 \$m, 5\$f, same label data as holotype but 7 Oct. – 6 Nov. 1959, 6 Dec, 1960, 9 Oct. – 25 Nov. 1963, 22 Oct, 1964, ANIC 31-035304 to 31-035321, ANIC GS 14790\$m, 14875\$m, 19327\$m, 19328\$f (ANIC, DEMV, BMNH).

Other material: Victoria: 1 \$m, 2 \$f, 37° 44.1'S 145°13.2E', Warrandyte, 6-31 Oct. 2004, 1-15 Oct. 2007, 1-15 Nov. 2008, D.J. Hilton, ANIC GS 14920 \$f, 14822\$m (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 with crosier-shaped aedeagus and very long, club-shaped saccus, gnathos tip fringed only along central 2/3, valva with costa convex in distal half and apex tapering, narrowly rounded, and juxta wide, band-shaped, with a median crease. Female genitalia with 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 59, 60, 69, 70). Wingspan: 8-12 mm. Head and thorax 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 with narrow grey-brown apex in a narrow band along costa from ¼ to apex, expanded into an irregular wider band beyond middle; with much fewer off-white scales scattered along dorsum beyond 1/4, reaching to middle of wing in distal third; with 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, about 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 darktipped 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 95-97). 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 x) in distal half with costa lightly convex and apex tapering, sharply rounded; saccus long (xx length of valva), 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.

Female genitalia (Fig. 130). Ovipositor lobes membranous, appressed, broadly ovate, with scattered bristles; posterior apophyses 1.7 x 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, Vic., 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*.

# Ogmograptis barloworum Horak sp. nov.

(Figs 71, 72, 98-100, 131)

### Material examined.

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

Lectotypes: Australian Capital Territory: 3 \$m, same data as holotype but 19 Sep. 1962, 29 Sep. & 20 Oct. 1964, ANIC 31-035323 to 31-03525 (ANIC).

Other material. Victoria: 1 \$f, 37°26'S 145° 39'E, Melbourne, Gembrook, Gilwell Park, at light, 30 Oct. 2009, Kallies, Marriott & Hilton, ANIC GS 14874\$f (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 71, 72). 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 along costa to 2/3 with unevenly scattered dark grey scales, 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.

Male genitalia (Figs 98-100). Gnathos strongly tapering to rounded tip with moderately long apical fringe around entire curvature; valva long, much (1.6-1.7x) wider in distal half, apex broadly rounded; saccus long (xx length of valva), 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. 131). Ovipositor lobes membranous, appressed, ovate, with scattered bristles; posterior apophyses 1.4 x 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 costal half and largely grey-black along dorsum, but there are somewhat similar undescribed species with additional black marks on 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, Vic., seems to be conspecific and is tentatively described and figured, but not included in the type series.

# Ogmograptis paucidentatus Horak sp. nov.

(Figs 73, 74, 101-103)

#### Material examined

Holotype \$m: '[35.27S 149.1E] Black Mt., ACT, Light Trap, 2 May 1963, I.F.B.Common', 'ANIC Database No. 31-035326', 'ANIC genitalia slide No. 19334\$m' (ANIC).

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

Diagnosis. Forewings white with scattered dark brown scales and usually 3 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 with 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 with 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 73, 74). Wingspan: (8.5) 11.5-13 mm. Head and thorax speckled with browntipped 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 101-103). Uncus tips short and blunt. Gnathos tapering to pointed tip with apical fringe of only a few teeth; valva long, wider (1.4x) in distal half and broadly rounded; saccus long (xx length of valva), 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 basal loop, crosier-shaped, 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 sclerotized tube below ostium, remainder of ductus narrow and lightly sclerotised, slightly widening near corpus bursae; corpus bursae ovate, anteriorly 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 exactly similar genitalia. The red-brown streak along the dorsum of the forewing and the unique gnathos tip readily characterise *O. paucidentatus*.

# Ogmograptis rodens Horak sp. nov.

(Figs 75, 104-106)

### Material examined

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

Paratypes: New South Wales: 1 \$m, same label data as holotype but 15 Sept. 1966, ANIC 31-053334, ANIC GS 14753\$m; 1 \$m, 34.23S 150.7E, CSIRO Experimental Farm Wilton, 3 Oct. 1974, V.J. Robinson, ANIC 31-0533333; (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 with 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 with costa convex in distal half and apex tapering, narrowly rounded, juxta in slide preparation folded and projecting as a long, narrow beak. Female genitalia with 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 (Fig. 75). 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; longitudinal grey-brown marks large but ill-defined, 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 nearby along 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 ¾; 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 104-106). Gnathos tip nearly parallel-sided, apex broadly rounded with fringe of few teeth only in centre of distal margin; valva long, wider (1.4x) in distal half and apex broadly rounded; valva moderately long, wider in distal half with costa lightly convex and 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 sub-median 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* could possibly be confused with other undescribed black and white mottled species, but the combination of the unique gnathos tip and the dorsally hugely projecting median shield of the juxta are diagnostic.

# Ogmograptis bignathifer Horak sp. nov.

(Figs 76, 107-109)

### Material examined

Holotype \$m: South Australia: '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 GS 18600\$m' (ANIC).

Diagnosis. Forewings with a 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 with 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 apex with a fringe along its entire margin, juxta with a long and narrow central plate.

# Description

Adult (Fig. 76). 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 longitudinally boldly marked with 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, more narrow 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 legs blackish.

Male genitalia (Figs 107-109). Gnathos highly complex, with lateral arms each branching into two arms each before the ventral arms meet to form the twice narrowed gnathos tip with a widened and weakly curved apex with a fringe along its entire margin; the upper branches from each gnathos arm are expanded into long, flat, paddle-shaped processes; valva moderately long, much wider (1.6-1.7x) in distal half and apex broadly rounded; saccus long (xx length of valva), 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.

### Ogmograptis inornatus Horak sp. nov.

(Figs 77, 110-112)

### Material examined.

Holotype \$m: Victoria: '[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\$m' (ANIC).

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

Diagnosis. Forewings white with scattered scales with grey-brown tips mainly in a band along costa and along dorsum, with ill-defined sprinklings of dark brown-tipped scales at 2/5 costa, near end of fold and in wing tip. Male genitalia with 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

Male (Fig. 77). 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 ill-defined patches of more densely sprinkled scales with dark brown tips: a variably developed small group in 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. Abdomen pale silvery grey, darker dorsally.

Male genitalia (Figs 110-112). Gnathos tip complex with sinuate lateral margins, with 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.

### 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 also 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 singletons in the collection, and nothing is known about their biology.

# Ogmograptis triradiata (Turner, 1926) comb. nov.

(Figs 78, 113, 114)

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

#### Material examined

Holotype \$m: New South Wales: 'Mt Wilson [Blue Mts, 33.5S 150.38E] N.S.W. 19.11.[19]23 [Turner]'; 'ANIC 31-035341'; 'ANIC GS 14824\$m' (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 with faintly sinuate aedeagus with weakly bulbous base, with short saccus strongly tapering to truncate apex, with a 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 (Fig. 78). Wingspan: 9 mm. 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 ochrous 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 113, 114). Uncus tips long, slender, pointed. 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 x 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 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 series of Cateristis, Cateristis eustyla Meyrick, 1889, is 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* by its 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 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.

# Ogmograptis centrospila (Turner) comb. nov.

(Fig. 79)

Opostega centrospila Turner, 1923: 179

Cateristis centrospila. – Nielsen, 1996 (comb.)

### Material examined.

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

Paralectotype \$m: Queensland: 'Brisbane [27.47S 153.03E] Aug.' [without abdomen]; 'ANIC 31-035340' (ANIC).

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 (Fig. 79). 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.

#### 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 fore wing, similar to *O. triradiata*, and is probably not conspecific with the lectotype.

## Ogmograptis bipunctatus Horak sp. nov.

(Figs 80, 81, 115, 116, 132)

#### Material examined.

Holotype \$m: New South Wales: '[35.12S 150.083E] 5 mls NE Nerriga, N.S.W., 27 Nov. 1962, I.F.B. Common & M.S. Upton', 'ANIC Database No. 31-035342', 'ANIC genitalia slide No 14783\$m' (ANIC).

Paratype \$f: New South Wales: same label data as holotype but ANIC 31-035343, ANIC GS 14786\$f (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 with straight slender aedeagus with bulbous base, with short saccus strongly tapering to rounded apex, with 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 with unmodified, spinulose, posteriorly directed ovipositor lobes, ductus bursae membranous, short, with sclerotised funnel below ostium, corpus bursae bottle-shaped, membranous.

## Description

Adult (Figs 80, 81). 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 115, 116). 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 x 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. 132). 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 membraneous; corpus bursae bottle-shaped with a long, slender, membraneous neck leading to ductus bursae and ductus seminalis, without spinules.

#### Ogmograptis pulcher Horak sp. nov.

(Figs 82, 117, 118)

Material examined.

Holotype \$m: '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\$m' (**ANIC**).

Paratypes: Victoria: 2\$m, same label data as holotype but ANIC 31-035345 & 31-035346, ANIC GS 14879\$m (ANIC, DEMV).

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 with straight gradually tapering aedeagus, with very short saccus with distal half not tapering, with a 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 (Fig. 82). 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 117, 118). 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 x 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 roundedtruncate and strongly projecting shield-shaped median plate with a prominent ventral bar; aedeagus straight, gradually tapering (tip broken in holotype).

### Unassigned to species group

## Ogmograptis notosema (Meyrick, 1922)

Cryphioxena notosema Meyrick, 1922: 507. – Nielsen, 1996.

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

#### Remarks

The single holotype of *O. notosema* has not been found. The species was based on material collected by Lower and sent 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 (pers. comm. E. D. Edwards). 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 supported by 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.

## **Molecular systematics**

A molecular systematic study 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 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. 133) suggest that the "ghost scribble" producing species are members of *Tritymba*, although there is a significant molecular divergence between the confirmed adult specimen and the larval specimens, comparable to that between the *maxdayi* and *scribula* species groups within *Ogmograptis*. For both *O. fraxinoides* and *O. scribula*, molecular sequences match for larvae and adults thus

confirming their utility for identifications. While sequences were only obtainable from 2 of the 3 *Ogmograptis* species groups, the phylogenetic results support those species group assignments.

#### **Discussion**

## 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 Ogmograptis 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 (Nielsen 1996a). The identity of *Cryphioxena* notosema Meyrick cannot be conclusively resolved as the holotype has not been located in the South Australian Museum, Adelaide. 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). In the Checklist (Nielsen 1996b), the taxon was given in its original combination, but in the Bucculatricidae next to Ogmograptis. However, the fact that Meyrick (1935) had referred it to *Ogmograptis* when describing that genus justifies including the species in Ogmograptis, in the absence of further information.

These 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 hide the eye and suggest an inanimate object like a bird dropping rather than a moth. 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 goups, the gracillarioid Bucculatricidae and the yponomeutoid Lyonetiidae, as well as in several gelechioid groups. Homoplasy, parallel developments of such an obvious trait, has long caused taxonomic confusion, and species of *Ogmograptis* have been described in or assigned to all the groups above. For similar reasons, the Bucculatricidae have long been incorrectly associated with the Lyonetiidae.

The large, widely distributed and highly derived genus *Bucculatrix* Zeller was long 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 known it is now evident that *Ogmograptis* also shares the other three attributes that Scoble and Scholtz (1984) listed as relating Leucoedemia and Bucculatrix needhami Braun, 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 apomorphies shared also by Tritymba and Bucculatrix. The first is a modified, slender tarsal claw on the prothoracic leg (Fig. 39) together with a pair of hugely enlarged, spatulate, dorso-distal setae on the meso- and metathoracic legs (Figs 41, 42), the second a highly modified last abdominal segment (Figs 54-56). None of these modifications were 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 only apparent 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 a hypothesis. Absence of the paddle-shaped modified setae could be important to the function of the hook-like slender prothoracic claw.

Position and rank of the Bucculatricidae have long been contentious, and Kuroko's (1964) taxonomic history of the Lyonetiidae follows the various assignments of *Bucculatrix*.

Assessments based on immature characters recognised early that the group deserved family status (Mackay 1972). Based on nine shared features, Davis and Robinson (1999) included the Bucculatricidae in the Gracillarioidea, together with Gracillariidae, Roeslerstammiidae and Douglasiidae. A pupa with free appendages and movable abdominal segments with a band of spines to push the pupa partially out of the cocoon before eclosion accounts for two of these gracillarioid characters, and a larva with mining early instars and a fully legged last instar for a third one. The ribbed cocoon, the strongly widened antennal scape, and the combination of a slender prothoracic claw with modified dorsal setae on the mesoand meta-tarsus distinguish Bucculatricidae from other Gracillarioidea. Modified tarsal setae have not been reported from any of the other three gracillarioid families, though there are few descriptions and illustrations of roeslerstammiid larvae (Moriuti 1978; Kyrki 1984) and only a single figure of a douglasiid larva (Heppner 1987). Absence of ocelli and presence of two rings of scales per antennal segment link the Bucculatricidae with the Roeslerstammiidae, and plesiomorphic male genitalia in both families have a bifid uncus and a gnathos with distally joined arms, structures lacking in Gracillariidae and Douglasiidae (Davis and Robinson 1999). Mutanen et al. (2010), in the supplementary figure 1 of their cladogram, show the Bucculatricidae plus Gracillariidae as the sister group of the Roeslerstammiidae, with the Douglasiidae far removed as an apoditrysian taxon. However, they state that 'the status of the bucculatricid complex as a gracillarioid taxon is ambiguous'.

With the Bucculatricidae now comprising four genera it is timely to re-evaluate this family. Adult morphology of the four genera now known 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. It 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 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 alone would identify the three genera as a monophyletic grouping. All have 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 which 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. Especially those of the male are highly diverse 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 specialized'. However, the description by Puplesis et al. (1992) of a species with a well-developed gnathos and a large saccus illustrates that complexity in this case 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 early development stage, 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. 56), presumably remnants of the 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. 133, Table 2), based on *cox1* and *18S*, confirms and refines the bucculatricid relationships derived from morphology as outlined above. An unnamed Australian species of *Bucculatrix* serves as outgroup in our molecular phylogeny, with *Tritymba* and *Ogmograptis* presenting as sister groups, both strongly supported. 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 (Edwards 1996).

In summary, the morphology of immatures and adults and molecular data 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 retained well-developed uncus and gnathos whilst in *Bucculatrix* the socii have become prominent and the uncus and gnathos 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 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 apomorphy 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 only known host for Tritymba and Ogmograptis, has a history on parts of Gondwana including Patagonia and Australia that makes such an association plausible (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 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 the majority of *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), suggesting that in *Bucculatrix* gall induction is not an ancestral trait.

# Insect-plant interactions between Ogmograptis and Eucalyptus

The tracks of the *Ogmograptis 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 which is contiguous with the phellogen (Fig. 22). 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. Hence formation of these distinctive tracks depends on a close interaction between the *Ogmograptis* larva and its eucalypt host tree. Development of the larva and the associated track is synchronised for each species within a narrow window and is correlated with host phenology, in particular with the cycle of bark shedding. 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 being prepared by Celia Barlow and Margaret McCully.

At present we can only point to the synchronicity of *Ogmograptis* larval activities with eucalypt phenology and tissue developments without providing any causal explanations. However, the close fit between host tree physiology and *Ogmograptis* life history suggests 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 two species of Opostegidae (Grossenbacher 1910, Kumata 1984, Davis and Stonis 2007). In the *Ogmograptis scribula* group, on the other hand, this behaviour is obligate and highly refined. Its eucalypt hosts usually shed only part of their outer bark in any given year, and the areas shed from year to year are not congruent. Active *Ogmograptis* tracks are restricted to bark due to be shed at the next bark dehiscence, and the larvae infallibly 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 yet discernible when the *Ogmograptis* larva bores its early mine, yet the larva unerringly bores at the correct level. Once the outer bark falls off the entire track is revealed at exactly this level, without fail, never dipping above or below (Figs 1-6). Furthermore, in order for her progeny to survive and develop, the female moth has to lay her eggs on an area of bark that will be shed in the coming summer, again at a time when we were not able to morphologically locate the phellogen.

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 and happen within a short time span, with at most 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 zigzag 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, presumably along the friable abscission layer of cork starting to be produced by the phellogen. The timing of the final moult exactly at the moment when the track becomes filled with callus tissue ensures that the necessary food is available for the last instar larva. It seems reasonable to consider this as more than a mere coincidence.

The most remarkable and unique aspect of the life history of the *Ogmograptis scribula* group is that the final instar larva returns to feeding on the callus filling the mine it has itself 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. There are only very few examples where a mining insect returns to the callus growing in its mine and actually feeds on it. *Liriomyza strigata* Meigen (Diptera: Agromyzidae), with its

forked track along the mid-rib of the leaf, and the species of *Nepticula* of the *argyropeza* group (Lepidoptera: Nepticulidae), which produce a slight thickening in the leaf petiole, are examples given. However, both larva feed as 'proper' leaf miners on the leaf blade between consuming callus tissue in their central mine channel. Two agromyzid *Phytomyza* species on thistles also mine in the mid-rib of leaves which becomes considerably swollen and appears like a gall, but again, both species also mine lateral tracks outside the thickened area. Among all the examples (Hering 1951, 1962), there is nothing remotely approximating the radical and obligatory switch of feeding mode observed in the *Ogmograptis scribula* group, complete with significant morphological changes between relevant larval instars.

The obvious question is what makes this callus grow, exactly at this moment, and only in this 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 often more pronounced around the excrements of the miner (Hering 1951). However, in the Ogmograptis track callus growth is restricted to the final, doubled-up zig-zags of the track, 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 2006/2007 the Eucalyptus racemosa ssp. rossii at Gunning hardly produced 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 just a fortuitous by-product, based on a simple wound reaction, or whether larval activity induces the callus growth. Two aspects of its behaviour indicate that the *Ogmograptis* larva may maximise production of callus in the latter part of its mine. Firstly, 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 doubled track zig-zags appears modified once the callus is present, as evidenced by discolouration (Figs 4, 12, 13). Note that this discolouration is not yet visible at the moment when the penultimate caterpillar is ready to moult (Fig. 9). Secondly, the life history of the larva is timed so that completion of the double track exactly coincides with the activity of the cork cambium.

Scanning electron microscope images of early and last instar larvae of *O. racemosa* and their tracks clearly show the radically different nature of the tissue the larva is feeding on

during the early borer and the later callus feeder phases. Whilst 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 any trace of callus cells (Fig. 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 (Fig. 22, 23). The stacks of cells are contiguous across phelloderm 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 wherever there was any 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 thickwalled 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.

In summary, the obligatory switch by the last instar larva of the *Ogmograptis scribula* group from feeding as a borer in the bark at the phellem 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 to callus growth, to help answer the question of whether it might be induced by larval activity beyond simple wounding and presence of frass.

The life history is known in detail only for the *Ogmograptis scribula* group, but our casual observations of fresh *Tritymba* tracks suggest that this genus has a similar biology. The track of the *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 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. However, whilst 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 has brought them to the surface of the bark.

## Host specificity of the Ogmograptis scribula group

As briefly outlined in the Biology paragraph, both *Ogmograptis* and *Tritymba* are probably confined to the genus *Eucalyptus* and possibly close relatives, but *Tritymba* feeds also on rough-barked eucalypt species where the scars of the tracks made in the vascular cambium never become visible on the surface but may be seen when the bark is stripped. Moore (1972) described and figured tracks of an unidentified insect which can only be those of *Tritymba* from many species of *Eucalyptus* and also from *Angophora floribunda* (Sm.) Sweet in New South Wales. Based on molecular data (Fig. 133), at least two *Tritymba* species have been found together on *E. racemosa* spp. *rossii*, and the very diverse tracks suggest there may be even more species on this one eucalypt. 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. With guidance from E. D. Edwards for a school project, J. Cooke surveyed in 1996 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. The results were later re-analysed and published (Cooke and Edwards 2007), demonstrating that 'scribble measurements differed significantly between all tree 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 based on ten 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 between the four species, and, more surprisingly, differences also in larval morphology between the three species examined. This pooled information for five species shows a definite but not exclusive correlation between species of *Ogmograptis* and its Eucalyptus host species.

Ogmograptis bark scribbles have been reported from 26 species of Eucalyptus (Brooker et al. 2002), listed in Table 1 according to the classification by Brooker (2000). All 26

species belong to the monophyletic subgenus *Eucalyptus* which is endemic to eastern 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 occur on skeletal and poor soils. Scribbles may densely cover the trunk, at variable density between even close trees, but in some species they may be infrequent. In species such as E. pilularis and E. delegatensis with a rough-barked trunk, the scribbles are restricted to the smooth-barked upper, larger branches. 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 scribbles there are only found on the two subspecies of E. racemosa. The resident population of Ogmograptis 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 assumption that species of the *scribula* group are restricted to some degree to a given eucalypt species. However, this is by no means 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. Ogmograptis 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 could be found on adjacent Angophora costata (Gaertn.) Britten. However, their rather irregular shape indicated that conditions on *Angophora* were less than ideal for the larva, and such scribbles were never found at any distance from E. racemosa.

Given the very long and apparently exclusive association of the *Tritymba – Ogmograptis* lineage with *Eucalyptus* and close relatives, the question as to parallel evolution between insects and host trees has to be asked. The *scribula* group is the most recent radiation within *Ogmograptis*, with only subtle morphological differences between species, and the four species studied are a very small sample. However, the unique track of *O. pilularis*, with the second half superimposed over the initial loose zigzags (Figs 5-6), possibly reflects the isolated position of its host which is the only eucalypt species with scribbles in the section *Pseudophloius* (Table 3). The other three species studied have hosts in two different series of the section *Cineraceae*. *Ogmograptis scribula* and *O. racemosa* both

have hosts in the series *Pauciflorae*, namely *E. pauciflora* and *E. racemosa*, while *O. fraxinoides* has two hosts in two different series, *E. pauciflora* in *Pauciflorae* and *E. fraxinoides* in *Fraxinales*. *Ogmograptis racemosa* on *E. racemosa* is the odd one out on scribble shape as the only observed species with an adjacent rather than parallel return track. A comprehensive study of possible co-evolution between species of the *scribula* group and their eucalypt hosts would be of great interest.

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#### References

Braun, A. F. (1963). The genus *Bucculatrix* in America north of Mexico (Microlepidoptera). *Memoir of the American Entomological Society* **18**, i-iii, 1-208, pls I-XLV.

Brooker, M. I. H. (2000). A new classification of the genus *Eucalyptus* L'Hér. (Myrtaceae). *Australian Systematic Botany* **13**, 79-148.

Brooker, M. I. H., Slee, A. V., Connors, J. R., and Duffy, S. M. (2002). 'EUCLID: Eucalypts of Southern Australia, (CD ROM) 2<sup>nd</sup> edn'. (CSIRO Publishing: Collingwood, Victoria.)

Cameron, S.L., Dowton, M., Castro, L.R., Ruberu, K., Whiting, M.F., Austin, A.D., Diement, K. and Stevens, J. (2008) The sequence of the mitochondrial genomes of two vespid wasps reveals a number of derived tRNA gene rearrangements. *Genome* **51**, 800-808.

Cameron, S.L., Sullivan, J., Song, H., Miller, K.B., and Whiting, M.F. (2009). A mitochondrial genome phylogeny of the Neuropterida (lace-wings, alderflies and snakeflies) and their relationship to the other holometabolous insect orders. *Zoologica Scripta* **38**, 575-590.

Common, I. F. B. (1990). 'Moths of Australia'. (Melbourne University Press: Carlton South, Melbourne.)

Cooke, J. and Edwards, T. (2007). The behaviour of scribbly gum moth larvae *Ogmograptis* sp. Meyrick (Lepidoptera: Bucculatricidae) in the Australian Capital Territory. *Australian Journal of Entomology* **46**, 269-275.

Davis, D.R., Landry, B. and Roque-Albelo, L. (2002). Two new Neotropical species of *Bucculatrix* leaf miners (Lepidoptera: Bucculatricidae) reared from *Cordia* (Boraginaceae). *Revue Suisse de Zoologie* **109**, 277-294).

Davis, D. R. and Robinson, G. S. (1999). The Tineoidea and Gracillarioidea. In 'Evolution, Systematics, and Biogeography'. Vol. 1. Handbook of Zoology: Lepidoptera, Moths and Butterflies'. (Ed. N. P. Kristensen.) pp 91-117 (Walter de Gruyter: Berlin and New York.)

Davis, D. R. and Stonis, J. R. (2007). A Revision of the New World Plant-Mining Moths of the Family Opostegidae (Lepidoptera: Nepticuloidea). *Smithsonian Contributions to Zoology* no. 625, i-v, 1-212.

Dugdale, J. S. (1988). Lepidoptera – annotated catalogue, and keys to family group taxa. *Fauna of New Zealand* no. 14, 1-262.

Edwards, E. D. (1996). Plutellidae. In 'Checklist of the Lepidoptera of Australia. Vol. 4. Monographs on Australian Lepidoptera'. (Eds E. S. Nielsen, E. D. Edwards and T. V. Rangsi.) p. 53. (CSIRO Publishing: Collingwood.)

Flannery, T. (2010). Here on Earth. 'An Argument for Hope'. (The Text Publishing Company: Melbourne.)

Folmer, O., Black, M., Hoeh, W., Lutz, R. and Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology & Biotechnology* **3**, 294-299.

Gandolfo, M. A., Hermsen, E. J., Zamaloa, M. C., Nixon, K. C., González, C. C., Wilf, P., Cúneo, N. R. and Johnson, K. R. (2011). Oldest known *Eucalyptus* macrofossils are from South America. PLoS ONE 6(6): e21084. doi:10.1371/journal.pone.0021084

Gentry, A. H. (1982). Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic functions, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* **69**(3), 557-593.

Gibbs, M. (1918). 'Snugglepot and Cuddlepie, their adventures wonderful'. (Angus & Robertson: Sydney.)

Grossenbacher, J. G. (1910). Medullary Spots: a Contribution to the Life History of Some Cambium Miners. *New York Agricultural Experiment Station Technical Bulletin* **15**, 49-65.

Heppner, J. B. (1987). Douglasiidae, p. 408-409. *In*: Stehr, F. W. (ed.). Immature Insects. x + 491 pp. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Hering, E. M. (1951). 'Biology of the Leaf Miners'. (Dr W. Junk: The Hague, Netherlands.)

Hering, E. M. (1962). Neue Blattminen-Studien II. *Deutsche Entomologische Zeitschrift*, N. F. **9**, 30-65.

Huelsenbeck, J.P. and Ronquist, F.R. (2001). MrBayes: Bayesian inference of phylogeny. *Biometrics* **17**, 754-755.

Kumata, T. (1984). Cambium Miners Making Pith Flecks in Broad-Leaved Trees – A Review of Cambium Miners (in Japan). *Hoppô Ringyô [Northern Forestry]* **36**(5), 6-15.

Kuroko, H. (1964). Revisional studies of the family Lyonetiidae of Japan (Lepidoptera). *Esakia* no. 4, 1-61, pls 1-17.

Kyrki, J. (1984). *Roeslerstammia* Zeller assigned to Amphitheridae, with notes on the nomenclature and systematics of the family (Lepidoptera). *Entomologica scandinavica* **14**, 321-329.

Ladiges, P. Y., Udovicic, F., and Nelson, G. (2003). Autralian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. *Journal of Biogeography* **30**, 989-998.

Ladiges, P. Y., Bayly, M. J., and Nelson, G. J. (2010). East-west continental vicariance in *Eucalyptus* subgenus *Eucalyptus*. In 'Beyond Cladistics. The Branching of a Paradigm'. (Eds D. M. Williams and S. Knapp.) pp. 267-302. (University of California Press: Berkeley and Los Angeles.)

Mackay, M. R. (1972). Larval sketches of some microlepidoptera, chiefly North American. *Memoirs of the Entomological Society of Canada* **88**, 5-83.

Maddison, W. and Maddison, D. (2003). MacClade ver 4.06. Sunderland: Sinauer Associates.

Meyrick, E. (1921). Descriptions of South African Micro-Lepidoptera. *Annals of the Transvaal Museum* **8**, 49-148.

Meyrick, E. (1922). Exotic Microlepidoptera 2(16), 481-512.

Meyrick, E. (1935). Exotic Microlepidoptera 4(2Q), 593-608.

Moore, K. M. (1972). Observations on some Australian forest insects. *Australian Zoologist* **17**(1), 30-39.

Moriuti, S. (1978). Amphitheridae (Lepidoptera): Four new species from Asia, *Telethera blepharacma* Meyrick new to Japan and Formosa, and *Sphenograptis* Meyrick transferred to the family. *Bulletin of University of Osaka Prefecture*, series B, **30**, 1-17.

Mosher, E. (1969). 'Lepidoptera Pupae. Five collected works on the pupae of North American Lepidoptera'. (Entomological Reprint Specialists: East Lansing.)

Mutanen, M., Wahlberg, N. and Kaila, L. (2010). Comprehensive gene and taxon coverage elucidates radiation patterns in moths and butterflies. *Proceedings of the Royal Society Biological Sciences Series B* **277**(1695):2839-2848.

Nielsen, E. S. (1996a). Lyonetiidae. In 'Checklist of the Lepidoptera of Australia. Vol. 4. Monographs on Australian Lepidoptera'. (Eds E. S. Nielsen, E. D. Edwards and T. V. Rangsi.) pp. 57-58. (CSIRO Publishing: Collingwood.)

Nielsen, E. S. (1996b). Bucculatricidae. In 'Checklist of the Lepidoptera of Australia. Vol. 4. Monographs on Australian Lepidoptera'. (Eds E. S. Nielsen, E. D. Edwards and T. V. Rangsi.) p.45. (CSIRO Publishing: Collingwood.)

Nielsen, E. S. and Common, I. F. B. (1991). Lepidoptera (Moths and Butterflies). In 'The Insects of Australia. Vol. 2'. (Ed. CSIRO.) pp 817-915. (Melbourne University Press: Carlton, Victoria.)

Pfeil, B. E. and Henwood, M. J. (2004). Multivariate analysis of morphological variation in *Eucalyptus* series *Psathyroxyla* Blakely (Myrtaceae): taxonomic implications. *Telopea* **10**(3), 711-724.

Posada, D. and Crandall, K.A. (1998). ModelTest: Testing the best-fit model of nucleotide substitution. *Bioinformatics* **14**, 817-818.

Puplesis, R., Seksjaeva, S. and Puplesiene, J. (1992). *Bucculatrix formosa* sp. n., a remarkable species from the Kugitangtau Mountains (Central Asia) (Lepidoptera: Bucculatricidae). *Nota lepidoperologica* **15**, 41-46.

Rambaut A. and Drummond A.J. (2007). Tracer v1.4. http://beast.bio.ed.ac.uk/Tracer

Robinson, G. S. (1976). The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. *Entomologistst's Gazette* **27**, 127-132.

Seksjaeva, S. V. (1995). New intrageneric groups within the genus Bucculatrix (Lepidoptera, Bucculatricidae) designated on the basis of the morphology of the male genitalia. *Entomological Review* **74**, 111-119.

Scoble, M. J. and Scholtz, C. H. (1984). A new, gall-feeding moth (Lyonetiidae: Bucculatricinae) from South Africa with comments on larval habits and phylogenetic relationships. *Systematic Entomology* **9**, 83-94.

Swofford D.L. (2002). PAUP\* Phylogenetic Analysis using Parsimony (\*and Other Methods) Ver. 4. (Sinauer Associates: Sunderland.)

Turner, A. J. (1923). New Australian Micro-Lepidoptera. *Transactions of the Royal Society of South Australia* **47**, 165-194.

Turner, A. J. (1926). Studies in Australian Lepidoptera. *Transactions of the Royal Society of South Australia* **50**, 120-155.

Upton, M. S. (1997). 'A Rich and Diverse Fauna. The history of the Australian National Insect Collection 1926-1991'. (CSIRO Publishing: Collingwood.)

Whiting, M.F. (2002). Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. *Zoologica Scripta* **31**, 93-104.

Wright, J. (1955). Scribbly-Gum. In 'The Two Fires'. (Angus and Robertson: Sydney.)

Zborowski, P. and Edwards, T. (2007). 'A guide to Australian Moths'. (CSIRO Publishing: Collingwood.)

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 2 <sup>nd</sup> 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 zigzags; larva moults near point B				
Track B-C	First pass of doubled zigzags which don't cross each other; larva feeds on bark tissue				
Point C	First turning loop of track				
Track C-D	Return track of doubled zigzags, either closely parallel in separate track ( <i>O. scribula</i> ) or joining and enlarging initial track ( <i>O. rossii</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				

**Table 2. Data for DNA samples** 

I DDM-		anna sampics		a4a	En a a le verter e	I coality data collector
LEPNo	DNANo	genus	species	stage	Eucalyptus	Locality, date, collector
LEP001		Ogmograptis	racemosa	larva	ssp.rossii	Barlow property, Gunning, NSW
LEP002		Ogmograptis	racemosa	larva	racemosa	Royal National Park, Uloola Falls Track, 20.xi.2008, D. Lewis
LEP003		Bucculatrix	sp.	larva	Commersonia	Bot. Garden, ACT, em. Jan. 2009, M. Horak
LEP004		Ogmograptis	scribula	larva	pauciflora	Bull's Head, ACT, coll. 8.iii.2008, collectors
LEP005		Ogmograptis	maxdayi	adult	?	Warrandyte, Vic., 1-15 Nov. 2008, D. J. Hilton
LEP006	3008	Ogmograptis	scribula	adult	pauciflora	Bull's Head, ACT, coll. 12.ii.2009, em. 8.iii.2009, M. Horak, Y.
						N. Su & P. Macnicol
LEP007	3009	Ogmograptis	racemosa	adult	ssp.rossii	Barlow property, Gunning, NSW, em. 20.iv.2009, C. Barlow
LEP009	3011	Ogmograptis	racemosa	adult	racemosa	3 km E Wedderburn, NSW, 18.iv.2007, D. Britton
LEP010	3012	Ogmograptis	fraxinoides	adult	fraxinoides	Piper's Lookout, Brown Mt., NSW, pupa coll. 14.iii.2009, em
						5.iv.2009, M. Horak
LEP011	3013	Ogmograptis	scribula	adult	pauciflora	Tallaganda, NSW, 11.vi.2008, G. Cocking & E. Edwards
					present	
LEP012	3014	Tritymba	sp. many larvae	larva	ssp.rossii	Barlow property, Gunning, NSW, 31.vii.2009, C. & P. Barlow
LEP013	3015	Tritymba	sp. no comb	larva	ssp.rossii	Barlow property, Gunning, NSW, 31.vii.2009, C. & P. Barlow
LEP014	3016	Tritymba	sp. early track	larva	ssp.rossii	Barlow property, Gunning, NSW, 3.viii.2009, C. & P. Barlow
LEP015	3017	Tritymba	sp. no photo	larva	ssp.rossii	Barlow property, Gunning, NSW, 31.vii2009, C. & P. Barlow
		-				
LEP190	4017	Ogmograptis	fraxinoides	larva	fraxinoides	Piper's Lookout, Brown Mt., NSW, 8.ii.2010, M. Horak
LEP191	4018	Ogmograptis	fraxinoides	larva	fraxinoides	Piper's Lookout, Brown Mt., NSW, 8.ii.2010, M. Horak
LEP192	4019	Ogmograptis	fraxinoides	larva	fraxinoides	Piper's Lookout, Brown Mt., NSW, 8.ii.2010, M. Horak
LEP193	4020	Ogmograptis	fraxinoides	larva	fraxinoides	Piper's Lookout, Brown Mt., NSW, 8.ii.2010, M. Horak
LEP194	4021	Ogmograptis	fraxinoides	larva	pauciflora	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010 Horak et al.
LEP195	4022	Ogmograptis	fraxinoides	larva	pauciflora	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010 Horak et al.
LEP196	4023	Ogmograptis	scribula	larva	pauciflora	Kosciuszko NP, Waterfall Track, NSW, 7.ii.2010 Horak et al
LEP198	4025	Ogmograptis	scribula	larva	pauciflora	Bull's head, ACT, 10.ii.2010, M. Horak & Y. N. Su
LEP199	4026	Ogmograptis	scribula	larva	pauciflora	Bull's head, ACT, 10.ii.2010, M. Horak & Y. N. Su
LEP200	4027	Ogmograptis	scribula	larva	pauciflora	Bull's head, ACT, 10.ii.2010, M. Horak & Y. N. Su
LEP201	4028	Ogmograptis	scribula	larva	pauciflora	Bull's head, ACT, 10.ii.2010, M. Horak & Y. N. Su
LEP204	4031	Ogmograptis	barloworum	adult	?	Gilwell Pk., Melbourne, Vic., 30 Oct. 2009, A. Kallies, P.
						Marriott & D. Hilton
LEP207	4034	Tritymba	sp.	adult	ssp.rossii	8 km NE Nerriga, NSW, 6.Dec.2008, E.D.Edwards & A. Kallies
X1		Tritymba	Sp.	larva	ssp. rossii	Barlow property, Gunning, NSW, 30.viii.2008, C. & P. Barlow

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

section	series	subseries	species
Pseudophloius			*pilularis Smith
1			*
Aromatica	Radiatae		*elata Dehnhardt
	Radiatae		croajingolensis Johnson and Hill
	Radiatae		*willisii ssp. falciformis Newman,
			Ladiges & Whiffin
	Insulanae		*nitida Hooker
Capillulus	Limitares		deuaensis Boland & Gilmour
37.1.1			
Nebulosa			olsenii Johnson & Blaxell
Eucalyptus	Regnantes		*fastigiata Deane & Maiden
Bucatypius	Strictae	Irregulares	*stricta Sieber & Springer
	Strictae	Irregulares	*triflora Maiden
	Strictae	Irregulares	*dendromorpha Johnson &
		11.100	Blaxell
	Strictae	Irregulares	*burgessiana Johnson & Hill
	Strictae	Regulares	cunninghamii Sweet
	Contiguae		kybeanensis Maiden & Cambage
Longitudinales			*stellulata Sieber ex DC.
Cineraceae	Fraxinales		*fraxinoides Deane & Maiden
	Fraxinales		*delegatensis Baker
	Pauciflorae		*pauciflora Sieber & Springel
	Psathyroxyla	Considenianae	multicaulis Blakely
	Psathyroxyla	Considenianae	andrewsii Maiden
	Psathyroxyla	Considenianae	?remota Blakely
	Psathyroxyla	Haemastomae	*haemastoma Smith
	Psathyroxyla	Haemastomae	*racemosa ssp. racemosa
			Cavanilles
	Psathyroxyla	Haemastomae	*racemosa ssp. rossii (Baker &
			Smith) Pfeil & Henwood
	Stenostomae		stenostoma Johnson & Blaxell
	Piperitales		*piperita Smith

## **Figure Captions**

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.

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).

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, Pupae 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).

Figs 22-29. 22, Cross section of outer bark of *Eucalyptus racemosa* ssp. *rossii* with callus-filled track of *Ogmograptis 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 *Ogmograptis* track (pg: phellem, cork cambium (arrows); pm: phellem; pd: phelloderm ). 24, Mouthparts of probably 3rd 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 3rd instar of *O. racemosa*, in ventral view. 27,

Probably 3rd 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 doubled track section of *O. racemosa*, bordered by normal phellem cells (black arrow). Scales = 0.05 mm (Fig. 24); 0.1 mm (Fig. 25, 26)

Figs 30-34. Larva and pupa of *Ogmograptis* spp. 30, Diagram of chaetotaxy of last instar larva of *O. racemosa*. 31, Head capsule of last instar larva of *O. racemosa*. 32, Pupa of *O. racemosa*, ventral view. 33, 34, Frontal process of pupa of *O. racemosa* male (33) and *O. fraxinoides* female (34), lateral view.

Fig. 35. Wing venation of *Ogmograptis racemosa*, male.

Figs 36-42. Last instar larva of *Ogmograptis scribula*, Sawpit Creek, Koszciusko NP, NSW. 36, Head, frontal. 37, Spinneret. 38, Last abdominal segment, posterior view, note square margin of anal shield. 39, Prothoracic tarsus with modified slender claw (basal part obliterated by undetermined fluid) and two normal distal setae. 40, Proleg with short row of crochets on inner side. 41, Mesothoracic tarsus with modified distal setae and normal claw. 42, Enlarged detail of modified, flattened distal seta. Scales = 0.1 mm (Fig. 36); 0.01 mm (Figs 37-42).

Figs 43-47. Last instar larva of *Ogmograptis fraxinoides*, Brown Mt., NSW. 43, Mouth parts, frontal view. 44, Mesothoracic leg with modified distal setae and normal claw. 45, Enlarged detail of mesothoracic tarsus with cone-shaped modified distal setae. 46, Last abdominal segment, posterior view, note square margin of anal shield. 47, Enlarged detail of anal prolegs, not absence of crochets. Scales = 0.1 mm (Figs 43, 46); 0.02mm (Figs 44, 47); 0.01 mm (Fig. 45).

Figs 48-53. Last instar larva of *Ogmograptis racemosa*, nr Gunning, NSW. 48, Head, lateral. 49, Enlarged detail of stemmata region (arrow indicating position of reduced 6<sup>th</sup> stemma). 50, Last abdominal segment, lateral view. 51, Last abdominal segment, posterior view, note rounded margin of anal shield. 52, Mesothoracic tarsus with modified distal setae and normal claw. 53, Enlarged detail of modified, flattened

distal seta. Scales = 0.1 mm (Figs 48, 51); 0.02 mm (Fig. 49); 0.05 mm (Fig. 50); 0.1 mm (Fig. 51); 0.01 mm (Figs 52, 53).

Figs 54-56. Internal skeleton in last abdominal segment of larva of *Ogmograptis* racemosa (54, 55) and *Bucculatrix* sp. (56). 54, Dorsal view, last instar. 55, Lateral view, penultimate instar. 56, Lateral view, penultimate instar.

Figs 57-60. Head of *Ogmograptis* spp., male. 57, 58, *O. fraxinoides*. 59, 60, *O. maxdayi*.

Figs 61-68. Adults of the *Ogmograptis scribula* group. 61, 62, *O. scribula*, male, Bull's Head, ACT (61), female, Sawpit Creek, Kosciuszko NP, NSW (62). 63, 64, *O. fraxinoides*, holotype male (63), paratype female (64). 65, 66, *O. racemosa*, holotype male (65), female paratype, nr Gunning, NSW (66). 67, 68, *O. pilularis*, holotype male (67), paratype female (68). Scale = 2 mm.

Figs 69-74. Adults of the *Ogmograptis maxdayi* group. 69, 70, *O. maxdayi*, paratype male (69), paratype female (70). 71, 72, *O. barloworum*, holotype male (71), paratype male (72). 73, 74, *O. paucidentatus*, paratype male (73), paratype female (rubbed specimen) (74). Scale = 2 mm.

Figs 75-82. Adults of the *Ogmograptis maxdayi* (75-77) and *O. triradiata* (78-82) groups. 75, *O. rodens*, holotype male. 76, *O. bignathifer*, holotype male. 77, *O. inornatus*, holotype male. 78, *O. triradiata*, holotype male. 79, *O. centrospila*, lectotype male. 80, 81, *O. bipunctatus*, holotype male (80), paratype female (81). 82, *O. pulcher*, holotype male. Scales = 2 mm; Figs 75-77 resp. Figs 78-82 same magnification.

Figs 83-88. Male genitalia of the *Ogmograptis scribula* group. 83-85, *O. scribula*; Lee's Spring, ACT, ANIC GS 14839 (83 genitalia, 84), H57 (83 aedeagus, 85). 86-88, *O. fraxinoides*; holotype, ANIC GS 14863 (86, 88), paratype ANIC GS 14861 (87).

Figs 89-94. Male genitalia of the *Ogmograptis scribula* group. 89-91, *O. racemosa*; paratype, nr Gunning, NSW, ANIC GS 14780 (89, 90); Wilton, NSW, ANIC GS 14771 (91). 92-94, *O. pilularis*; holotype (92, 93), paratype, ANIC GS14772 (94).

Figs 95-100. Male genitalia of the *Ogmograptis maxdayi* group. 95-97, *O. maxdayi*; holotype (95, 96), paratype, ANIC GS 14790 (97). 98-100, *O. barloworum*; paratype, GS 19331 (98, 99), holotype (100).

Figs 101-106. Male genitalia of the *Ogmograptis maxdayi group*. 101-103, *O. paucidentatus*; holotype (101, 102), paratype ANIC GS 19335 (103). 104-106, *O. rodens*; holotype (104, 105), paratype ANIC GS 14753 (106).

Figs 107-112. Male genitalia of the *Ogmograptis maxdayi* group. 107-109, *O. bignathifer*, holotype. 110-112, *O. inornatus*; holotype (110, 111), paratype ANIC GP 14869 (112).

Figs 113-118. Male genitalia of the *Ogmograptis triradiata* group. 113, 114, *O. triradiata*, lectotype. 115, 116, *O. bipunctatus*, holotype. 117, 118, *O. pulcher*, holotype.

Figs 119-124. Female genitalia of the *Ogmograptis scribula* group. 119-121, *O. scribula*, Lee's Spring, ACT, ANIC GS 14791 (119, 120), ANIC GS 14776 (121). 122-124, *O. fraxinoides*, paratypes, ANIC GS 14862 (122), ANIC GS 14838 (123, 124).

Figs 125-129. Female genitalia of the *Ogmograptis scribula group*. 125, 126, *O. racemosa*; paratype, Botanical Garden, ACT, ANIC GS 14784; paratype, nr Gunning, NSW, ACT GS 14773 (126). 127-129, *O. pilularis*, paratypes, ANIC GS 14840 (127), ANIC GS 14752 (128).

Figs 130-132. Female genitalia of the *Ogmograptis maxdayi* (130, 131) and *triradiata* (132) groups. 130, *O. maxdayi*, paratype, ANIC GS 19328. 131, *O. barloworum*, Gembrook, Vic. 132, *O. bipunctatus*, paratype, ANIC GP 14786.

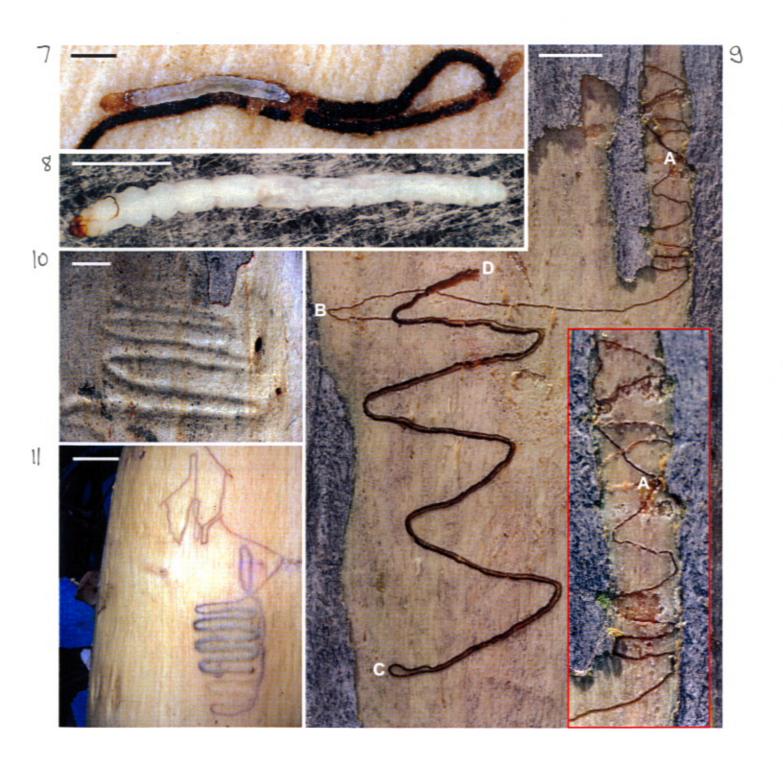
Fig. 133. Molecular phylogeny based on *cox1* and *S18*.

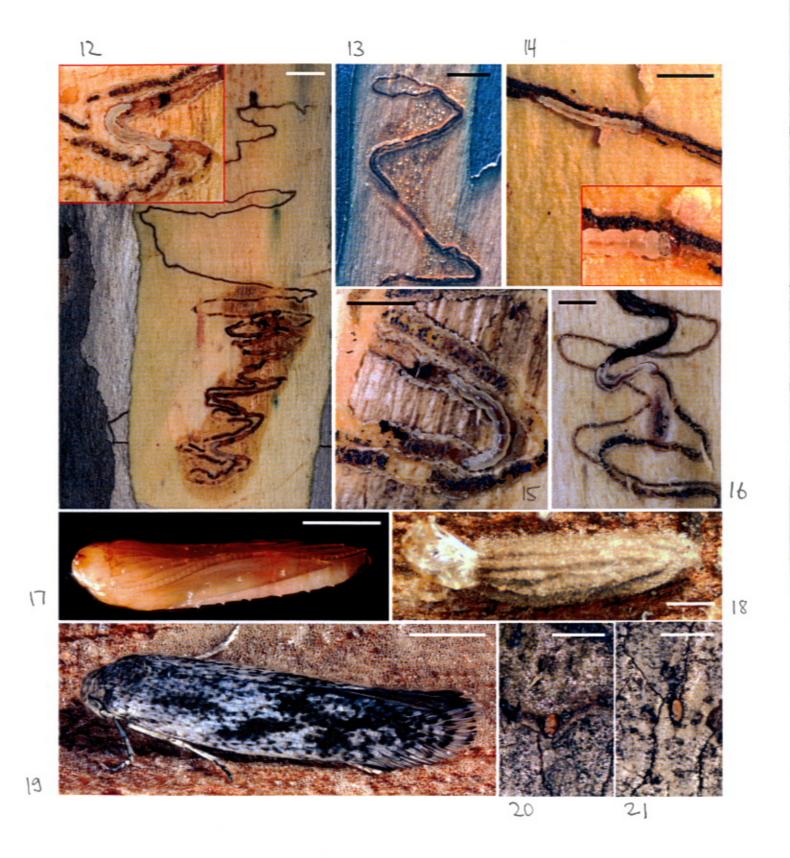
Table 1. Generalised description of tracks of *Ogmograptis* larvae of the *scribula* group (bark scribbles). The track descriptions apply to all the species except where noted for a specific species. See Figs 2, 4, 5, 9.

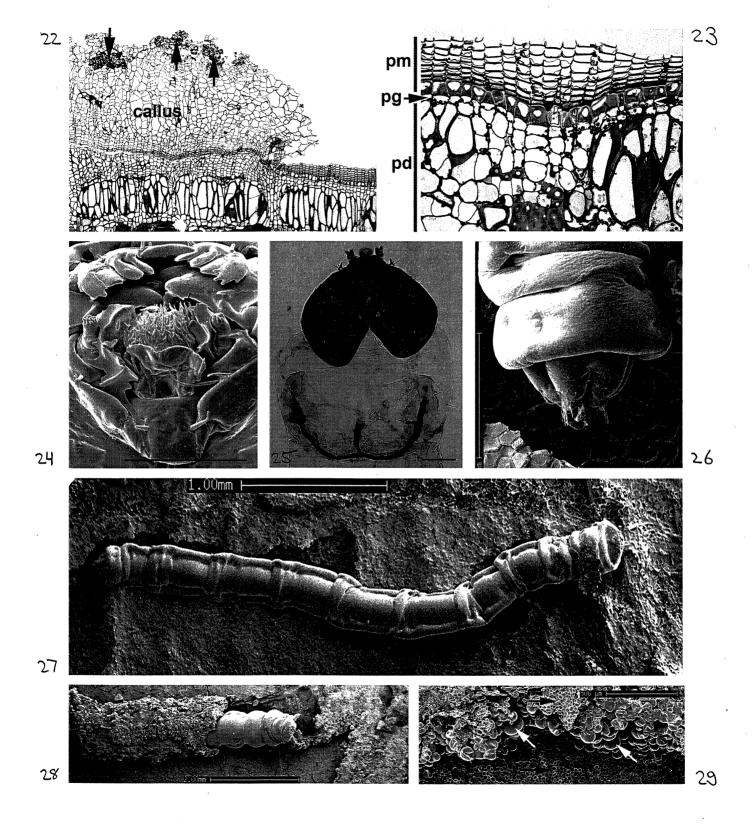
Table 2. Data for DNA samples.

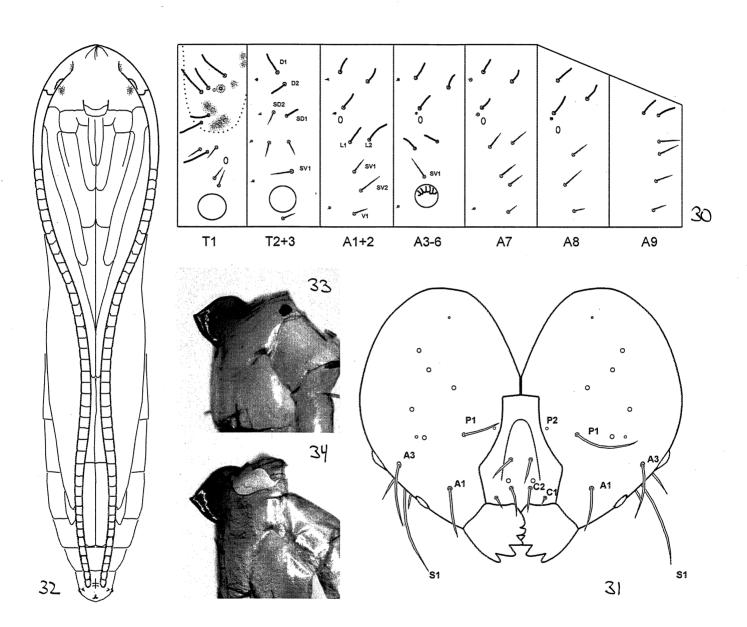
Table 3. Species of subgenus *Eucalyptus* of which scribbles have been recorded (following system of Brooker 2000)

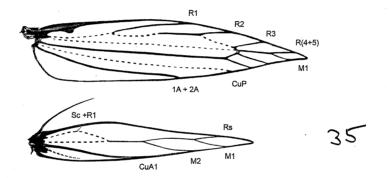


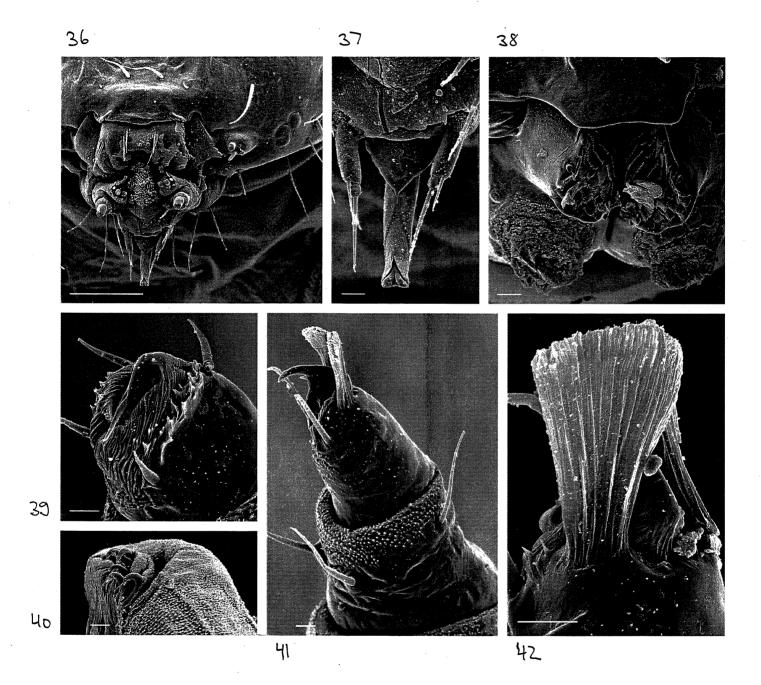


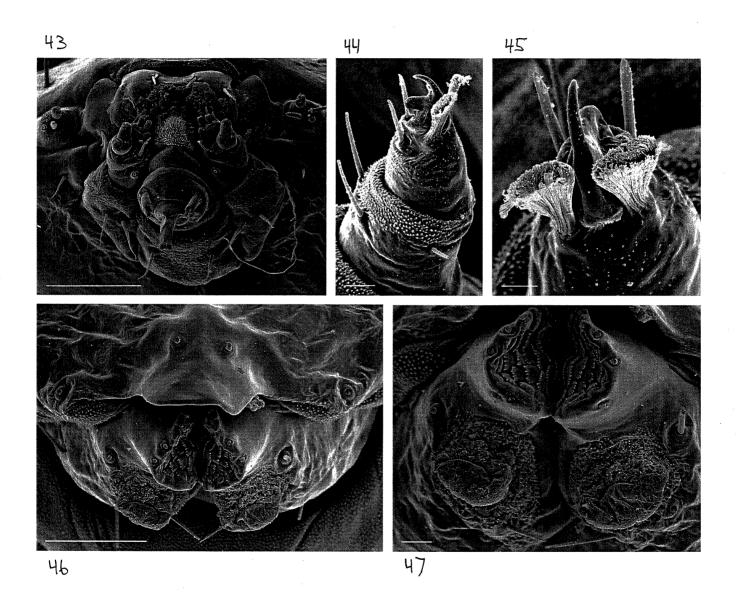


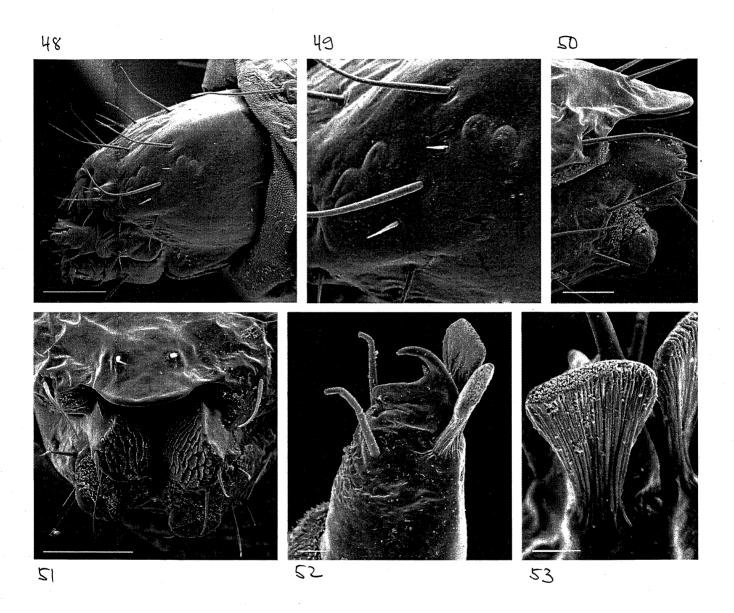


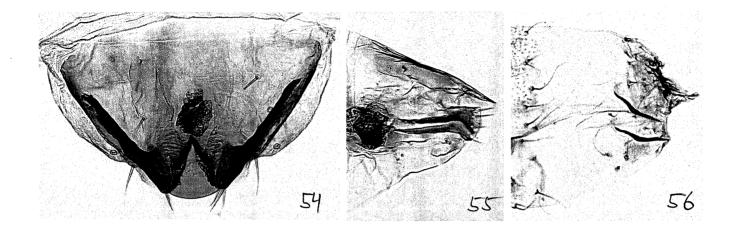


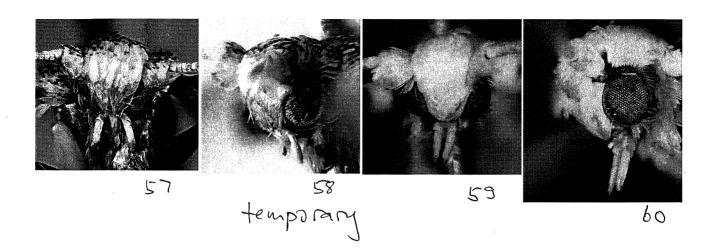


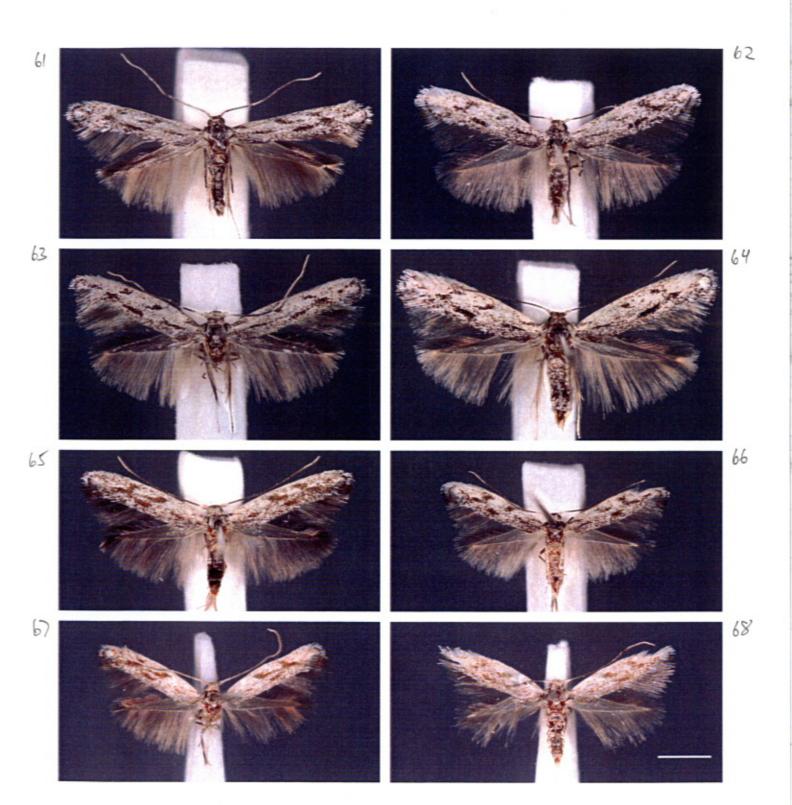


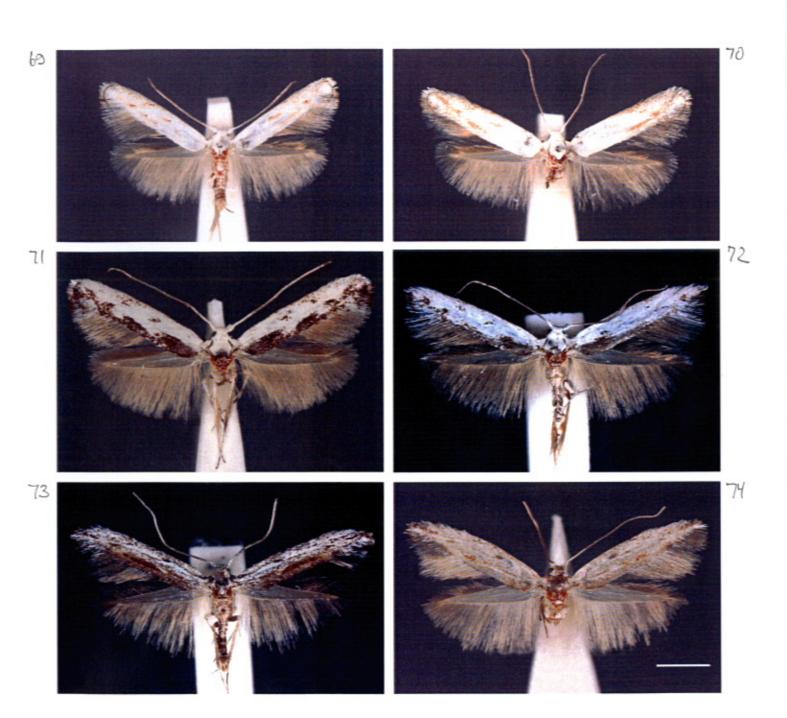


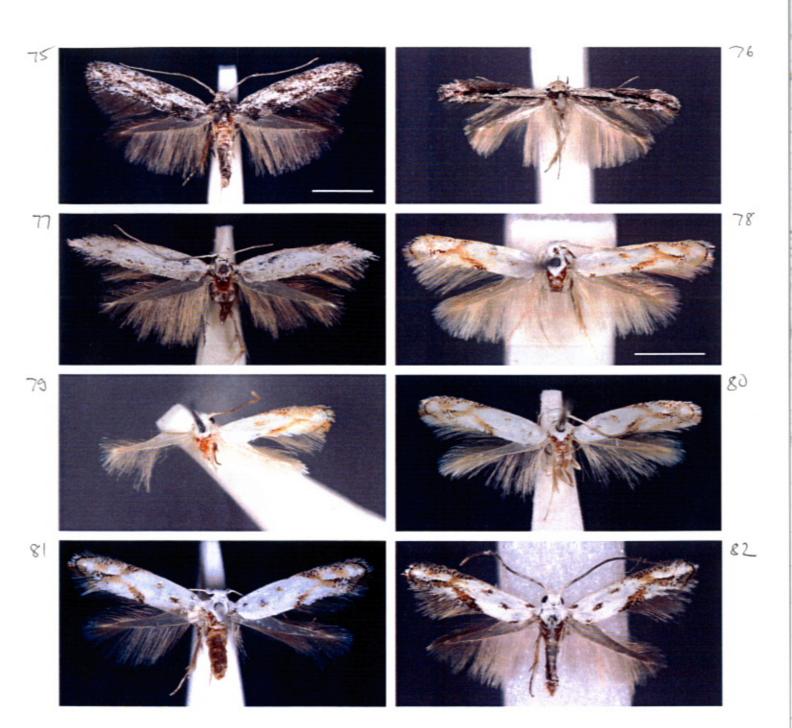


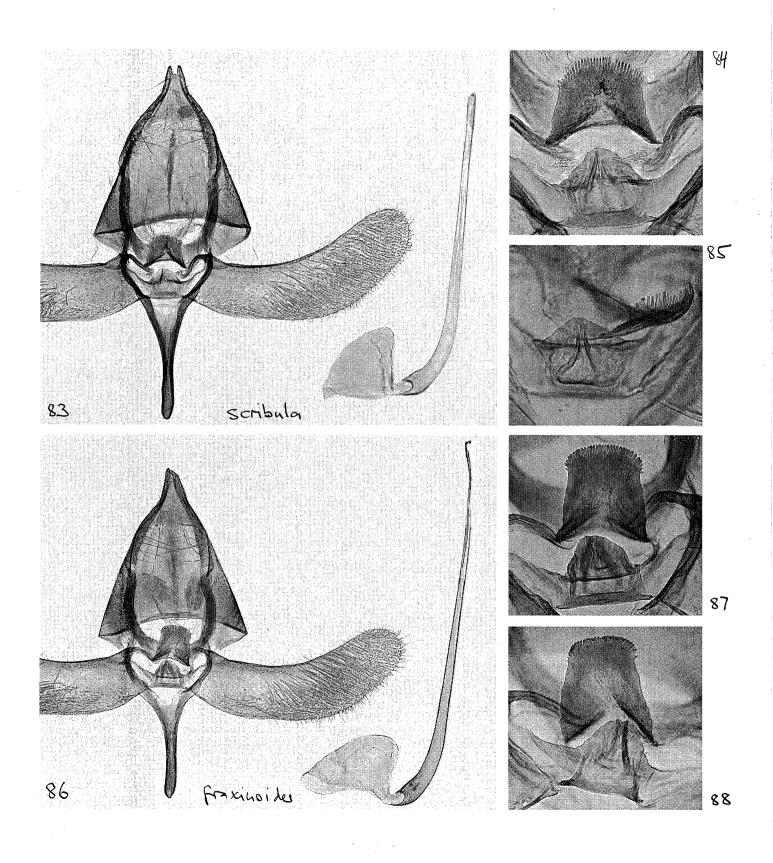


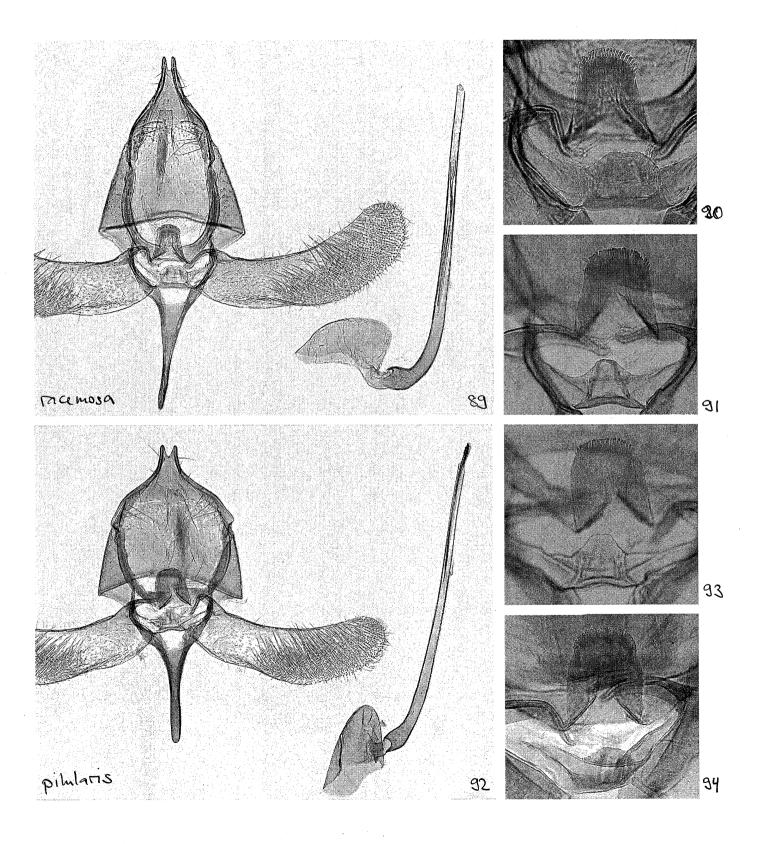


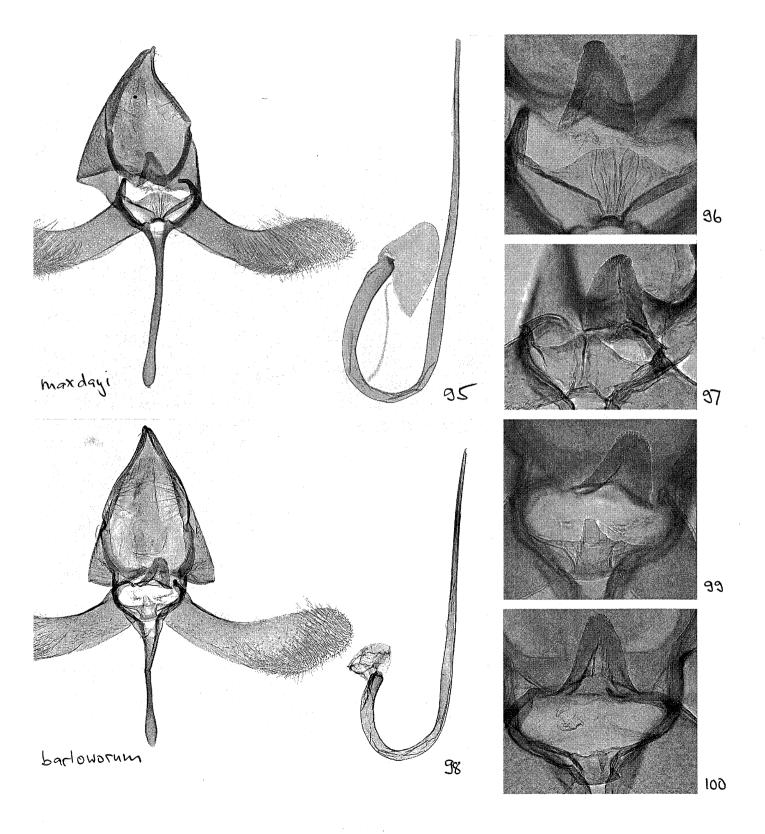


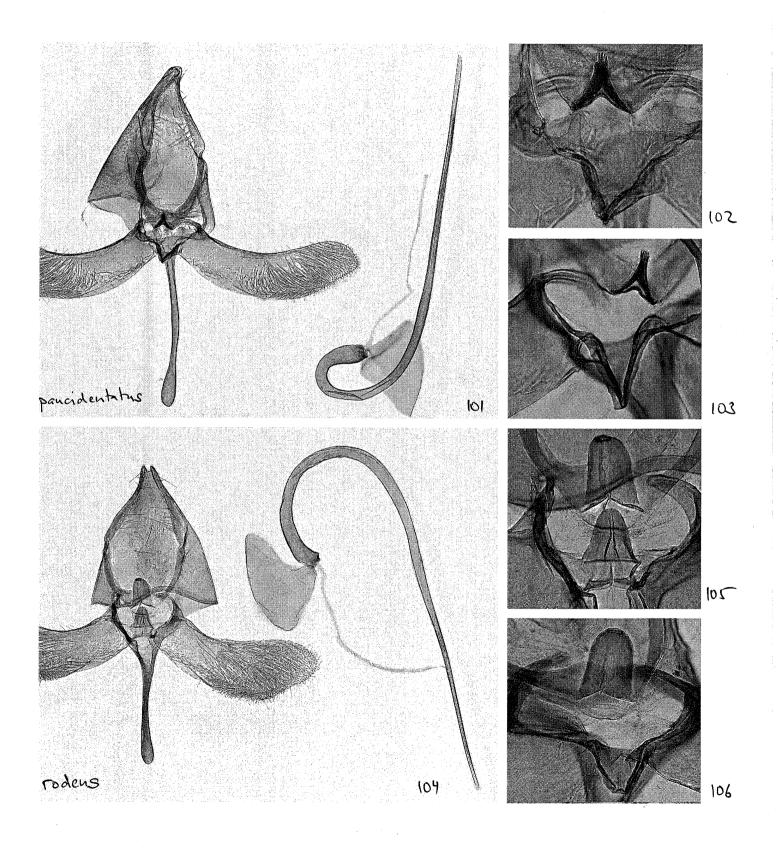


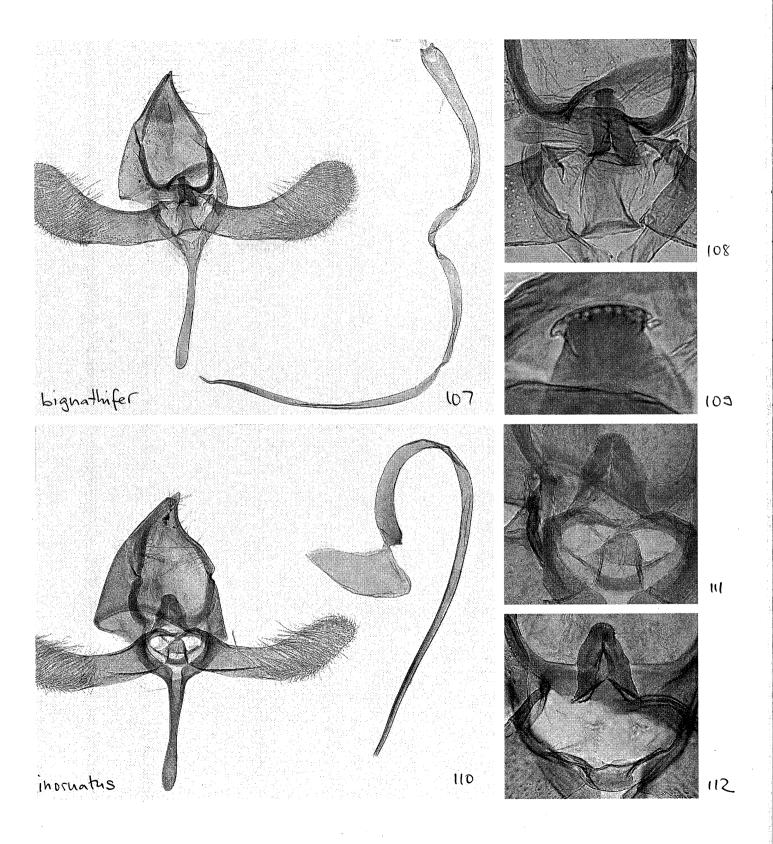


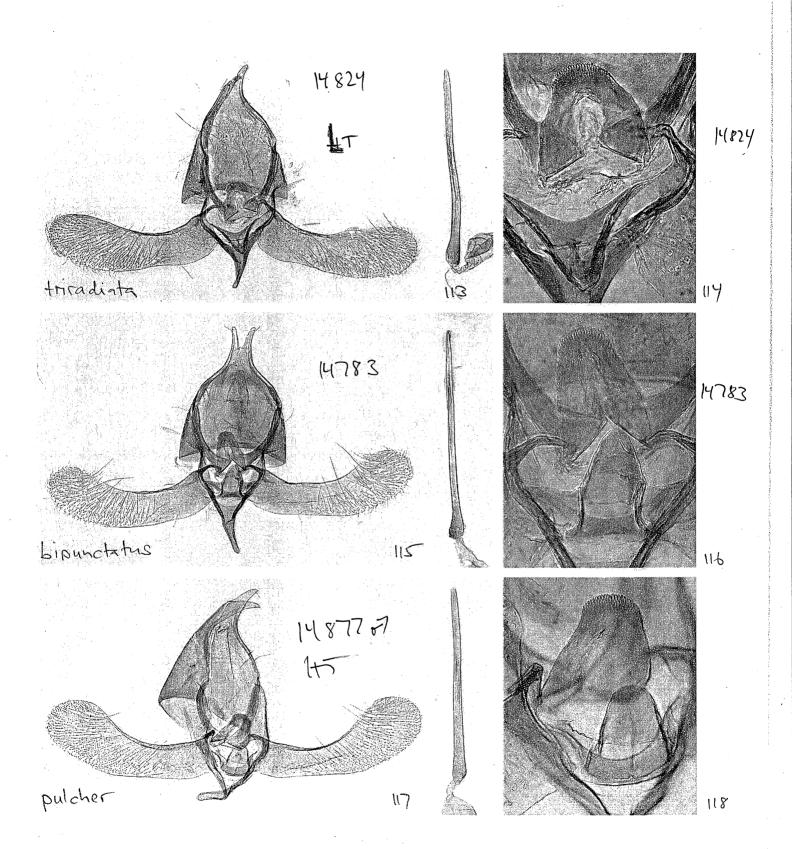


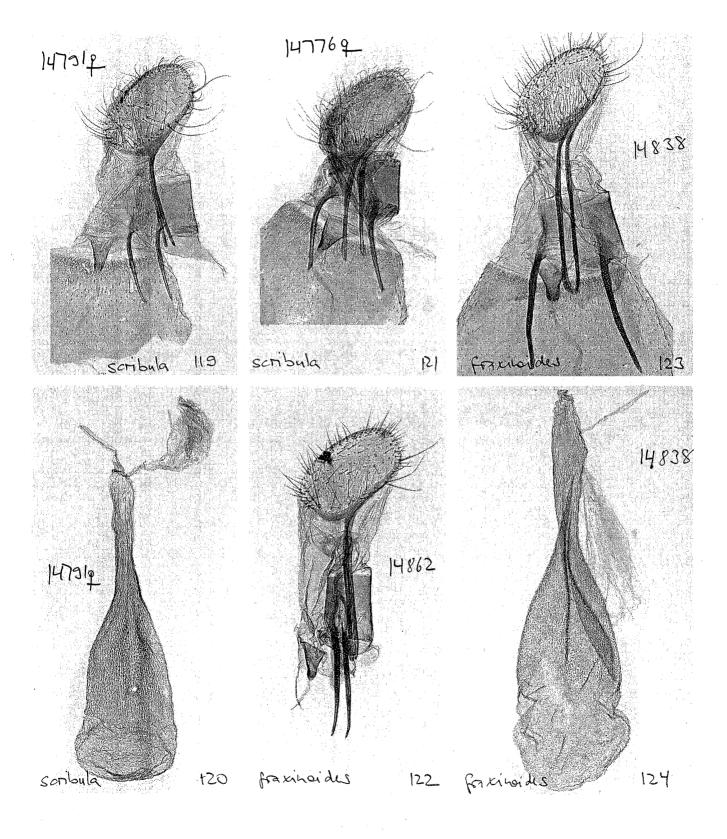


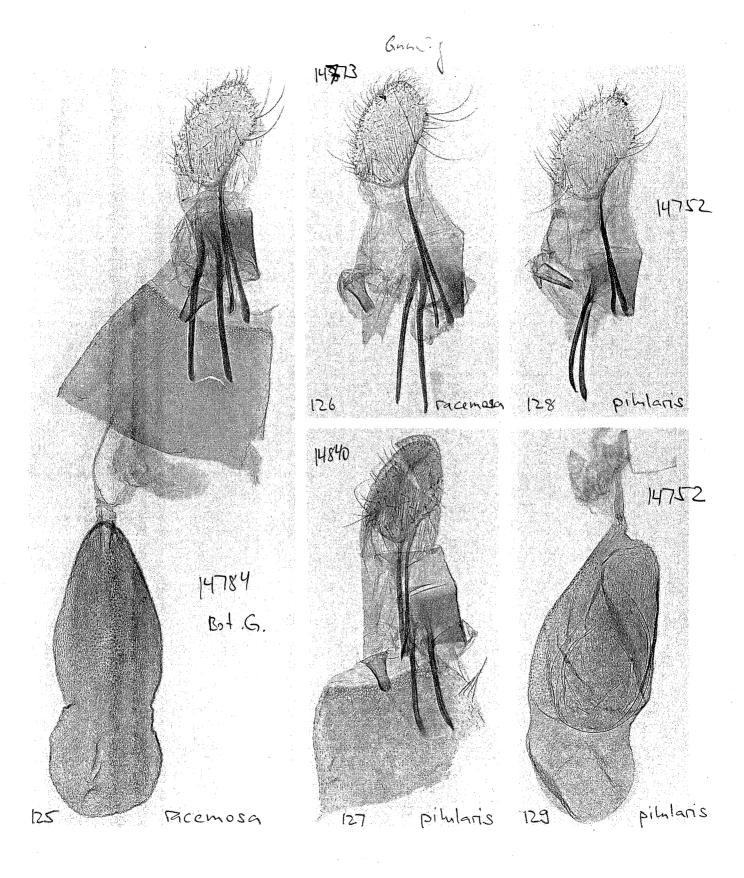


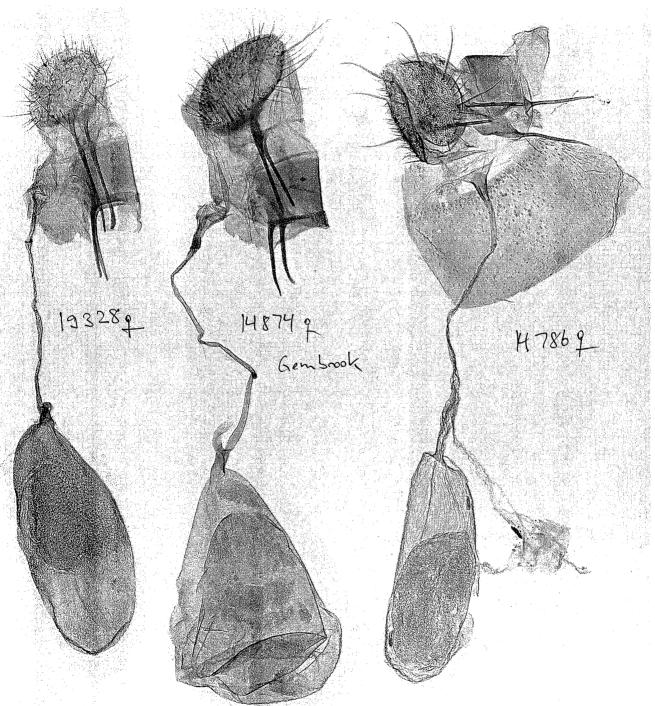












130 maxdayi

131 Barlowopum

132 bipunctatus

