



# Systematic revision of the *Ogyris idmo* (Hewitson, 1862) species group (Lepidoptera: Lycaenidae): implications for the conservation management of Australia's most threatened butterflies

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## ABSTRACT

Lycaenid butterflies of the *Ogyris idmo* species group are endemic to Australia and obligatorily associated with *Camponotus* ants. Several species are threatened with extinction, but there are considerable uncertainties with the present classification. Here, the taxonomy of the species group is revised based on molecular and morphological data. Mitochondrial sequence data were obtained from GenBank for *Ogyris* Angas, 1847, from cytochrome oxidase I (*COI*) and cytochrome *b* (*cytb*) (total of 1203 bp), and a phylogeny of the genus was reconstructed using Maximum Likelihood methods. Based on these molecular data, adult morphology and other evidence, the following eight taxa are recognised in this species group: *Ogyris otanes* (C. & R. Felder, 1865), *Ogyris arcana* M.R. Williams & Hay, 2001 **stat. rev.**, *Ogyris arcana arcana* M.R. Williams & Hay, 2001 **comb. nov.**, *Ogyris arcana sublustris* M.R. Williams & Hay, 2001 **comb. nov.**, *Ogyris halmaturia* (Tepper, 1890), *Ogyris halmaturia halmaturia* (Tepper, 1890), *Ogyris halmaturia waterhouseri* (Bethune-Baker, 1905) **stat. rev.**, *Ogyris idmo* (Hewitson, 1862), *Ogyris subterrestris* Field, 1999 and *Ogyris petrina* Field, 1999 **stat. rev.** The female of *Ogyris halmaturia halmaturia* is described for the first time. Phylogenetic relationships among the six species are as follows: (*O. otanes* + *O. arcana*) + (*O. halmaturia* + (*O. idmo* + (*O. subterrestris* + *O. petrina*))). The life history switch from phytophagy (*O. otanes* and *O. arcana*) to entomophagy (suspected myrmecophagy) within this species group has led to diversification of four species, a most unusual evolutionary pattern within the Lycaenidae globally. The taxonomic changes proposed herein affect some of the most threatened Australian butterflies and their conservation status is discussed.

**ZooBank:** [urn:lsid:zoobank.org:pub:B9A6F558-DD47-47DF-AC9C-A71270B6EE09](https://zoobank.org/pub/B9A6F558-DD47-47DF-AC9C-A71270B6EE09)

**Keywords:** *Camponotus*, conservation status, critically endangered, endangered, entomophagy, Loranthaceae, myrmecophagy, Santalaceae, systematics, Theclinae, threatened species, vulnerable.

## Introduction

The genus *Ogyris* Angas, 1847 is a diverse thecline genus in the tribe Ogyrini endemic to Australia and New Guinea, with several distinct species groups defined on the basis of ecological or structural relationships (Braby and Müller 2022). The *Ogyris idmo* (Hewitson, 1862) species group is currently understood to include four morphologically similar species, all endemic to southern and south-western Australia. Although members of all other *Ogyris* species groups are phytophagous, with larvae specialising on aerial-stem mistletoes in the family Loranthaceae (Braby 2000), most members of the *O. idmo* species group are entomophagous, with suspected predatory associations with *Camponotus terebrans* (Lowne, 1865) (Formicinae) ants (Pierce 1995; Field 1999; Braby and Douglas 2008; Grund 2010; Schmidt *et al.* 2014; Williams *et al.* 2020). The

exception to this is *Ogyris otares* (C. & R. Felder, 1865), which is ecologically unique in being the only species in which the larvae are associated with the foliage of root hemiparasites in the family Santalaceae (Burns and Angel 1952; Williams *et al.* 1992; Hart and Powell 1997; Williams and Hay 2001). Santalaceae is closely related to Loranthaceae and both families are classified in the order Santales (Nickrent *et al.* 2010).

The taxonomy and nomenclature of this group of butterflies have been contentious and highly dynamic for the duration of the investigation period. This uncertainty has been compounded by the fact that the species in this complex are generally rarely encountered without targeted efforts and that the species can be highly localised. As such, previous workers often had few (usually poor quality) specimens available for study and this has hindered species delimitation in this group of morphologically similar species.

At least five taxa in this species group are of conservation significance. At the state level, *Ogyris otares otares* and *O. halmaturia* (Tepper, 1890) are listed as Critically Endangered (CR), and *O. subterrestris subterrestris* Field, 1999 is listed as Endangered (EN) in Victoria under the *Flora and Fauna Guarantee Act* 1988 (Taylor *et al.* 2018). Additionally, *O. subterrestris petrina* is listed as CR in Western Australia under the *Biodiversity Conservation Act* 2016 and is also listed as CR under the federal *Environmental Protection and Biodiversity Conservation Act* (1999), and *O. halmaturia* is listed internationally as EN under the IUCN Red List Categories (Young *et al.* 2021). *Ogyris otares sublustris* M.R. Williams & Hay, 2001 is recognised as a taxon of national concern (Geyle *et al.* 2021) but is currently not listed under any legislation. Although notably less threatened, concerns for the protection of *O. idmo* populations have also been raised, with the species extirpated from almost a third of all known sites (Williams *et al.* 2020).

The purpose of this study is to re-examine the morphology of the *Ogyris idmo* species group and re-analyse the mtDNA sequence data presented by Schmidt *et al.* (2014) in this context. Taxonomic resolution of the *O. idmo* species group is imperative because all taxa are of conservation concern and many are threatened with extinction.

## Materials and methods

### Taxon sampling and molecular data

The mitochondrial DNA regions cytochrome oxidase *I* (*COI*) and cytochrome *b* (*cytb*) were obtained from NCBI GenBank (Supplementary Table S1) and included in the phylogenetic analysis. This dataset comprised 83 sequences covering seven in-group taxa and 12 outgroup taxa. The data were assembled, trimmed and aligned using Geneious (ver. 11.1.5, Biomatters, New Zealand, see <https://www.geneious.com>). Information on taxon sampling, PCR and sequencing is

discussed by Schmidt *et al.* (2014) and Beaver *et al.* (2023) who obtained these sequences prior to our study.

### Phylogenetic analysis

Phylogenetic relationships of *Ogyris* species were inferred by Maximum Likelihood methods. The *COI* and *cytb* alignments were concatenated in Geneious and the final alignment was a contig of 83 sequences with a total length of 1203 nucleotides (*COI* 626 bp, *cytb* 577 bp). Maximum Likelihood analysis was performed using IQ-TREE (ver. 2.2.0, see <https://www.iqtree.org/>; Minh *et al.* 2020). The best model was GTR + F + I + G4 that was chosen according to Bayesian Information Criterion using ModelFinder (see <https://www.iqtree.org/ModelFinder/>; Kalyaanamoorthy *et al.* 2017). Branch and clade support were assessed by ultrafast bootstrapping approximation with 1000 replicates (Hoang *et al.* 2018) and the Shimodaira–Hasegawa-like approximate likelihood-ratio test (SH-like aLRT) with 1000 replicates. Node values were considered robust if these were recovered with ultrafast bootstrap values of or above 95, and Shimodaira–Hasegawa-like approximate likelihood-ratio test values of or above 80. The resulting best tree was rooted with *Acrodipsas myrmecophila* as the outgroup and visualised using FigTree (ver. 1.4.4, see <https://tree.bio.ed.ac.uk/software/figtree/>) and Adobe Photoshop (ver. 2022, 24.0, Adobe Inc., San Jose, CA, USA).

### Morphological data

Internal morphology of the male genitalia was examined through dissection. The abdomen was removed and soaked in 10% KOH for 8–15 min at 85–90°C to dissolve internal musculature and viscera. Cleared sclerites were stained with Chlorazol black diluted with 30% ethanol. Completed dissections were fixed in 95% ethanol and 100% isopropanol. Dissections were stored within glycerol and assigned a unique identifier that was also attached to the pinned specimen. Stored dissections were either pinned next to the specimen or affixed to the same pin on which the set specimen was mounted. Dissections were imaged and measured using a Leica M205A microscope and stacked using Helicon Focus (ver. 5.3, see <https://helicon-focus.software.informer.com/5.3/>) with the dissection floating in gel as described by Su (2016).

The genitalia of male *Ogyris* spp. were studied and compared by dissecting specimens of each taxon as follows. *Ogyris otares otares*: 1♂ Genitalia No. EPB-169 – Kingscote, KI, SA, 21 JAN. 1952, F.E. Parsons, ANIC Database no. 31 020437 (ANIC); 1♂ Genitalia No. EPB-183 – Big Desert, V. 27 m. N. Yanac, 6 DEC. 1973. B. D.F. Crosby, ANIC Database no. 31-020454 (ANIC); *Ogyris otares arcana*: 1♂ Genitalia No. EPB-170 – Stirling Ranges, WA. 2 NOV 1988, R.W. Hay, ANIC Database no. 31 019933 (ANIC); *Ogyris otares sublustris*: 1♂ Genitalia No. EPB-171 – 2 km S of Leeman, WA. 16 OCT 1985, R.W. Hay, ANIC Database

no. 31 019976 (ANIC); *Ogyris subterrestris subterrestris*: 1♂ Genitalia No. EPB-185 – 13.5 km ENE of Waikerie, SA, 19 OCT. 2021, E.P. Beaver & E.F.M. Fisher (ANIC); *Ogyris subterrestris petrina*: 1♂ Genitalia No. EPB-184 – Lake Douglas, Kalgoorlie, WA, 28 SEP. 1988, J.W.C. d'Apice, ANIC database no. 31 034646 (ANIC); 1♀ Genitalia slide M1127 – Lake Douglas, 12 km SW of Kalgoorlie, WA, 1 FEB. 82, A.J. Graham, PARATYPE, ANIC Database no. 31 019585 (ANIC); 1♂ Genitalia slide M1132 – Lake Douglas, 12 km SW of Kalgoorlie, WA, 22 OCT 1985, A.J. Graham, PARATYPE, ANIC Database no. 31 019589 (ANIC); 1♂ Genitalia tube 208 – Lake Douglas, 12 km SW of Kalgoorlie, WA, 1 FEB. 82, A.J. Graham, PARATYPE, ANIC Database no. 31 019584 (ANIC); *Ogyris idmo*: 1♂ Genitalia No. MFB-029 – Port Denison, WA, 29 SEP. 2002, M.F. Braby (ANIC); 1♂ Genitalia No. MFB-157 – South Perth, WA, 10 DEC. 1901, H.M. Giles (ANIC); 1♂ Genitalia No. MFB-161 – Mundaring, WA, 26 NOV. 1985, R. Hay (ANIC). *Ogyris halmaturia*: 1♂ Genitalia No. MFB-158 – Flinders Chase NP [exact locational data withheld], Kangaroo Island, SA, NOV. 2014, R.V. Glatz & D.A. Young (DESS); 1♂ Genitalia No. MFB-159 – Flinders Chase NP [exact locational data withheld], Kangaroo Island, SA, NOV. 2014, R.V. Glatz & D.A. Young (DESS); 1♂ Genitalia No. MFB-162 – Flinders Chase NP [exact locational data withheld], Kangaroo Island, SA, NOV. 2015, R.V. Glatz & D.A. Young (DESS); 1♂ Genitalia No. MFB-028 – Ngarkat CP, 28 km N Keith, SA, 10 NOV. 2005, M. Moore (ANIC); 1♂ Genitalia No. MFB-160 – Ngarkat CP, 28 km N Keith, SA, 30 OCT. 2007, M.F. Braby & M. Moore (ANIC).

The following abbreviations refer to repositories at which material has been examined:

AMS, Australian Museum, Sydney.  
 ANIC, Australian National Insect Collection, Canberra.  
 DESS, D'Estrees Entomology and Science Services, Kangaroo Island, SA.  
 NHMUK, Natural History Museum, London (formerly BMNH).  
 NMV, Museums Victoria, Melbourne.  
 SAMA, South Australian Museum, Adelaide.  
 WAM, Western Australian Museum, Perth.

## Results

### Molecular phylogeny

The *Ogyris idmo* species group was resolved as a monophyletic lineage with strong support (BS = 95, SH aLRT = 86.8, BI = 0.99) (Fig. 1). A larger clade containing all descendants with a *Camponotus*-associated life history was also strongly supported (BS = 99, SH aLRT = 98.7, BI = 1.0) (Fig. 1). Based on the well-supported phylogeny, relationships of the six species we recognised in the *O. idmo* group were as follows: (*O. otales* + *O. arcana* stat. rev.) + (*O. halmaturia* + (*O. idmo* + (*O. subterrestris* + *O. petrina* stat.

rev.))). Topology and support values for the *O. idmo* species group were largely congruent with those in Schmidt *et al.* (2014). The notable differences were that in our study that included additional *Ogyris* taxa, the clade containing *O. idmo* + (*O. subterrestris* + *O. petrina* stat. rev.) had a bootstrap support of 99 compared with 95 in Schmidt *et al.* (2014) and the clade containing *O. otales* + *O. arcana* stat. rev. was resolved as a sister lineage to the remainder of the *O. idmo* species group with higher support (BS = 95) compared with only weak support (BS = 57) in Schmidt *et al.* (2014).

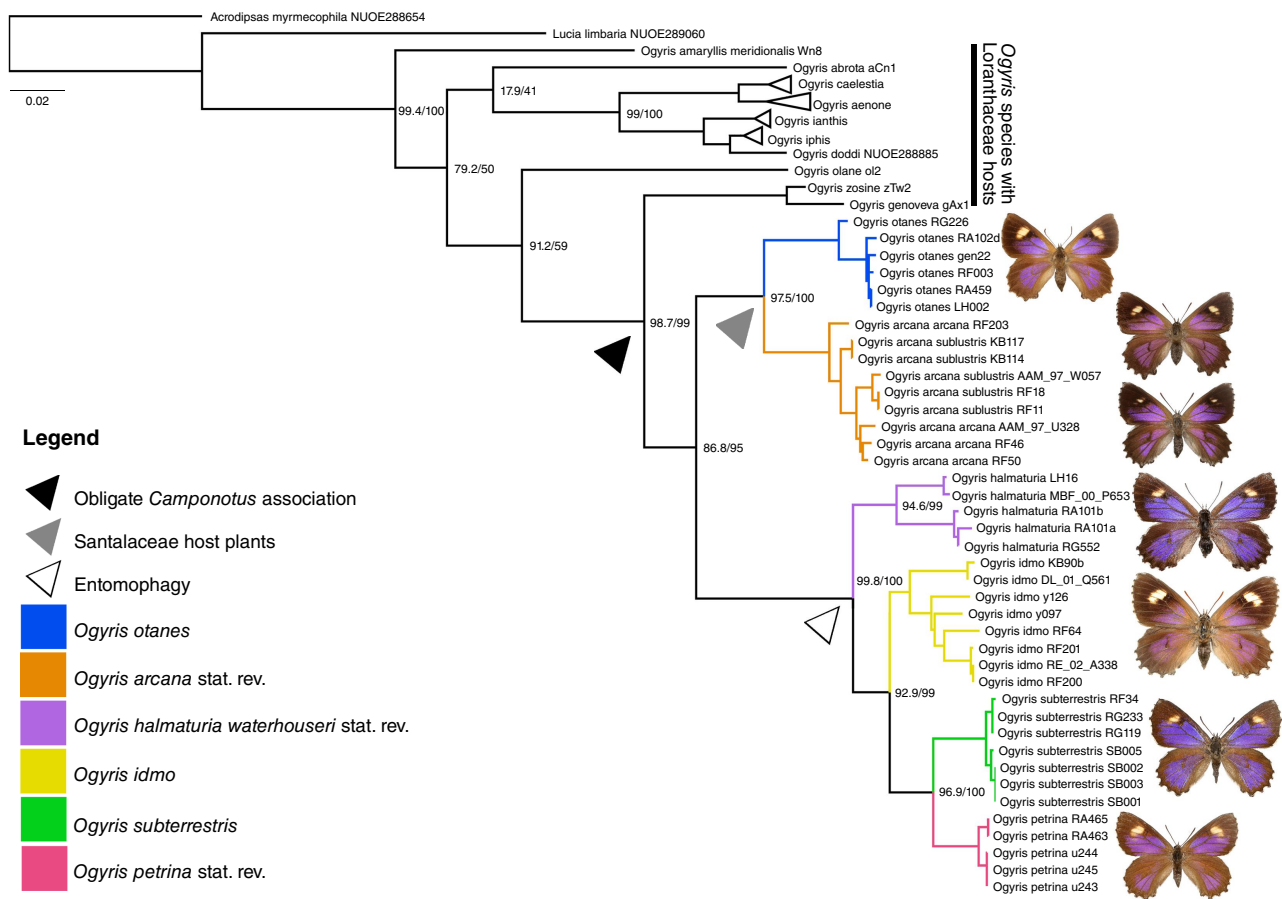
Uncorrected *p*-distances between the species of interest are summarised in Table 1 as median values. Variation of within-group sequence similarity was wide, ranging from 0–0.5% for outgroup *O. ianthis* to 0.319–4.31% for *O. halmaturia*.

## Taxonomy

The genus *Ogyris* was named twice with the same name based on different type species, first by Angas (1847) and later by Westwood in Doubleday and Westwood (1851). This confusing nomenclatural problem was clarified by Edwards (1996). The legacy of this synonym is apparent in the nomenclatural accounts for each taxon in this work, whereby most authors post-1996 refer to *Ogyris* Angas, 1847, but earlier authors were unaware of Angas (1847), and referred to the genus *Ogyris* Westwood, 1851 instead.

The *Ogyris idmo* species group (Fig. 1–8) as referred to by Schmidt *et al.* (2014) is informally defined by the combination of: (1) the presence of a cream forewing postmedian spot or patch in females; (2) ecological association with *Camponotus* ants; (3) behaviour of adults resting on the ground; (4) the hindwing termen relatively rounded with the tornus not produced or sometimes weakly produced in the male; and (5) all species have subterranean life histories. The larvae emerge from the ground to feed nocturnally in two species. The species pairs *O. genoveva* (Hewitson, 1853) and *O. zosine* (Hewitson, 1853) are closely related and sister to the *O. idmo* group but do not meet criteria 3 and 4. These species are canopy butterflies instead and the hindwing tornus is strongly produced.

On the basis of molecular and morphological evidence, we recognise eight taxa in the strictest sense (six species and two subspecies) in the *O. idmo* group as follows: *Ogyris otales* (C. & R. Felder, 1865), *Ogyris arcana* M.R. Williams & Hay, 2001 stat. rev., *Ogyris arcana arcana* M.R. Williams & Hay, 2001 comb. nov., *Ogyris arcana sublustris* M.R. Williams & Hay, 2001 comb. nov., *Ogyris halmaturia* (Tepper, 1890), *Ogyris halmaturia halmaturia* (Tepper, 1890), *Ogyris halmaturia waterhouseri* (Bethune-Baker, 1905) stat. rev., *Ogyris idmo* (Hewitson, 1862), *Ogyris subterrestris* Field, 1999 and *Ogyris petrina* Field, 1999 stat. rev.



**Fig. 1.** Maximum Likelihood phylogeny of *Ogyris* species inferred from mitochondrial *COI* and *cytb*, showing our revised taxonomy. Focal clades for six species comprising the *Ogyris idmo* group are highlighted in colour. The obligate host-ant *Camponotus* association is designated by a black arrowhead and ant entomophagy is designated with a white arrowhead. Node labels represent SH-aLRT values (left) and bootstrap support values (right). Twelve outgroup taxa are included and the tree is rooted with *Acrodipsas myrmecophila*. Scale bar represents substitutions per site.

**Table 1.** Uncorrected *p*-distances of *Ogyris idmo* species group based on a mitochondrial sequence alignment (fragment length = 1203 bp: *COI* 1–626, *cytb* 627–1203).

|                         | <i>O. otnes</i> | <i>O. arcana</i> | <i>O. halmaturia</i> | <i>O. idmo</i> | <i>O. subterrestris</i> | <i>O. petrina</i> |
|-------------------------|-----------------|------------------|----------------------|----------------|-------------------------|-------------------|
| <i>O. otnes</i>         |                 |                  |                      |                |                         |                   |
| <i>O. arcana</i>        | 5.07            |                  |                      |                |                         |                   |
| <i>O. halmaturia</i>    | 9.07            | 8.71             |                      |                |                         |                   |
| <i>O. idmo</i>          | 9.11            | 9.14             | 5.68                 |                |                         |                   |
| <i>O. subterrestris</i> | 9.39            | 9.23             | 6.55                 | 5.10           |                         |                   |
| <i>O. petrina</i>       | 10.09           | 9.56             | 6.87                 | 5.19           | 3.62                    |                   |

Subspecies of *O. arcana* are not displayed here as these were non-monophyletic (see Taxonomy section) and sequences of *O. halmaturia halmaturia* were not available for inclusion.

The *O. idmo* species group contains taxa that are morphologically very similar to each other. Careful corroboration of locality and biological information will assist in confirming identification. Females may be distinguished from males by the presence of a yellowish-cream postmedian spot or patch on the dorsal surface of the forewing.

Key to males

- 1 Dorsal forewing with narrow dark brown margin, 1.0–1.8 mm at apex.....*O. idmo*, Fig. 5a
- Dorsal forewing with broad dark brown margin, greater than 2 mm at apex.....2
- 2 Hindwing without prominent tornal projection.....3

## OGYRINI Waterhouse &amp; Lyell, 1914

## Ogyris Angas, 1847

Type species: *Ogyris amaryllis* Hewitson, 1862 by subsequent monotypy.

## Ogyris otanes (C. &amp; R. Felder, 1865)

(Fig. 1, 2, 3a–d, 6a–d.)

*Ogyris otanes* C. & R. Felder, 1865, p. 217, pl. XXVIII, fig. 1–3; Kirby (1871), p. 425; Miskin (1890), pp. 23–24; Lower (1893), p. 9; Tepper (1893), pp. 284–285; Anderson and Spry (1893), p. 101; Seitz (1926), p. 940, fig. 161g; Waterhouse (1903b), p. 249; Waterhouse (1903a), p. 29; Bethune-Baker (1905), pp. 275–277; Waterhouse and Lyell (1914), p. 121, pl. 18, fig. 404, 408, pl. 19, fig. 426, 427; Bethune-Baker (1916), p. 390; Tindale (1923), pp. 347–348, pl. XXIX, fig. 16–19; Waterhouse (1932), p. 184, pl. XXV, fig. 10; Waterhouse (1937), p. 120; Common (1964), p. 96, fig. 370–371; Burns and Rotherham (1969), p. 98; D’Abrera (1971), p. 320; McCubbin (1971), p. 84; Common and Waterhouse (1972), p. 342, pl. 34, fig. 10, 10A; Crosby (1972), pp. 6–7; Quick (1973), p. 15; Crosby (1974b), p. 58; Quick (1974), pp. 60–61; Crosby (1976), pp. 15–16; Fisher (1978), pp. 194–196, pl. 11, fig. 7–9; Common and Waterhouse (1981), pp. 480–481, pl. 41, fig. 10, 10A; Fisher (1985), p. 7; Hill and Michaelis (1988), pp. 14, 36; Fisher (1993), pp. 11–12; F. Douglas (unpubl. data, 1995), pp. 18–23, fig. 3; Grund (1996), p. 97; Grund (1999), pp. 47–48; Grund (2003), p. 71. [Genus *Ogyris* Westwood, 1851].

*Ogyris atanes* C. & R. Felder, 1865 – Burns and Angel (1952), pp. 183–186, pl. VII. [Misspelling of *O. otanes*].

*Ogyris otanes* (C. & R. Felder, 1865). – Edwards (1996), p. 250; Field (1997), p. 391; Hunt *et al.* (1998), p. 116; Eastwood and Fraser (1999), pp. 511; Field (1999), pp. 252; Edwards *et al.* (2001), pp. 258–259; Sands and New (2002), pp. 288–290; Pierce (2002), pp. 747; Young (2004), pp. 64–65, fig. 11; Orr and Kitching (2010), pp. 244–245; Braby *et al.* (2011), pp. 29–36. [Genus *Ogyris* Angas, 1847].

*Ogyris otanes* C. & R. Felder, 1865 ‘local form 1’ – Dunn and Dunn (1991), pp. 367, 458.

*Ogyris otanes* (C. & R. Felder, 1865) ‘eastern form’ – Braby (2000), pp. 396, 710–712, pl. 50, fig. 3.

*Ogyris otanes otanes* (C. & R. Felder, 1865). – Williams and Hay (2001), p. 55–56, 62; Braby (2004), pp. 242–243, 316; Braby and Douglas (2008), pp. 315–318, 326; Grund (2010), pp. 114–120; Braby (2010), pp. 14, 16, 35, 70; New (2011), pp. 101–103, 142, 148, 154, 163; Schmidt *et al.* (2014), pp. 473–484; Braby (2016), pp. 266–267, 350; Taylor *et al.* (2018), table S3; Sankowsky (2020), p. 315; Geyle *et al.* (2021), pp. 101, 103.

*Ogyris idmo* Hewitson, 1862 – Tepper (1893), pp. 284–285. [Incorrectly considered to be a senior synonym of *O. otanes*].

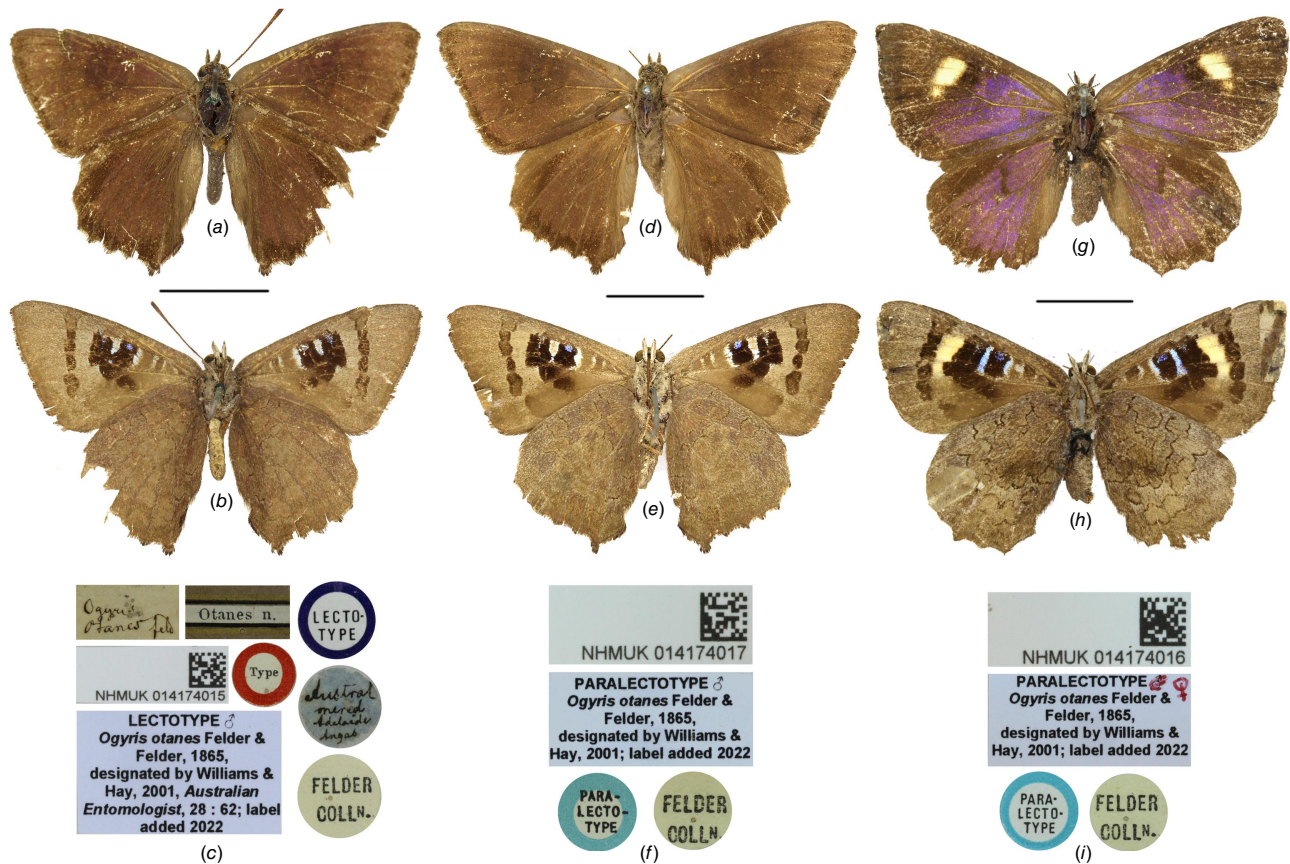
*Ogyris halmaturia* Tepper, 1890 – Waterhouse (1903b), p. 249; Waterhouse (1903a), p. 29; Waterhouse and Lyell (1914), p. 121; Bethune-Baker (1916), p. 390; Tindale (1923), pp. 347–348. [Incorrectly considered to be a junior synonym of *O. otanes* in whole or in part].

*Ogyris halmaturia* (Tepper, 1890). – Braby and Douglas (2008), pp. 315–319, fig. 7–9. [Incorrectly considered to be a junior synonym of *O. otanes*].

- Hindwing with prominent tornal projection.....6
- 3 Ventral forewing with blue scales below discal cell, postmedian band angled sharply towards tornus and not displaced medially.....  
.....*O. subterrestris*, Fig. 5f
- Ventral forewing without blue scales below discal cell, postmedian band displaced medially.....4
- 4 Ventral colouration predominately cinnamon–brown, medial area of hindwing without distinct black marking.....*O. petrina*, Fig. 5j
- Ventral colouration predominately silver–grey, medial area of hindwing with distinctive black patch of scales.....5
- 5 Dorsal wing margins broader, 4 mm, ventral forewing apex with double line of charcoal–black tending to brown scales against light grey background.....*O. halmaturia halmaturia*, Fig. 4a, b
- Dorsal wing margins narrower, 2.0–2.5 mm, ventral forewing apex unmarked.....*O. halmaturia waterhousei*, Fig. 4i, j
- 6 Ventral surface light yellowish to cinnamon–brown, hindwing tornal projections shorter, narrower.....*O. otanes*, Fig. 3b
- Ventral surface dark brown to grey–brown, with distinctive hindwing markings, tornal projections longer, broader.....7
- 7 Ventral hindwing generally plain dark brown .....  
.....*O. arcana arcana*, Fig. 3f
- Ventral hindwing generally suffused with light grey scales, particularly in background area around markings.....  
.....*O. arcana sublustris*, Fig. 3j

## Key to females

- 1 Ventral forewing with blue scales below discal cell, postmedian band angled in straight line towards termen, not curved or displaced along any part.....*O. subterrestris*, Fig. 5h
- Ventral forewing with blue scales in discal cell, postmedian band not straight.....2
- 2 Ventral ground colour predominately light brown or light cinnamon brown.....3
- Ventral ground colour predominately silver–grey or dark brown, with only highlights of lighter brown at most.....4
- 3 Dorsal forewing with double black line at end of discal cell, set on lighter reddish–brown scales.....*O. petrina*, Fig. 5k
- Dorsal forewing with only black scales at end of discal cell.....  
.....*O. otanes*, Fig. 3c
- 4 Ventral hindwing without distinctive central patch of black scales, tornal lobes prominent.....5
- Ventral hindwing with distinctive central patch of black scales, tornal lobes reduced.....6
- 5 Ventral wings dark brown, with markings similar colouration to background, cream dorsal forewing postmedian spot larger.....  
.....*O. arcana arcana*, Fig. 3g, h
- Ventral wings covered with light grey suffusion, predominately over background but occasionally on hindwing markings, cream dorsal forewing postmedian spot smaller.....*O. arcana sublustris*, Fig. 3k, l
- 6 Dorsal forewing with violet or blue scales not reaching cream postmedian spot, overall wing margins broader, cinnamon–coloured scales extensive in basal areas.....*O. idmo*, Fig. 5c
- Dorsal forewing with purple or blue scales meeting with cream postmedian spot, margins narrower, with or without very few cinnamon–coloured scales in basal wing area.....7
- 7 Cream forewing postmedian spot reduced, rarely extending beyond vein  $M_3$  as a scattering of cream scales, ventral forewing apex with double line of brown markings over light grey background.....  
.....*O. halmaturia halmaturia*, Fig. 4c–f
- Cream forewing postmedian spot large, usually extending beyond vein  $M_3$  as a distinct clean patch of scales, ventral forewing apex plain or with few broken brown markings.....  
.....*O. halmaturia waterhousei*, Fig. 4g, h, k, l



**Fig. 2.** Type specimens of *Ogyris otanes* C. & R. Felder, 1865 in the NHMUK showing dorsal and ventral views, and labels: (a–c) lectotype male; (d–f) paralectotype male; (g–i) paralectotype female. Scale bar: 10 mm. Images by J. Tennant.

## Type material

**Lectotype.** Australia: South Australia: ♂ ‘Austral. Merid. Adelaide Angas’, ‘*Ogyris otanes* Feld.’, ‘FELDER COLL<sup>N</sup>’, ‘*Otanes* n.’, ‘Type’ [on red label], ‘LECTO-TYPE’ [on blue label], ‘LECTOTYPE ♂ *Ogyris otanes* Felder & Felder, 1865 designated by Williams & Hay, 2001, *Australian Entomologist*, 28: 62; label added 2022’, ‘NHMUK 014174015’ (NHMUK) (Fig. 2a–c).

**Paralectotypes.** Australia: South Australia: 1♂ ‘PARA-LECTO-TYPE’ [on blue label], ‘FELDER COLL<sup>N</sup>’, ‘PARALECTOTYPE ♂ *Ogyris otanes* Felder & Felder, 1865, designated by Williams & Hay, 2001; label added 2022’, ‘NHMUK 014174015’, ‘NHMUK 014174017’ (NHMUK) (Fig. 2d–f). 1♀ ‘PARA-LECTO-TYPE’ [on blue label], ‘FELDER COLL<sup>N</sup>’, ‘PARALECTOTYPE ♀ *Ogyris otanes* Felder & Felder, 1865, designated by Williams & Hay, 2001; label added 2022’, ‘NHMUK 014174015’, ‘NHMUK 014174016’ (NHMUK) (Fig. 2g–h).

## Other material examined

85 ♂, 70 ♀ in the ANIC, variously from across the known South Australian and Victorian distribution.

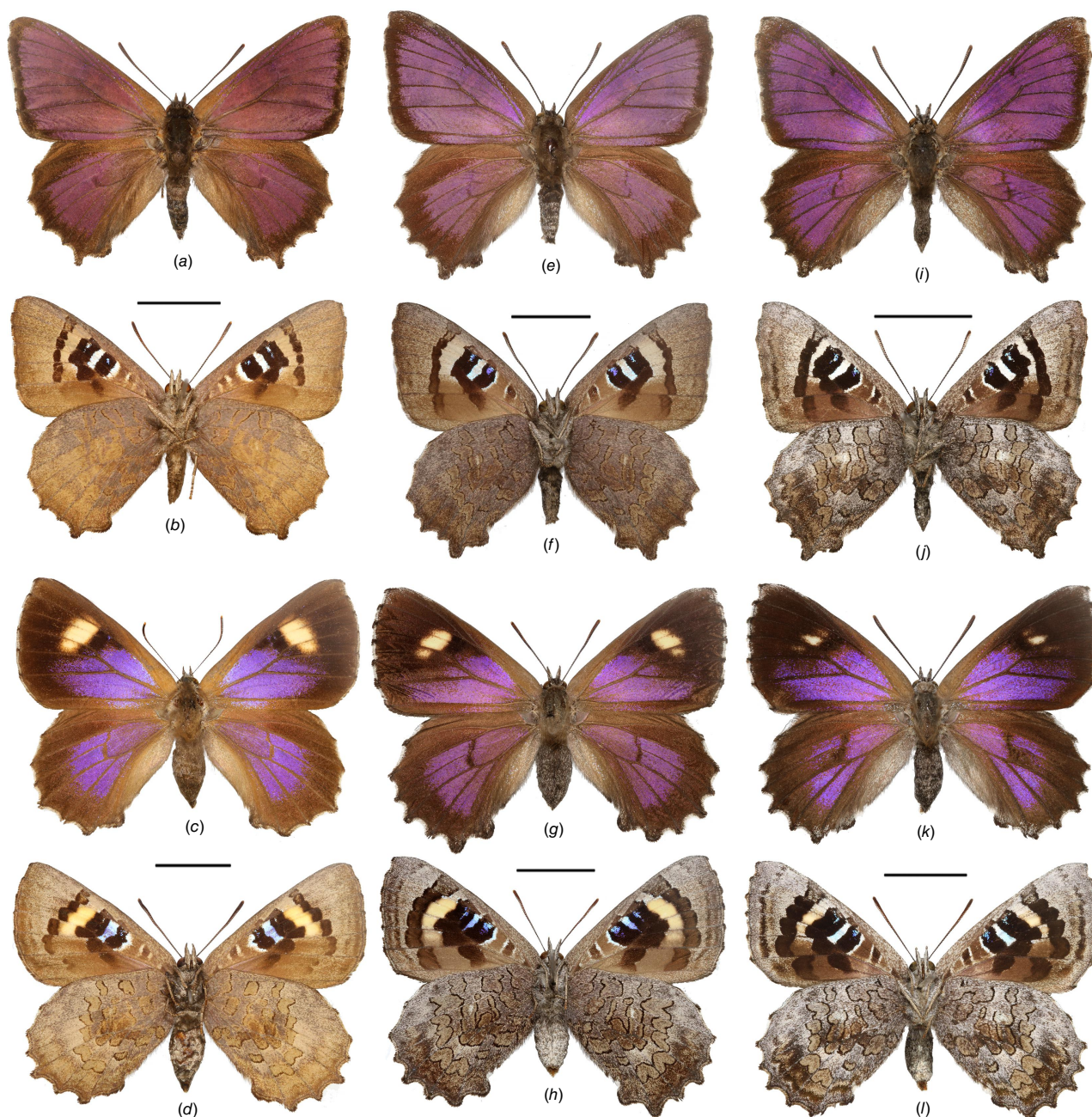
## Remarks

Felder and Felder (1865) originally described and illustrated both sexes of *Ogyris otanes* C. & R. Felder, 1865 based on three syntypes (2♂, 1♀, now in NHMUK) but no types were referenced (Edwards et al. 2001). Bethune-Baker (1905) examined and referred to the syntypes of Felder and Felder

(1865) but did not refer to an individual specimen. Tindale (1923) referred to types, stating that, ‘The type of *O. otanes* came from Adelaide...’ (p. 347). Edwards et al. (2001) interpreted Tindale’s (1923) reference to a type as qualifying as a lectotype designation but this is questionable because Tindale (1923) did not indicate which of the three syntypes were being referred to. Subsequently, Williams and Hay (2001, p. 62) made an intentional, unambiguous and explicit lectotype designation by providing the label data of one of the syntype males in NHMUK. We consider the action of Williams and Hay (2001) to constitute a valid lectotypification under Article 74 of the ‘International Code of Zoological Nomenclature’ (International Commission on Zoological Nomenclature 1999), thereby fixing the name *otanes* to this species. The three types were not illustrated; the lectotype male (Fig. 2a–c) is illustrated for comparison with the paralectotype male (Fig. 2d–f) and paralectotype female (Fig. 2g–i).

## Distribution

This species occurs patchily in the Gulf Country and Lower South-East South Australia and north-western Victoria (Braby 2000, 2016) and formerly occurred in western New South Wales where the species is currently considered locally extinct.



**Fig. 3.** Adults of *Ogyris otanes* and *O. arcana* stat. rev. showing dorsal and ventral views: (a–d) *O. otanes*; (a, b) male from Big Desert, VIC; (c, d) female from Kingscote, SA; (e–l) *O. arcana* stat. rev.; (e–h) *O. arcana arcana* comb. nov. from Stirling Range, WVA; (e, f) male; (g, h) female; (i–l) *O. arcana sublustris* comb. nov. from Leeman, WVA; (i, j) male; (k, l) female. Scale bars: 10 mm.

### Common name

Small bronze azure.

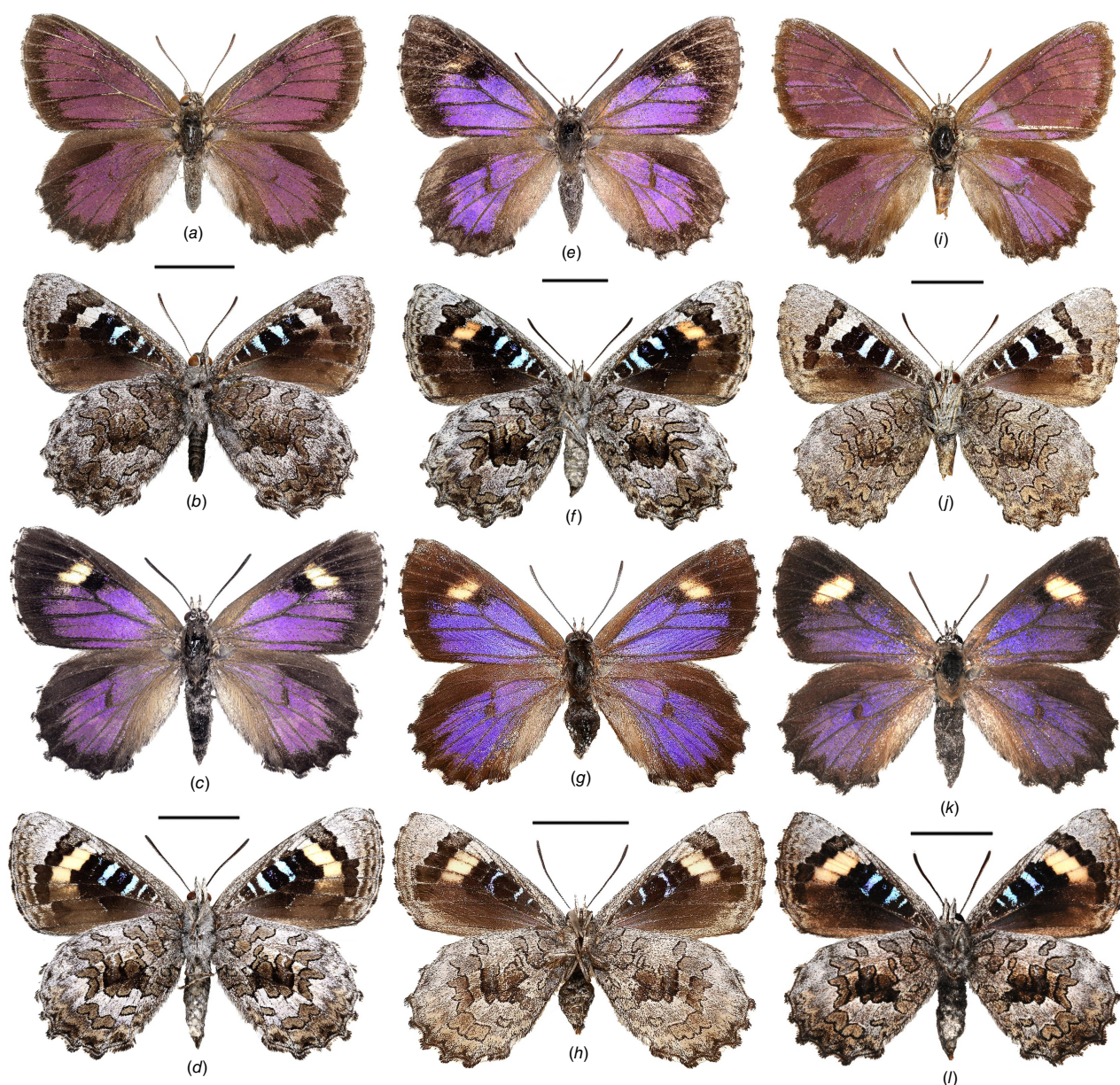
### *Ogyris arcana* M.R. Williams & Hay, 2001, stat. rev.

Two subspecies are recognised here, the nominate subspecies *O. arcana arcana* M.R. Williams & Hay, 2001 comb. nov. and *O. arcana sublustris* M.R. Williams & Hay, 2001 comb. nov.

### *Ogyris arcana arcana* M.R. Williams & Hay, 2001, comb. nov.

(Fig. 1, 3e–h, 6e–h.)

*Ogyris otanes* C. & R. Felder, 1865 – Waterhouse and Lyell (1914), p. 121; Waterhouse (1932), p. 184; Common (1964), p. 96; Burns and Rotherham (1969), p. 98; McCubbin (1971), p. 84; Common and Waterhouse (1972), p. 342; Crosby (1972), p. 7; Fisher (1978),



**Fig. 4.** Adults of *Ogyris halmaturia* showing dorsal and ventral views: (a–f) *O. halmaturia halmaturia* from Kangaroo Island, SA; (a, b) male; (c, d) female; (e, f) female showing variation with reduced forewing spot; (g–l) *O. halmaturia waterhouseri* stat. rev. from Ngarkat, SA; (g, h) *O. halmaturia waterhouseri* stat. rev. female showing variation with reduced forewing spot; (i, j) male; (k, l) female. Scale bars: 10 mm. Images g, h by F. Douglas.

p. 196; Williams *et al.* (1992), pp. 55–60; Fisher (1993), p. 11; Hay *et al.* (1994), pp. 31, 31, pl. 4, fig. 7–9. [Genus *Ogyris* Westwood, 1851]. [Misidentifications in literature].

*Ogyris* sp. – Field (1987), p. 113.

*Ogyris otanes* C. & R. Felder, 1865 – Hay (1989), pp. 42, 43. [Misspelling of *O. otanes*].

*Ogyris otanes* C. & R. Felder, 1865 ‘local forms 2 & 3’ – Dunn and Dunn (1991), p. 367. [Genus *Ogyris* Westwood, 1851].

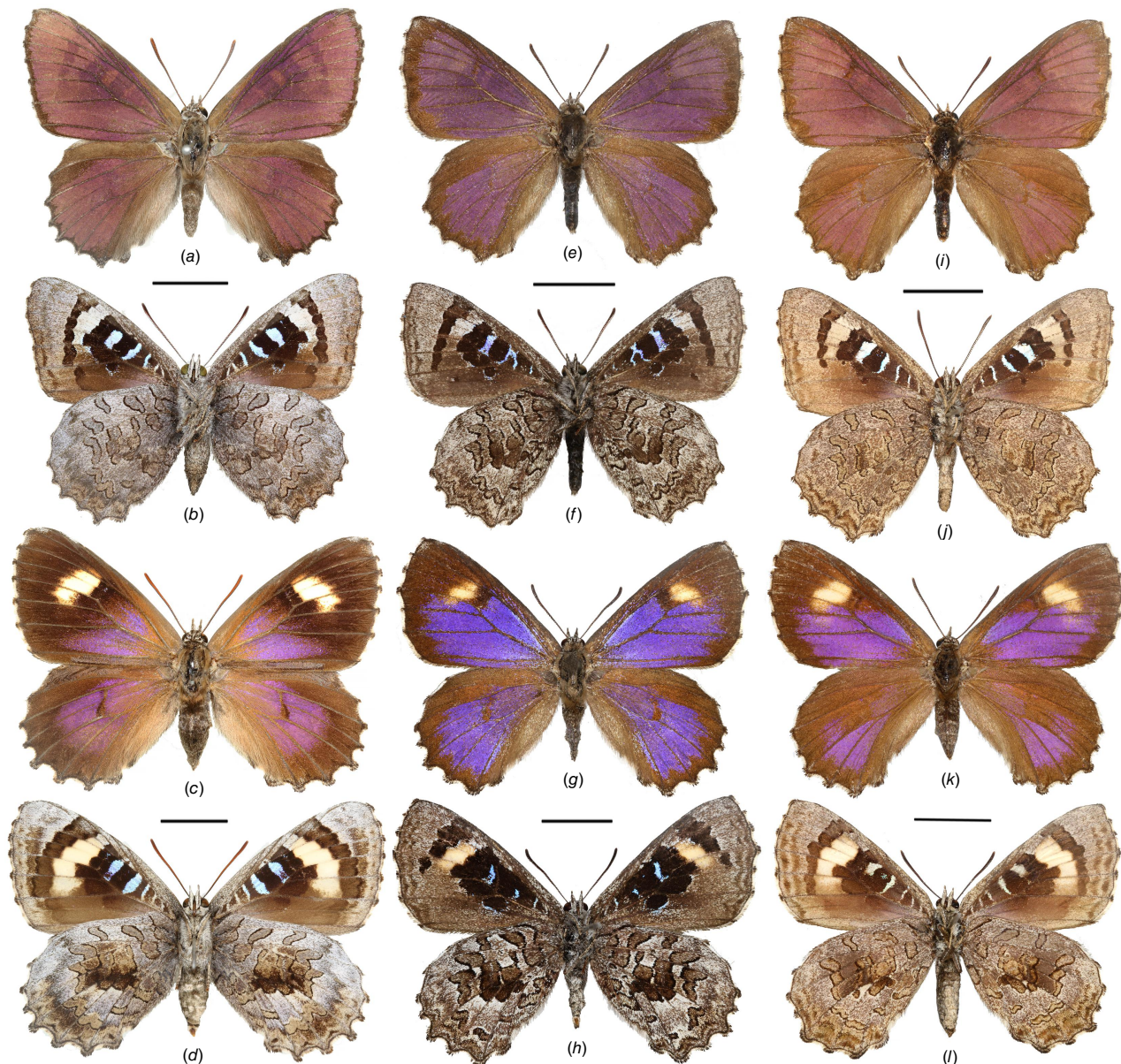
*Ogyris otanes* (C. & R. Felder, 1865) – Williams *et al.* (2012), pp. 50–51. [Misidentification in literature]. [Genus *Ogyris* Angas, 1847].

*Ogyris otanes* (C. & R. Felder, 1865) ‘south-western form’ – Braby (2000), pp. 710–712, pl. 50, fig. 3b. [Genus *Ogyris* Angas, 1847].

*Ogyris otanes arcana* M.R. Williams & Hay, 2001, pp. 59–61, fig. 5–8; Sands and New (2002), p. 288; Braby (2010), p. 35; Schmidt *et al.* (2014), pp. 473–484; Braby (2016), pp. 266–267, 350; Sankowsky (2020), p. 315.

## Type material

**Holotype.** Australia: Western Australia: ♂ ‘Stirling Ra, 7 Dec. 1990, M.R. Williams’ (WAM). [Illustrated in Williams and Hay (2001), p. 57, fig. 5].



**Fig. 5.** Adults of *Ogyris idmo*, *O. subterrestris* and *O. petrina* stat. rev. showing dorsal and ventral views: (a–d) *O. idmo* from Mundaring, WA; (a, b) male; (c, d) female; (e–h) *O. subterrestris*; (e, f) male from 6 km south of Colignan, VIC; (g, h) female from Pooginook, SA; (i–l) *O. petrina* stat. rev. from 12 km SW of Kalgoorlie, WA; (i, j) male; (k, l) female. Scale bars: 10 mm.

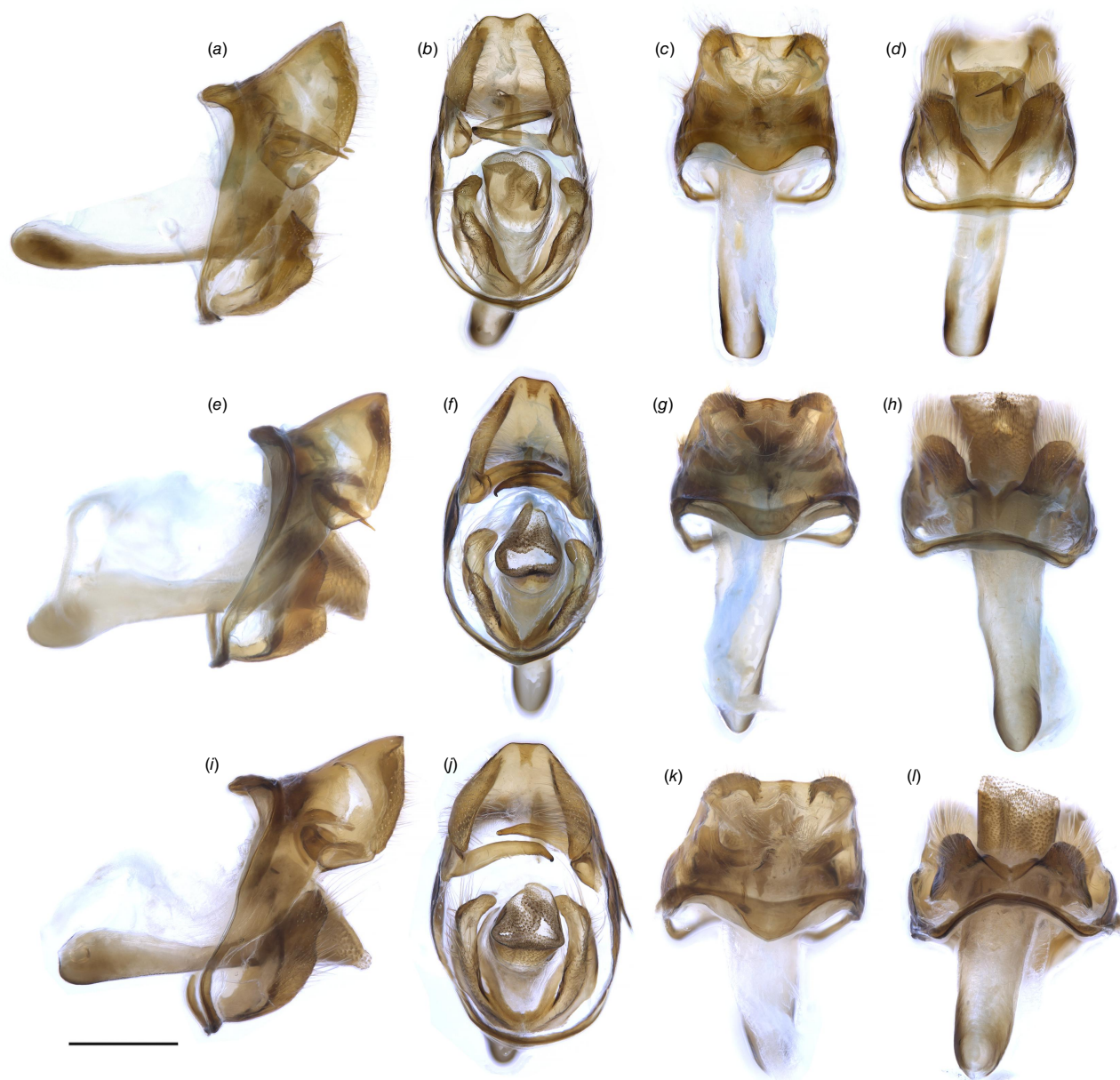
### Other material examined

20 ♂, 17 ♀ in the ANIC, from the Stirling Range, Wylie Scarp, and Cape Arid, WA.

### Diagnosis

*Ogyris arcana* can be distinguished from *O. otnes* by the following 10 character states that are more easily discerned in freshly emerged or reared specimens: (1) The forewing of *O. arcana* males is more elongate, with a straighter termen and more pointed apex than that of *O. otnes* males. This character appears to hold true for females but is most

evident in males. (2) The hindwing of *O. arcana* males is more elongate or slightly narrower than that of *O. otnes* males. (3) The tornal projection at the end of vein  $CuA_2$  on the hindwing is more pronounced in both sexes of *O. arcana* than that in *O. otnes*. (4) In females, the yellow postmedian spot on the upperside of the forewing is smaller in *O. arcana* than that in *O. otnes*, especially in the subspecies *O. arcana sublustis*. In *O. otnes*, the spot is not only generally broader but almost always extends beyond vein  $M_3$ , whereas in *O. arcana* the spot extends beyond this vein in only about half of the specimens examined ( $n = 38$ ); when present the spot is usually very faintly developed. (5) In *O. arcana*



**Fig. 6.** Male genitalia of *Ogyris* spp.: (a–d) *O. otanes*, genitalia number EPB-183 (ANIC); (e–h) *O. arcana arcana* comb. nov., genitalia number EPB-170 (ANIC). (i–l) *O. arcana sublustris* comb. nov., genitalia number EPB-171 (ANIC). Shown are lateral (a, e, i), posterior (b, f, j), dorsal (c, g, k) and ventral (d, h, l) views. Scale bar: 500 μm.

females, the upperside of the hindwing has a distinct black transverse bar along the discocellular vein, whereas in *O. otanes* females this bar is usually absent or if present, very faintly developed as a narrow black line. (6, 7) In both sexes of *O. arcana*, the apex on the upperside of the forewing and tornus (tornal projection and tornal lobe) on the upper side of the hindwing have a dusting or suffusion of grey scales, a pattern element that is absent in *O. otanes*. (8, 9) The underside (i.e. subapical region of forewing and entire hindwing) ground colour is dark brown to grey in both sexes of *O. arcana*, being particularly dark in *O. arcana*

*arcana* males, but light yellowish to cinnamon-brown in both sexes of *O. otanes*. Moreover, the underside markings of the hindwing in *O. arcana* are more pronounced and well developed (reminiscent of *Ogyris oroetes*), with a darker hue or tone towards the termen, especially in the subspecies *O. arcana sublustris*, whereas in *O. otanes* the markings are usually more obscure and the colour pattern more uniform, particularly in males. One exception to this is that female specimens particularly from Kangaroo Island are occasionally more distinctly patterned in this respect. (10) The cilia (scale fringe) are white and conspicuous in both

wings of *O. arcana*, whereas these are grey and less conspicuous in *O. otanes*.

Williams and Hay (2001) noted that males of *O. arcana* are darker than those of *O. otanes*; however, the upperside ground colour varies in males of both species. Williams and Hay (2001) also noted that the anal or tornal lobe of the hindwing is more accentuated in *O. arcana* but this feature is not applicable due to also being well developed in *O. otanes*. In females, the iridescent purple areas on the upperside vary in extent and colour in both species and are therefore not diagnostic.

The two species further differ in the male genitalia according to the following five character states: (1) the space at which the vinculum meets with the uncus is more concave in *O. arcana*, less so in *O. otanes*; (2) the valvae are elongate in *O. arcana* with a subtle medial concavity, whereas in *O. otanes* this concavity is deeper with the dorsal and ventral lobes more prominent, and ventral lobe more rounded; (3) the phallus is medially broader in *O. arcana*, whereas this is very narrow in *O. otanes*; (4) the sacculus of *O. arcana* is rugose with a basal triangular projection, whereas this is smooth in *O. otanes*; (5) the brachia are thicker and more heavily sclerotised in *O. arcana* but much finer and less sclerotised at the apex in *O. otanes*.

A new description is not required (see Williams and Hay 2001).

## Remarks

Waterhouse and Lyell (1914, p. 121) first drew attention to the western population from the Stirling Range, WA, provisionally placing the material under *O. otanes* (C. & R. Felder, 1865) but noted that these 'possibly represent a distinct race'. Waterhouse and Lyell's (1914) comment was based on three worn specimens (1♂, 2♀) collected in 1911 preserved in AMS (Williams *et al.* 1992). The population was subsequently rediscovered in 1988 by P.S. Valentine, H.H. Bollam and R.W. Hay (Hay 1989; Williams *et al.* 1992). Hay (1989, p. 43) remarked that, 'Classification of the species is being researched and all indications point to a distinct new W.A. species.' Williams *et al.* (1992) and Hay *et al.* (1994), however, later regarded this to most likely be an undescribed subspecies of *O. otanes*. Braby (2000), following Williams *et al.* (1992) and Dunn and Dunn (1991), provisionally treated the population as a distinct form of *O. otanes* and referred to this as the 'south-western form'. Subsequently, Williams and Hay (2001) formally described and illustrated the taxon as a subspecies of *O. otanes*, listing 81 paratypes (38♂, 43♀) in CALM (now in WAM) and various private collections. Braby (2000) and Williams and Hay (2001) provided a diagnosis and collectively listed five character states by which *Ogyris arcana* differs from *O. otanes*. Examination of additional material preserved in the ANIC since that publication have confirmed these differences but also revealed an additional five characters.

Therefore we treat *O. arcana* as a species distinct from *O. otanes* based on the large number of morphological differences including differences in the male genitalia (total of 15 characters), together with the molecular phylogenetic evidence presented by Schmidt *et al.* (2014) (see also Fig. 1) and the large *p*-distance, which is >5% (Table 1).

## Distribution

*Ogyris arcana arcana* occurs in the south-west of Western Australia, from the Stirling Range to as far east as Wylie Scarp (Williams and Hay 2001; Braby 2016).

## Common name

Dark bronze azure. Williams *et al.* (1992) proposed the name 'western dark azure' for this species, a name that we suggest modifying to include the group name 'bronze azure'.

***Ogyris arcana sublustris* M.R. Williams & Hay, 2001, comb. nov.**

(Fig. 1, 3i–l, 6i–l.)

*Ogyris* sp. – Field (1987), pp. 112–113.

*Ogyris otanes* C. & R. Felder, 1865 – Field (1990), pp. 77, 78; Williams *et al.* (1995), p. 95; Hart and Powell (1997), pp. 185–190. [Genus *Ogyris* Westwood, 1851]. [Misidentifications in literature].

*Ogyris otanes* C. & R. Felder, 1865 'local form 2' – Dunn and Dunn (1991), p. 367. [Genus *Ogyris* Westwood, 1851].

*Ogyris* sp. aff. *otanes* – Grund (1998), p. 66.

*Ogyris otanes* (C. & R. Felder, 1865) 'western coastal form' – Braby (2000), pp. 710–712, pl. 50, fig. 3c. [Genus *Ogyris* Angas, 1847].

*Ogyris otanes sublustris* M.R. Williams & Hay, 2001, pp. 56–59, fig. 1–4; Sands and New (2002), p. 288; Braby (2010), p. 35; Schmidt *et al.* (2014), pp. 473–484; Braby (2016), pp. 266–267, 350; Sankowsky (2020), p. 315.

## Type material

**Holotype.** Australia: Western Australia: ♂ 'Port Denison, 13 Nov. 1993, M.R. Williams' (WAM). [Illustrated in Williams and Hay (2001), p. 57, fig. 1].

## Other material examined

74 ♂, 56 ♀ in the ANIC, from Leeman and Port Denison, WA.

## Diagnosis

Williams and Hay (2001) provided a comprehensive diagnosis on how *Ogyris arcana sublustris* is distinguished from the nominate subspecies. Several character state differences were listed, including: (1) smaller body size; (2) paler (grey) underside ground colour in both sexes; (3) reduced pale

yellow postmedian spot on the forewing in females; and (4) a more pronounced subterminal band on the underside of forewing in males. The male genitalia were not included in the original diagnosis; however, we have discovered that the two subspecies differ slightly in shape of the male valvae, with *O. arcana sublustris* (Fig. 6i–l) having smoother, less concave valvae than nominate *O. arcana* (Fig. 6e–h).

## Remarks

Field (1987) first drew attention to the distinctiveness of this taxon from Western Australia, classifying this as a species of *Ogyris* allied to *O. otanes* (C. & R. Felder, 1865). Dunn and Dunn (1991) commented on the unusual wing phenotype of the adults and referred to the population(s) as a local form ('No. 2') of *O. otanes*. Braby (2000) illustrated a female, diagnosed the population and treated this as the 'western coastal form' of *O. otanes*. Subsequently, Williams and Hay (2001) formally described and illustrated the taxon as a subspecies of *O. otanes* and provided a detailed diagnosis on how *O. otanes sublustris* M.R. Williams & Hay, 2001 is distinguished from *O. otanes arcana* M.R. Williams & Hay, 2001. These authors listed 124 paratypes (39♂, 85♀) in CALM (now in WAM) and various private collections. Braby (2010) again highlighted the distinctive wing pattern elements of *O. otanes sublustris* and called for further evidence to establish whether the observed morphological differences were correlated with molecular, ecological and behavioural characteristics. Following the molecular phylogeny based on mtDNA (*COI* and *cytb*) published by Schmidt et al. (2014) (see also Fig. 1), *sublustris* clearly belongs with *O. arcana* and not with *O. otanes*.

## Distribution

*Ogyris arcana sublustris* occurs on the western coast of Western Australia, from near Lancelin northwards to Port Denison (Hart and Powell 1997; Williams and Hay 2001; Braby 2016).

## *Ogyris halmaturia* (Tepper, 1890)

Two subspecies are recognised here, the nominate subspecies *O. halmaturia halmaturia* (Tepper, 1890) and *O. halmaturia waterhouserii* (Bethune-Baker, 1905) stat. rev.

## *Ogyris halmaturia halmaturia* (Tepper, 1890)

(Fig. 4a–f, 7a–d.)

*Ogyris halmaturia* Tepper, 1890, p. 12; Tepper (1893), p. 285; Hill and Michaelis (1988), pp. 14, 36. [Genus *Ogyris* Westwood, 1851].

*Ogyris halmaturia* Tepper. – Seitz (1926), p. 940. [Misspelling of *O. halmaturia*].

*Ogyris halmaturia* (Tepper). – Grund (2010), pp. 114–120; Braby et al. (2011), pp. 29–36; New (2011), pp. 21, 99, 103–104, 148; Schmidt et al. (2014), pp. 473–484; Braby (2016), pp. 268–269, 350. [Genus *Ogyris* Angas, 1847].

*Ogyris halmaturia halmaturia* Tepper. – Tindale (1923), p. 348, pl. XXIX, fig. 20. [Genus *Ogyris* Westwood, 1851].

*Ogyris idmo* Hewitson, 1862. – Lower (1893), p. 9; Waterhouse (1903a), p. 29. [Incorrectly considered to be a senior synonym of *O. halmaturia*].

*Ogyris idmo* (Hewitson, 1862). – Edwards (1996), p. 250. [Incorrectly considered to be a senior synonym of *O. halmaturia*].

*Ogyris idmo halmaturia* Tepper. – Waterhouse (1932), pp. 179–180; Common (1964), p. 96; Burns and Rotherham (1969), p. 98; D'Abrera (1971), p. 320; McCubbin (1971), p. 84; Common and Waterhouse (1972), pp. 341–342; Fisher (1978), pp. 193–194; Common and Waterhouse (1981), p. 479; Fisher (1985), p. 7; Dunn and Dunn (1991), pp. 366, 457. [Genus *Ogyris* Westwood, 1851].

*Ogyris idmo halmaturia* (Tepper). – Edwards (1996), p. 250; Moore (1999), p. 12; Field (1999), pp. 252–253; Braby (2000), pp. 396, 712–714; Edwards et al. (2001), pp. 254–255; Sands and New (2002), pp. 282–284. [Genus *Ogyris* Angas, 1847].

*Ogyris waterhouserii* (Bethune-Baker, 1905). – Braby and Douglas (2008), pp. 315–329, fig. 4–6.

## Type material

**Lectotype.** Australia: South Australia: ♂ 'Queenscliffe, 1 mile N.W. very shy, ♀, 20.11.86. Tepper' [in Tepper's original handwriting]; 'Ogyris halmaturia Tepper, Type female = ♂, Kangaroo Island | n348, vide, TRSSA. 1923'; 'SAMA Database No. 31-001699' (SAMA). [♂ *O. halmaturia*, illustrated in Tindale (1923), pl. XXIX, fig. 20; Braby and Douglas (2008), p. 319, fig. 4–6].

**Paralectotypes.** Australia: South Australia: 1♂ 'Queenscliffe, ♂, 1 m. N.W. very shy, 21.11.86. Tepper' [in Tepper's original handwriting]; 'Ogyris halmaturia Tepper, Type male, =not type, Kangaroo Island | vide TRSSA 1923, p. 389', 'Ogyris otanes ♂ not halmaturia'; 'SAM Database No. 31-001700' (SAMA) [=♂ *O. otanes*, illustrated in Tindale (1923), pl. XXIX, fig. 16]. 1♂ 'Queenscliffe, 1 m. N.W. very shy, 20.11.86. Tepper' [in Tepper's original handwriting]; 'Ogyris halmaturia Tepper, Cotype male, Kangaroo Island | vide TRSSA 1923, p. 389'; 'Ogyris otanes ♂ not halmaturia'; 'SAM Database No. 31-001701' (SAMA) [=♂ *O. otanes*]. 1♂ 'Queenscliffe, 1 mile N.W., in scrub. ♂, 20.11.86. Tepper' [in Tepper's original handwriting]; 'Ogyris halmaturia, Queenscliffe, Kang. Island, Nov. 1886., legit J.G.O. Tepper'; 'Bethune-Baker Coll. B.M. 1927-471.' (NHMUK) [=♂ *O. otanes*, illustrated in Braby and Douglas (2008), p. 319, fig. 7–9].

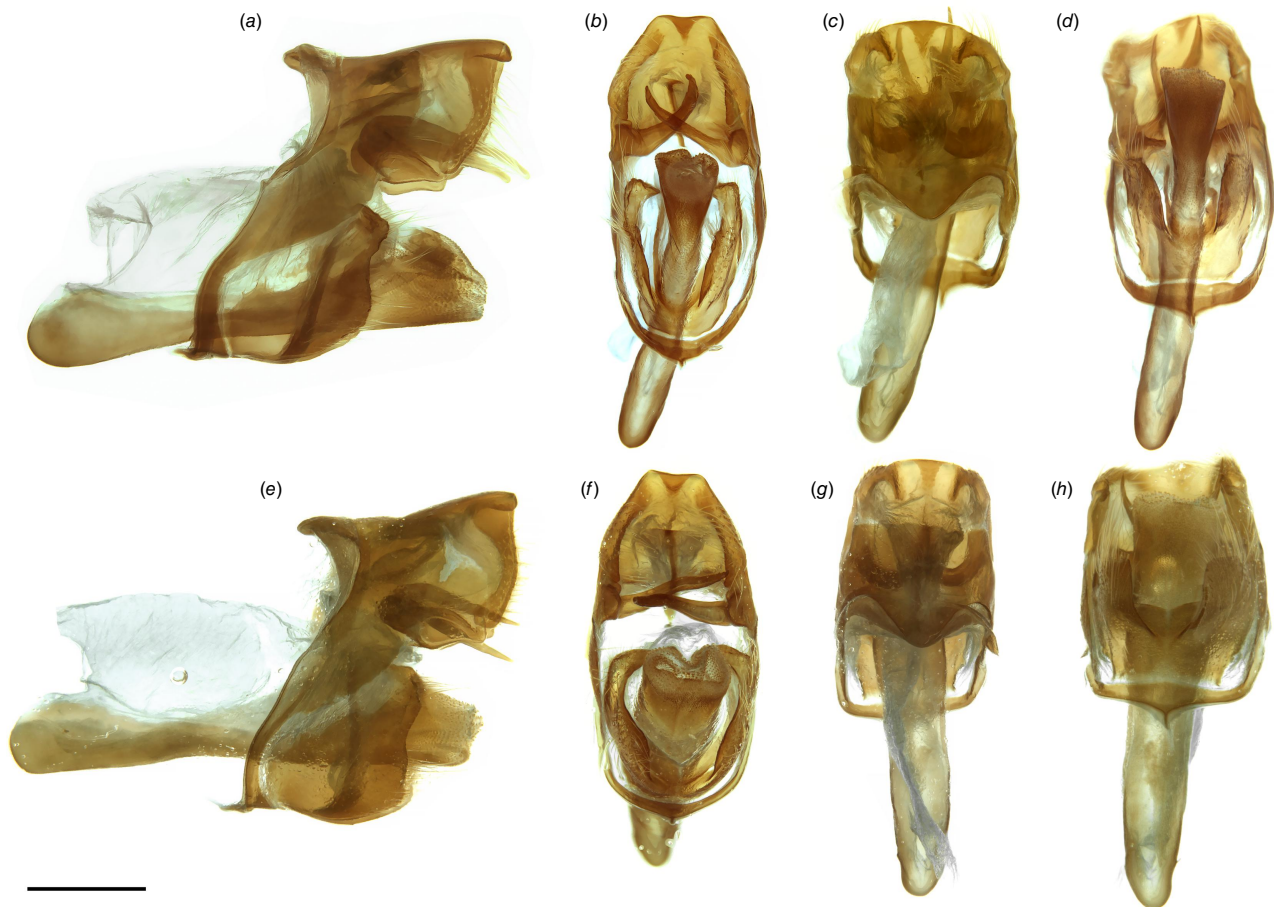
## Other material examined

An additional 40 specimens (23♂, 17♀) were examined in the ANIC and DESS, from Kangaroo Island, SA.

## Description of female

### Head

Dorsally and ventrally covered in dense light grey scales. Antennae 5–7 mm long, broadest distally, dorsally densely packed with scales, ventral surface without scales; dark brown, slight reddish hue in middle, lateral two-thirds



**Fig. 7.** Male genitalia of *Ogyris halmaturia*: (a–d) *O. halmaturia halmaturia*, genitalia number MFB-158 (DESS); (e–h) *O. halmaturia waterhouseri* stat. rev., genitalia number MFB-160 (ANIC). Shown are lateral (a, e), posterior (b, f), dorsal (c, g) and ventral (d, h) views. Scale bar: 500  $\mu$ m.

from head with white scales on distal aspect of each antennomere; 45–47 antennomeres, each with scattering of short black spines on lateral and ventral surfaces, particularly towards distal end; scape in deep socket, ovoid, appressed mandarin-like. Labial palp elongate, with three palpomeres, light grey to white, middle longest, apex acuminate, tipped with darker scales.

### Thorax

Patagium dark grey; tegula cinnamon-brown; meso- and metathorax dark grey interspersed with cinnamon-coloured scales. Ventral surface predominately light grey, interspersed with dark grey scales. Legs light grey, midleg with antenna brush organ vestigial, almost entirely absent, tibia and tarsi of all legs ventrally and laterally covered with many short black spines; tarsi with paired prominent claws and paired associated setae; aerolium triangular, larger on mid- and hindlegs.

### Wings

Forewing length 15–23 mm ( $\bar{x}$  = 20.6 mm  $\pm$  2.54 s.d.,  $n$  = 12); near triangular, with costa slightly convex, termen

convex medially, tornus rounded, dorsum straight; upper-side dark iridescent rich violet over brown; costal, marginal and apical areas black, light cinnamon-brown in basal area of costa; veins brown; black spot at end of discal cell; small cream-yellowish to cream postmedian spot between vein  $M_3$  and  $M_1$ , rarely larger between  $M_3$  and  $R_5$ ; cilia white, brown at ends of veins; underside ground colour, dark charcoal to brown basally, light silvery-grey at apex, grey at tornus, with complex patterns; discal cell black with 4–5 irregular longitudinal sky-blue markings, interspersed with dark blue; yellowish-cream to cream postmedian band from  $M_3$  to  $CuA_1$ , variable in extent and suffused with mid-brown in basal median area, followed by charcoal-coloured postmedian band from costa to  $CuA_2$ , sometimes merging with dark background, slightly displaced distally at  $M_3$ ; two dark brown parallel subterminal bands, variable in intensity but always present; cilia white, brown at ends of veins. Hindwing sub-ovoid in shape, with costa convex, apex indistinct from termen, termen crenulate with short, rounded projections at ends of veins, tornal lobe reduced, dorsum with weakly defined anal lobe, otherwise slightly convex medially; upperside

colour pattern similar to forewing except without cream spot; inner margin light cinnamon-grey; prominent dark brown band at end of discal cell; underside ground colour, broadly light silvery-grey interspersed with highly variable complex markings from basal to marginal area, markings ovoid, irregularly squarish in basal area, becoming heart-shaped towards marginal area, each marking bordered by black, interiorly interspersed with cinnamon-brown and grey; variable black central patch between irregularly shaped markings; submarginal area light brown, with broken black subterminal line; cilia light grey, black at ends of veins.

### Abdomen

Tergites covered with dark grey scales; sternites with light grey to white scales. Female genitalia not dissected – this feature is diagnostically uninformative in *Ogyris* spp. among closely related species (Beaver et al. 2023).

### Variation

Variation was observed in the size and shape of the dorsal and ventral postmedian forewing spot, the ventral discal forewing cell patterns and the ventral hindwing patterns.

### Remarks

Braby and Douglas (2008) and Braby et al. (2011) discussed the taxonomic status and complex nomenclatural history of this species. For over 75 years (from 1932 to 2008) *Ogyris halmaturia* (Tepper, 1890) was considered to be a junior synonym or subspecies of *O. idmo* (Hewitson, 1862) but both Braby and Douglas (2008) and Grund (2010) treated this as a distinct species according to fundamental differences in juvenile and adult morphology. Tindale (1923) had previously considered *O. halmaturia* to be a distinct species but this was not accepted by Waterhouse (1932). Confusion in nomenclature of this species has arisen because Tepper (1890) had a mixed series representing two different species, one of Tepper's (1890) syntypes was incorrectly sexed (the male was thought to be the female), and historically most previous authors (Lower 1893; Tepper 1893; Waterhouse 1903a, 1903b; Waterhouse and Lyell 1914; Bethune-Baker 1916; Tindale 1923) had failed to render a valid and unambiguous lectotype designation. The introduction of a second name, that is, *Ogyris waterhouseri* (Bethune-Baker, 1905), added further complexity. Braby et al. (2011) concluded that the name *O. halmaturia* had priority over *O. waterhouseri* based on the action of Tindale (1923) who was the first to make a valid lectotype designation, even though Tindale's (1923) type designation was confusing in that Tepper's (1893) concept of *O. halmaturia* was partly synonymised under *O. otares*.

The type locality of *O. halmaturia* is north-west of Kingscote, SA and we restrict the concept of the nominate subspecies to Kangaroo Island. The South Australian Gulf

Country and Kangaroo Island region have a complex geological and climatic history, with many potential biogeographic filters present that may have influenced subspeciation in the recent past. Indeed, the Kangaroo Island population is genetically distinct (D. J. Lohman, pers. comm.) from the mainland populations. The subspecies was last recorded on the island at 'Rocky River', in 1934, leading Braby and Douglas (2008) to conclude that it was possibly extinct. However, the subspecies was rediscovered on Kangaroo Island in 2014 after a lapse of 80 years. Prior to the rediscovery, only two females were historically known from Kangaroo Island, both in AMS (G.A. Waterhouse Collection): a specimen that was collected in December 1926 by F. W. Jones and another is without a locality label. While both historical localities for this species are valid historical Kangaroo Island place names, the actual collection locations referred to may likely not necessarily coincide with the areas currently recognised by these terms in the present day. Since Tepper (1890) only described the male of *O. halmaturia* (that was mistaken for the female), the female of the nominate subspecies has not been described. Hence, we provide a description and illustrations of female *O. halmaturia halmaturia* to distinguish the taxon and for comparison with females of the mainland subspecies.

### Distribution

*Ogyris halmaturia halmaturia* occurs only on Kangaroo Island, SA.

### Common name

Eastern bronze azure. Braby and Douglas (2008) proposed the common name 'eastern bronze azure' for this species, a name that we recommend be adopted for *O. halmaturia*.

### *Ogyris halmaturia waterhouseri* (Bethune-Baker, 1905), stat. rev.

(Fig. 1, 4g–l, 7e–h.)

*Ogyris idmo* Hewitson, 1862. – Miskin (1890), p. 24; Anderson and Spry (1893), pp. 101, 104; Lower (1893), p. 9; Waterhouse (1903a), p. 29. [Misidentifications in literature or incorrectly considered to be a senior synonym of *O. halmaturia*].

*Ogyris waterhouseri* Bethune-Baker, 1905, pp. 273–274; Waterhouse and Lyell (1908), pp. 162, 165–166; Kershaw (1908), pp. 163–164; Seitz (1926), p. 940; Peters (1971), p. 26. [Genus *Ogyris* Westwood, 1851].

*Ogyris waterhouseri* (Bethune-Baker, 1905). – Braby and Douglas (2008), pp. 315–329, fig. 1–3, 14–17. [Genus *Ogyris* Angus, 1847].

*Ogyris idmo waterhouseri* Bethune-Baker. – Waterhouse and Lyell (1914), p. 122, pl. 18; Burns (1931), pp. 131–132; Burns and Angel (1952), p. 183; Common (1964), p. 96; Burns and Rotherham (1969), p. 98; D'Abrera (1971), p. 320; McCubbin (1971), p. 84; Quick (1972), pp. 9–10.

*Ogyris idmo waterhousei* Bethune-Baker. – Common (1964), p. 96. [Misspelling of *O. waterhousei*].

*Ogyris halmaturia waterhousei* Bethune-Baker. – Tindale (1923), p. 348.

*Ogyris idmo halmaturia* Tepper. – Waterhouse (1932), pp. 179–180; Common and Waterhouse (1972), pp. 341–342; Crosby (1974a), p. 65; Fisher (1978), pp. 193–194, pl. 10, fig. 11–13; Common and Waterhouse (1981), p. 479; Dunn and Dunn (1991), pp. 366, 457; F. Douglas (unpubl. data, 1995), pp. 6–10, fig. 1; Grund (1999), pp. 47–48; Grund (2003), p. 71. [Genus *Ogyris* Westwood, 1851]. [Considered to be a senior synonym of *O. waterhousei*].

*Ogyris idmo halmaturia* (Tepper). – Edwards (1996), p. 250; Hunt *et al.* (1998), pp. 113–116; Moore (1999), p. 12; Field (1999), pp. 252–254, 259, fig. 13–16; Braby (2000), pp. 396, 712–714, pl. 50, fig. 5b; Edwards *et al.* (2001), pp. 254–255; Sands and New (2002), pp. 282–284; Braby (2004), pp. 242–243, 316; New *et al.* (2007), p. 245. [Genus *Ogyris* Angus, 1847]. [Considered to be a senior synonym of *O. waterhousei*].

*Ogyris halmaturia* Tepper. – Hill and Michaelis (1988), pp. 14, 36. [Genus *Ogyris* Westwood, 1851].

*Ogyris halmaturia* (Tepper). – Grund (2010), pp. 114–120; Braby *et al.* (2011), pp. 29–36; New (2011), pp. 21, 99, 103–104, 148; Schmidt *et al.* (2014), pp. 473–484; Braby (2016), pp. 268–269, 350. [Genus *Ogyris* Angus, 1847].

## Type material

**Lectotype.** Australia: Victoria: ♂ [Grampians]; ‘Victoria’; ‘Type’; L128; ‘L128, *Ogyris waterhousei* B-B’; ‘G.A. Waterhouse Collection’; ‘FIG. 400 Underside IN ‘THE BUTTERFLIES OF AUSTRALIA’, by WATERHOUSE & LYEELL, was taken from this specimen | KL20205’ (AMS). [Illustrated in Waterhouse and Lyell (1914), pl. 18, fig. 400; Braby and Douglas (2008) p. 319, fig. 1–3].

**Paralectotype.** Australia: Victoria: ♀ [Grampians]; ‘*Ogyris waterhousei* B-B’; ‘Ex wll Miskin’; ‘G.A. Waterhouse Collection’; ‘FIG. 402 Underside IN ‘THE BUTTERFLIES OF AUSTRALIA’, by WATERHOUSE & LYEELL, was taken from this specimen | KL20208’ (AMS) [Illustrated in Waterhouse and Lyell (1914), pl. 18, fig. 402].

## Other material examined

Braby and Douglas (2008) listed 54 specimens (29 ♂, 25 ♀) within the ANIC, AMS, NMV and SAM, variously from mainland South Australia and Western Victoria that we have re-examined.

## Diagnosis

The following four character states distinguish *O. halmaturia waterhousei* from *O. halmaturia halmaturia*: (1) males have the black dorsal forewing margin narrower than that of the nominate subspecies; (2) females usually have the cream dorsal forewing postmedian spot larger, whereas in *O. halmaturia halmaturia* the spot is smaller, never extending cleanly beyond vein  $M_3$ ; indeed in some specimens the spot is almost absent (Fig. 4e). Sometimes, *O. halmaturia halmaturia* specimens have a few cream scales beyond  $M_3$  (Fig. 4c); however, these do not coalesce to form a discrete patch as seen in typical *O. halmaturia waterhousei*. The extent of this pattern is somewhat variable in *O. halmaturia waterhousei*; typically, specimens (Fig. 4k) exhibit a large clean spot but in some atypical specimens (Fig. 4g) this may

be reduced. (3) Both sexes of *O. halmaturia waterhousei* have the apical area of the ventral forewing unmarked, particularly between the costa and  $M_1$ , whereas in *O. halmaturia halmaturia* this area has a double broken charcoal–black tending to dark brown line of crescent-shaped markings; (4) females have the dorsal basal area blue, whereas in the nominate subspecies this is violet purple, with a richer basal cinnamon suffusion.

There are also several diagnostic differences in the male genitalia of the two subspecies: (1) the valvae of *O. halmaturia waterhousei* (Fig. 7e–h) are uniformly broader, with the apices rounded, whereas in *O. halmaturia halmaturia* (Fig. 7a–d) the apices are more truncate and with a more concave posterior margin; (2) the saccus of *O. halmaturia waterhousei* is narrower than in the nominate subspecies, particularly in lateral view; and (3) the brachia of *O. halmaturia waterhousei* are slightly shorter and broader than in *O. halmaturia halmaturia*.

## Remarks

Miskin (1890) provided a description of the male of this taxon based on material from Victoria and South Australia under the name *Ogyris idmo* Hewitson, 1862, not realising this was an undescribed species. Anderson and Spry (1893) described and illustrated both sexes from the Grampians in western Victoria (see Waterhouse and Lyell 1908), also under the name *O. idmo* and similarly failed to realise this was an unnamed species. Miskin’s (1890) revision of *Ogyris* was published (in February 1890) before Tepper (1890) introduced the name *O. halmaturia*, 15 years before Bethune-Baker (1905) described *Ogyris waterhousei*. Edwards *et al.* (2001) and Braby and Douglas (2008) reviewed the type material, type locality and nomenclature of *Ogyris waterhousei* (Bethune-Baker, 1905). Bethune-Baker (1905) described the species from Victoria based on material dispatched by G. A. Waterhouse (see Waterhouse and Lyell 1908) but did not indicate the number of specimens available. Braby and Douglas (2008) concluded that Bethune-Baker had at most three syntypes (1♂, 2♀) and that the type locality was most likely the Grampians based on the plate index for the lectotype male illustrated by Waterhouse and Lyell (1914, pl. 18, fig. 400) and referred to by Peters (1971) as the holotype. However, re-examination of *O. waterhousei* material in AMS and G. A. Waterhouse’s original register indicated that only two specimens (1♂, 1♀) were sent to England and subsequently returned to Australia. These type specimens have the label ‘*Ogyris waterhousei* B-B’ in Bethune-Baker’s original handwriting. Edwards *et al.* (2001) considered Peters’ (1971) incorrect reference to a ‘holotype’ as a lectotype designation. We agree with the conclusion of Edwards *et al.* (2001) and consider the second (female) specimen, referred to above, in AMS and illustrated by Waterhouse and Lyell (1914, pl. 18, fig. 402), a paralectotype.

## Distribution

*Ogyris halmaturia waterhouseri* was at one time broadly distributed across mainland Gulf Country South Australia and western Victoria; however, the species is locally extinct in most localities and currently known only from the central-southern section of the Eyre Peninsula and Ngarkat Conservation Park, South Australia (Braby and Douglas 2008), in which the presence has not been confirmed for a number of years.

## *Ogyris idmo* (Hewitson, 1862)

(Fig. 1, 5a–d, 8a–d.)

*Ogyris idmo* Hewitson, 1862, p. 2, pl. I, fig. 3–4; Hewitson (1863), p. 2; Kirby (1871), p. 425; Miskin (1891), p. 72; Waterhouse (1903b), pp. 248–249; Waterhouse (1903a), p. 29; Bethune-Baker (1905), pp. 269, 271, 273–275, 290, fig. 10, 10a; Seitz (1926), p. 940, fig. 161g; Waterhouse (1937), p. 120; Hay et al. (1994), p. 31, fig. 10–13; Grund (1998), p. 66. [Genus *Ogyris* Westwood, 1851].

*Ogyris idmo* (Hewitson). – Edwards (1996), p. 250; Eastwood and Fraser (1999), pp. 510; Pierce (2002), pp. 747, 750; Braby and Douglas (2008), pp. 315–326, fig. 10–12; Williams (2009), pp. 37–43; Grund (2010), pp. 114–120; Orr and Kitching (2010), pp. 244–245; Braby (2010), pp. 16, 71; New (2011), pp. 101, 103; Williams et al. (2012), pp. 52–53; Schmidt et al. (2014), pp. 473–484; King and Williams (2014), pp. 199–201, fig. 1; Braby (2016), pp. 268–269, 350; Williams et al. (2020), pp. 221–247, fig. 4–6; Sankowsky (2020), p. 316. [Genus *Ogyris* Angus, 1847].

*Ogyris idmo idmo* Hewitson. – Waterhouse and Lyell (1914), pp. 121–122, pl. 18, fig. 405–406; Waterhouse (1932), p. 179, pl. XXV, fig. 3; Common (1964), p. 96, fig. 368; Burns and Rotherham (1969), pp. 98–99, fig. 73; McCubbin (1971), p. 84; D'Abrera (1971), p. 320; Common and Waterhouse (1972), p. 341, pl. 34, fig. 3, 3A; Atkins (1978), pp. 25–27; Common and Waterhouse (1981), pp. 478–479, pl. 41, fig. 3, 3A; D'Abrera (1984), p. 127; Hill and Michaelis (1988), p. 36; Field (1990), pp. 76–77; Dunn and Dunn (1991), p. 366; Field (1992), pp. 12–16; Williams et al. (1995), p. 94. [Genus *Ogyris* Westwood, 1851].

*Ogyris idmo idmo* (Hewitson). – Field (1997), pp. 390–391; Moore (1999), p. 12; Field (1999), pp. 251–259, fig. 9–12, 17–20; Braby (2000), pp. 712–714, pl. 50, fig. 5; Edwards et al. (2001), p. 255; Sands and New (2002), p. 285; Grund (2003), p. 71. [Genus *Ogyris* Angus, 1847].

*Ogyris* sp. aff. *idmo* – Hay et al. (1994), p. 31, fig. 14–15. [Cape Arid population].

*Ogyris orontas* Hewitson, 1862, p. 2, pl. I, fig. 8–9; Hewitson (1863), p. 2; Kirby (1871), p. 425; Miskin (1890), p. 24; Anderson and Spry (1893), p. 101; Waterhouse (1903b), pp. 248–249; Waterhouse (1903a), p. 29; Bethune-Baker (1905), pp. 269, 274–275; Seitz (1926), p. 940; Edwards (1996), p. 250; Field (1999), pp. 252. [Junior objective synonym of *O. idmo*].

*Ogyris otrontas* Hewitson. – Tepper (1893), p. 285. [Misspelling of *orontas*].

## Type material

**Lectotype.** *Ogyris idmo*. Australia: Western Australia: ♀ 'Swan River., 43.14. | *Ogyris idmo* Type Hewitson'; 'Type'; 'LECTO-TYPE'; 'NHMUK

014175794'; 'LECTOTYPE ♀ *Ogyris idmo* Hewitson, 1862' (NHMUK). [Illustrated in Hewitson (1862), p. 2, pl. I, fig. 3–4; Braby and Douglas (2008), p. 319, fig. 10–12].

**Paralectotype.** *Ogyris idmo*. Australia: Western Australia: ♀ 'Swan River | 43 14'; 'Swan River.'; 'PARA-LECTO-TYPE'; 'NHMUK 014175795'; 'PARALECTOTYPE *Ogyris idmo* Hewitson, 1862' (NHMUK).

**Holotype.** *Ogyris orontas*. Australia: Western Australia: ♂ 'Orontas Hewitson'; 'Type'; 'Holo-type'; 'Type'; 'Bethune-Baker Coll. B.M. 1927-471'; 'NHMUK 014175793'; 'HOLOTYPE ♂ *Ogyris orontas* Hewitson, 1862' (NHMUK) [Illustrated in Hewitson (1862), p. 2, pl. I, fig. 8–9].

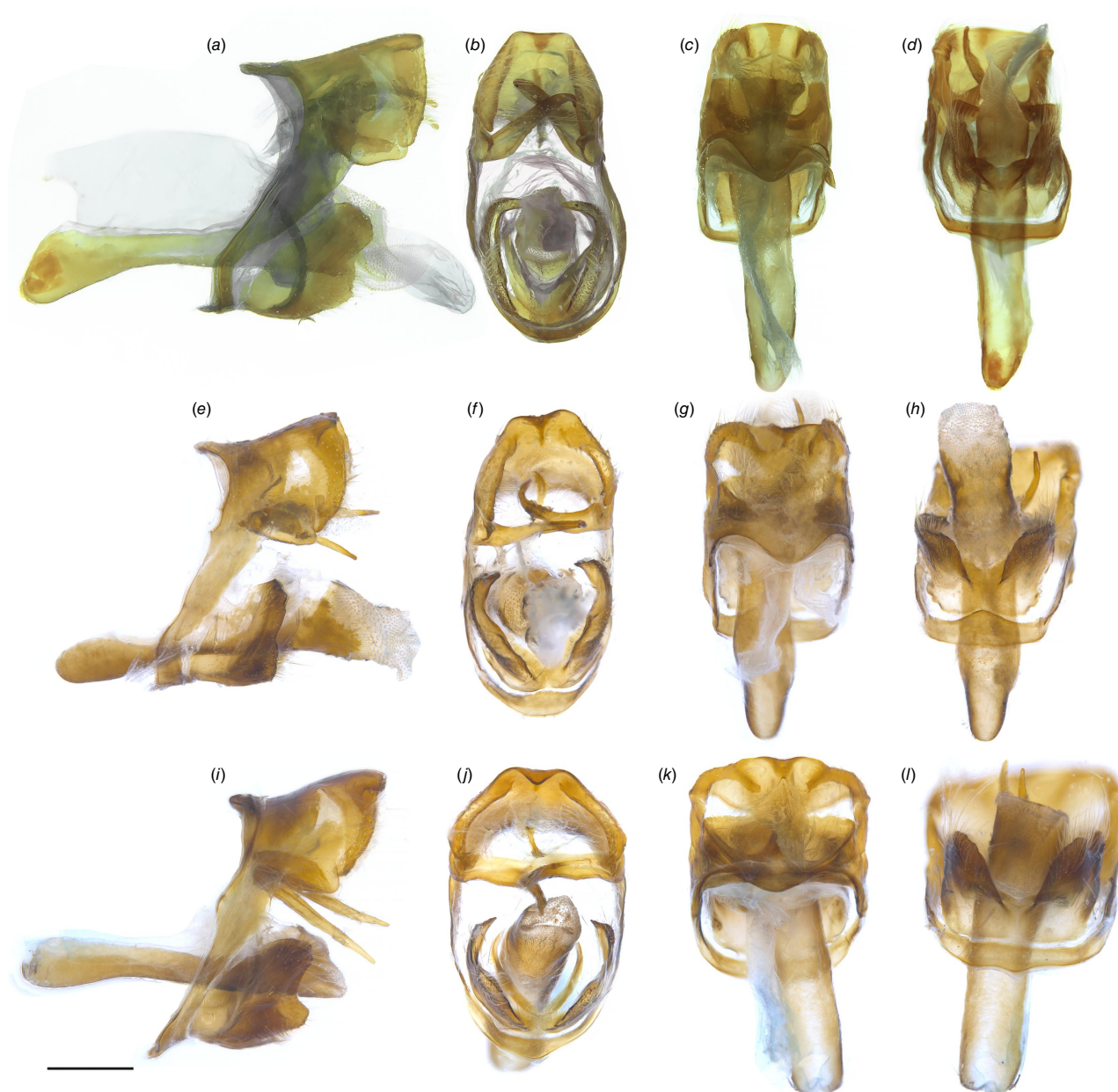
## Other material examined

64 ♂, 55 ♀ in the ANIC, from south-western WA.

## Remarks

Hewitson (1862) described and illustrated *Ogyris idmo* Hewitson, 1862 based on two females and *Ogyris orontas* Hewitson, 1862 based on a single male, all in the NHMUK. The following year, Hewitson (1863) realised the sexes of the two species were conspecific and synonymised *O. orontas* under *O. idmo* (Hewitson 1863), an action subsequently followed by Kirby (1871), Miskin (1890), Waterhouse (1903a, 1903b) and Bethune-Baker (1905) amongst others. The type locality of *O. orontas* was simply given as 'Australia' but no further detail was provided about from which part of Western Australia the specimen was collected. Braby and Douglas (2008) examined Hewitson's (1863) syntypes of *O. idmo* from Western Australia and designated one of the females from the Swan Coastal Plain near Perth as the lectotype.

Recent collections of this species indicate a species complex in south-western Western Australia (Williams et al. 2020) in which there are four distinct populations that we are currently investigating: (1) a bivoltine population restricted to banksia woodland or jarrah-banksia-wandoo woodland in the Swan Coastal Plain and from sites 60–80 km east of Perth (east of the Darling Escarpment) in which adults fly in late spring (November–December) and again in early autumn (February–April); both sexes fly during the morning and afternoon, and males perch to locate females; and the dorsal iridescent basal areas of females are purple. (2) A more widely distributed population that occurs in a variety of habitats in the mesic, higher rainfall areas of the south-western corner (generally > 500 mm mean annual rainfall) that is strictly univoltine (mainly in October and November but in some locations adults appear as early as September or as late as December); diurnal activity of the sexes is temporally partitioned, with females flying during the morning (10:00–12:00 hours) and males in the afternoon (> 13:00 hours), and where males patrol to locate females; and the iridescent areas of females are purple, with the colour varying from bright purple to dull dark purple. (3) A semi-arid population restricted to mallee heath or mallee shrubland in the south-eastern



**Fig. 8.** Male genitalia of *Ogyris* spp.: (a–d) *O. idmo*, genitalia number MFB-161 (ANIC); (e–h) *O. subterrestris*, genitalia number EPB-185 (ANIC). (i–l) *O. petrina* stat. rev., genitalia number EPB-184 (ANIC). Shown are lateral (a, e, i), posterior (b, f, j), dorsal (c, g, k) and ventral (d, h, l) views. Scale bar: 500  $\mu$ m.

subcoastal area, from Scaddan to Cape Arid, in which the mean annual rainfall varies from ~400–500 mm; adults are univoltine, flying in spring (September–November); females fly predominately in the morning and males in the afternoon; and the iridescent areas of females are blue. (4) A semi-arid population that occurs in shrubland in the transition zone between the South-western and Eyrean Provinces of low rainfall (~300–400 mm mean annual rainfall); adults are univoltine, emerging mainly in spring (September–November) and males and females appear to fly together

during the day, from mid-morning to early afternoon; and the iridescent areas of females are violet. Further work is being undertaken by the authors to clarify the ecological and taxonomic boundaries of these four populations.

### Distribution

*Ogyris idmo* occurs in south-western Western Australia; see Williams *et al.* (2020) and the above remarks concerning distribution within this region.

## Common name

Large bronze azure.

## *Ogyris subterrestris* Field, 1999

(Fig. 1, 5e–h, 8e–h.)

*Ogyris idmo halmaturia* Tepper, 1890. – *Common and Waterhouse* (1981), p. 479; *Dunn and Dunn* (1991), p. 366. [Genus *Ogyris* Westwood, 1851]. [Misidentifications in literature].

*Ogyris* sp. aff. *idmo* – F. Douglas (unpubl. data, 1995), pp. 11–17, fig. 2; *Field* (1997), pp. 389–392; *Grund* (1997), pp. 8–9; *Moore* (1999), p. 12–17; *Eastwood and Fraser* (1999), pp. 510.

*Ogyris subterrestris subterrestris* Field, 1999, pp. 251–259, fig. 1–4; *Braby* (2000), pp. 714–715, pl. 50, fig. 4b; *Edwards et al.* (2001), p. 259; *Pierce* (2002), pp. 747, 750; *Douglas and Allen* (unpubl. data, 2002, pp. 1–16); *Sands and New* (2002), pp. 293–295; *Grund* (2003), p. 71; *Braby* (2004), pp. 242–243, 316; *Braby and Douglas* (2008), pp. 315, 326, 327; *Williams and Williams* (2008), p. 16; *Grund* (2010), pp. 114–120; *Braby* (2010), pp. 19, 71; *New* (2011), pp. 101–105; *Douglas* (2012), pp. 1–37; *Field* (2013), pp. 248–249; *Schmidt et al.* (2014), pp. 473–484; *Braby* (2016), pp. 268–269, 350; *Taylor et al.* (2018), table S3; *Geyle et al.* (2021), pp. 101, 103; *Orr and Kitching* (2010), pp. 244–245; *Sankowsky* (2020), p. 316; *Murdoch* (2021), pp. 7–8; *Murdoch* (2022), pp. 22–24; *Murdoch and Murdoch* (2023), p. 21; *Ley* (2023), pp. 86–87.

## Type material

**Holotype.** Australia: Victoria: ♀ ‘Pink Lakes, Murray-Sunset NP, 15 km N Lima, Victoria, 35°03.45’S, 142°43.13’E, 20.x.1996, R.P. Field’; ‘NMV T-17264’ (NMV). [Illustrated in *Field* (1999), p. 254, fig. 1–2].

**Paratypes.** Australia: Victoria: 1♀, 1♂: ‘Mildura. Vic. 16 October. 1972, B.H. Vardy’; D.F. Crosby collection donated ANIC 1987’; ‘M f 14’ [male with label ‘M m 2’]; (ANIC). *Field* (1999) listed a further 19 paratypes (14 ♂, 5 ♀) in NMV and the private collection of B.H. Vardy.

## Other material examined

12 ♂, 11 ♀ in the ANIC from north-west VIC and SA.

## Remarks

Although *O. subterrestris* was named and described relatively recently, historical specimens of this species were collected 51–111 years ago: 1♂ from Broken Hill, NSW (1912), 1♀ from Lake Hattah (given as Lake Waltah) (1918) and 2♂, 4♀ from Mildura, Vic (1972) (*Field* 1999). The specimens from Broken Hill and Mildura were referred to by *Common and Waterhouse* (1981) and *Dunn and Dunn* (1991) under the name *Ogyris idmo halmaturia* before the realisation that these specimens belonged to a distinct species. *Field* (1999) and *Braby* (2000) also placed two females from Koonibba Mission near Ceduna, SA (in SAMA) under this species but this is erroneous because these specimens are actually *O. halmaturia waterhousei* (see *Braby and Douglas* 2008).

## Distribution

*Ogyris subterrestris* occurs in the South Australian Riverland area and in far north-western Victoria (*Field* 1999; *Braby* 2000, 2016; *Braby and Douglas* 2008). The species is considered to be locally extinct in south-western New South Wales.

## Common name

Mallee bronze azure. The name ‘mallee bronze azure’ is suggested for this species (*Braby et al.* 1997). *Ogyris subterrestris* has previously been known as arid bronze azure, as proposed by *Field* (1999) but the reasons for suggesting this change are twofold. *Field* (1999) reasoned that ‘arid bronze azure’ was a more appropriate name as the species was known ‘from mallee and non-mallee areas’. Contrary to this, the localities referred to, Broken Hill, NSW, Mildura, Vic and near Ceduna, SA, are all localities at which mallee is or was historically present or where *O. subterrestris* does not actually occur. A further impetus for this common name reappraisal is that the name arid bronze azure has been utilised extensively for conservation planning for *O. petrina* stat. rev., a species that also occurs within a drier environment than *O. subterrestris* and is plausibly more suitable.

## *Ogyris petrina* Field, 1999, stat. rev.

(Fig. 1, 5i–l, 8i–l.)

*Ogyris* sp. – *Field* (1987), p. 113; *Field* (1990), pp. 77, 80; *Field* (1992), pp. 13–16; *Field* (1997), pp. 389–391.

*Ogyris idmo idmo* Hewitson, 1862 – *Dunn and Dunn* (1991), p. 366. [Genus *Ogyris* Westwood, 1851]. [Misidentification in literature].

*Ogyris* sp. aff. *idmo* – *Eastwood and Fraser* (1999), pp. 510–511.

*Ogyris subterrestris petrina* *Field*, 1999, pp. 255–257, fig. 5–8; *Braby* (2000), pp. 714–715, pl. 50, fig. 4a; *Edwards et al.* (2001), p. 259; *F. Douglas and G. G. Allen* (unpubl. data, 2002), p. 1; *Sands and New* (2002), pp. 291–292; *Braby* (2004), pp. 242–243, 316; *Williams and Williams* (2006), pp. 20–23; *Braby and Douglas* (2008), p. 326; *Williams et al.* (2008), pp. 1–13; *Williams and Williams* (2008), pp. 1–17, fig. 1–2; *Braby* (2010), p. 71; *Gamblin et al.* (2010), pp. 55–58; *New* (2011), p. 105; *Douglas* (2012), pp. v, 1, 17; *Braby et al.* (2014), p. 108; *King and Williams* (2014), p. 199–201; *Schmidt et al.* (2014), pp. 475–481; *Braby* (2016), pp. 268–269, 350; *Taylor et al.* (2018), table S3; *Williams et al.* (2020), pp. 223, 239, 244; *Sankowsky* (2020), p. 316; *Geyle et al.* (2021), pp. 101, 103; *Australian Geographic* (2022), p. 97; *Western Australian Biodiversity Science Institute* (2022), pp. 1–20, fig. 1a.

*Ogyris subterrestris* *Field*, 1999 – *Orr and Kitching* (2010), p. 244; *Williams et al.* (2012), pp. 54–55. [Misidentification in literature].

## Type material

**Holotype.** Australia: Western Australia: ♀ ‘Lake Douglas, 12 km SW of Kalgoorlie. 12.xi.1989, R.P. Field’; ‘NMVT-17268’ (NMV). [Illustrated in *Field* (1999), p. 254, fig. 5–6].

**Paratypes.** Australia: Western Australia: 10 ♂, 3 ♀: 1 ♂ labelled as for the holotype except with date '1.2.82'; 'genitalia tube 208'; 'K m 20'; 'ANIC Database No. 31 019584'. 1 ♂ labelled similarly except with date '22 Oct 1985, 'K m 19'; 'Genitalia slide M1132'; 'Legs on slide'. 'ANIC Database No. 31 019589'. A further 7 ♂ and 2 ♀ with date '16 Dec 1986', one female with 'K f 16'; 'ANIC Database No. 31 019587', the other with 'K f 19'. 1 ♀ labelled similarly except with date '17 Dec 1986'; 'K f 17'; 'ANIC Database No. 31 019586'. 1 ♂ 'Lake Douglas WA, 22 Nov 1991, L.R. Ring' (ANIC). Field (1999) listed a further 58 paratypes (32 ♂, 26 ♀) in NMV and WAM.

## Other material examined

23 ♂, 10 ♀ in the ANIC, all from the type locality.

## Diagnosis

*Ogyris petrina* can be distinguished from *O. subterrestris* by the following 14 character states: (1) In female *O. petrina*, the pale yellow dorsal forewing postmedian spot is irregular but larger and distinctly divided by vein  $M_3$ , forming a small faint cream patch posteriorly between  $M_3$  and  $CuA_1$ , whereas this spot is smaller in *O. subterrestris*. (2) In female *O. petrina*, the dorsal iridescent purple central area on the hindwing does not extend anteriorly to vein  $M_1$  and does not extend proximally to the base, whereas the blue area is far more extensive in *O. subterrestris*. (3) In both sexes, the dorsal forewing of *O. petrina* is predominately brownish-purple without a strong bronze sheen to brown marginal areas, whereas in *O. subterrestris* this is bluer with a cinnamon-bronze sheen. (4) In both sexes of *O. petrina*, the brown markings on the ventral hindwing are poorly defined, compared to the highly complex and distinct grey markings in *O. subterrestris*; furthermore, there is a prominent dark grey to charcoal central marking in *O. subterrestris* that is absent in *O. petrina*. (5) The ventral hindwing of *O. petrina* lacks the contrasting grey postmedian patches between veins  $M_3$  and  $CuA_2$  that are prominent in *O. subterrestris*. (6) In female *O. petrina*, the dorsal forewing is deep iridescent purple, whereas in *O. subterrestris* this is brighter bluish-purple or blue. (7) In female *O. petrina*, the dorsal forewing has a double line of black scales at the end of the discal cell, divided medially by cinnamon-coloured scales, whereas in *O. subterrestris* this marking consists of a single broad black bar. (8) In female *O. petrina*, the dorsal hindwing discal bar is very obscure and surrounded by brown scales but is distinct in *O. subterrestris*. (9) The ventral ground colour of both sexes of *O. petrina* is a distinctive light cinnamon-brown but is generally dark grey in *O. subterrestris*, with highlights of light silvery-grey. (10) In both sexes of *O. petrina*, the ventral forewing has the area below the cubital vein a cinnamon-coloured gradient, from dark brown basally to light brown towards the dorsum and termen, whereas in *O. subterrestris* this feature is extensively and uniformly charcoal-grey towards the dorsum and termen without a gradient. (11) The ventral double subterminal bands in both wings of both sexes of *O. petrina*

are more widely spaced, whereas this feature is narrower and less extensive in *O. subterrestris*, especially in the forewing. (12) In both sexes of *O. petrina*, the posterior section of the dark brown ventral forewing postmedian band is parallel to the termen, whereas this band is inclined sharply towards the termen or tornus in *O. subterrestris*. (13) In both sexes of *O. subterrestris*, the ventral forewing has two small patches of black edged with blue below the discal cell, whereas in *O. petrina* these patches are absent or, if present, dark brown without the blue markings. (14) The ventral forewing of both sexes of *O. petrina* has the patterns in the discal cell cream and usually transverse, whereas these are usually circular and blue in *O. subterrestris*.

The following diagnostic male genitalia characters have been identified between *O. petrina* (Fig. 8i–l) and *O. subterrestris* (Fig. 8e–h): (1) the vinculum of *O. petrina* has a strong medio-lateral expansion, whereas in *O. subterrestris* this is expressed as a small point; (2) the vinculum apex and saccus in *O. petrina* appear straight in lateral view, whereas in *O. subterrestris* the vinculum is displaced dorsally so as to appear recurved. In ventral view (Fig. 8h) this is apparent by way of a more triangular saccus in *O. subterrestris* and not straight as in *O. petrina* (Fig. 8l). (3) In *O. petrina*, the uncus is narrower and more triangular, with the dorsal projection enlarged compared with that of *O. subterrestris*; and (4) the valvae of *O. petrina* have a clearly defined ventral lobe or projection, with the apex broad and blunt, whereas in *O. subterrestris* the ventral lobe is poorly defined, weakly triangular and the apex is distinctly acuminate.

The adult stage has previously been illustrated in colour by Field (1999), Braby (2000) and Williams and Williams (2006).

## Remarks

This species was originally discovered from Lake Douglas near Kalgoorlie, WA, by the late Alan Graham in 1982 (Braby 2000; Williams and Williams 2006; Gamblin *et al.* 2010), although investigations of material in the NHMUK revealed that a historic specimen (a single female) had been collected from the Kalgoorlie district in 1911 but the true identity had remained unrecognised (Field 1999; Williams and Williams 2006). Over many years, the taxonomy of the species was subsequently investigated by Field (1987, 1990, 1992, 1997), who considered this to be an undescribed taxon closely related to *Ogyris idmo* (Hewitson, 1862). Field (1999) eventually described and treated this as a subspecies of *Ogyris subterrestris* Field, 1999 although no justification was provided for this taxonomic arrangement. Field (1999) gave a diagnosis for the species *O. subterrestris* but not *O. petrina*. The only diagnostic information given for the latter taxon is provided in the Key on page 252, where two character states for females and three character states for males were included by which this taxon can be differentiated from *O. subterrestris*. The male genitalia were never

examined in Field's (1999) treatment of this taxon; only those of *O. subterrestris* were examined (Field 1999, fig. 22). Examination of a larger series of specimens in the ANIC and comparative study of the male genitalia have revealed additional characters by which the two taxa are distinguished. Schmidt et al. (2014) demonstrated that, based on molecular phylogenetic data, *O. petrina* was a monophyletic lineage more closely related to *O. subterrestris* from eastern Australia than to *O. idmo*. We treat *O. petrina* as a species distinct from *O. subterrestris* based on the large number of morphological differences including differences in the male genitalia (total of 18 characters), together with the molecular phylogenetic evidence presented by Schmidt et al. (2014) (see also Fig. 1) and the large *p*-distance, that is >3% (Table 1).

## Distribution

*Ogyris petrina* is known only from a few scattered localities near Kalgoorlie and Mukinbudin in the Goldfields and north-eastern Wheatbelt regions of Western Australia (Field 1999; Williams and Williams 2006; Gamblin et al. 2010; Western Australian Biodiversity Science Institute 2022). The population near Kalgoorlie was extirpated in 1993 (Williams et al. 2012).

## Common name

Arid bronze azure.

## Discussion

We currently consider the *O. idmo* species group to contain six species and two subspecies (i.e. 8 taxa) based on an integrative taxonomic approach that includes a detailed appraisal of adult morphology, including wing colour and pattern elements, and morphology of male genitalia, together with a reanalysis of the molecular phylogenetic data presented in Schmidt et al. (2014). This taxonomic revision brings the total number of species recognised in *Ogyris* to 18 and in the tribe Ogyrini to 20.

Recognition of both *Ogyris arcana* and *O. petrina* as distinct species is based on the divergent morphology correlated with the reciprocal monophyly compared with that of the previously proposed sister subspecies status. Moreover, the uncorrected *p*-distances between these taxa (Table 1) are larger than those of sister species in the *O. aenone* complex (Beaver et al. 2023). Furthermore, the total number of adult morphological character state differences between these two species pairs (15 for *O. arcana* and *O. otares*, and 18 for *O. petrina* and *O. subterrestris*) is similar to that recorded for the sister species *O. aenone* (Waterhouse, 1902) and *O. caelestia* Beaver & Braby, 2023, in which there are 20 character state differences (Beaver et al. 2023). This

number does not include other known character differences, such as divergent life histories or differences in the morphology of the immature stages. These differences, coupled with the apparently deeper molecular divergence, may suggest that the *O. idmo* species group is morphologically conservative compared with other *Ogyris* species groups. Although molecular data from this group have been publicly accessible since 2014 (Schmidt et al. 2014), no additional morphological investigation has been undertaken until this study. While often useful for species delimitation, mitochondrial sequence data alone were notably not useful for resolving subspecies concepts within *Ogyris* in two other studies (Schmidt and Hughes 2007; Schmidt et al. 2014).

Two species, *O. arcana* and *O. halmaturia*, contain allopatric subspecies. In Western Australia, the two taxa *O. arcana arcana* and *O. arcana sublustris* are not reciprocally monophyletic according to neutral divergence markers (mtDNA) (Schmidt et al. 2014) (Fig. 1) but are otherwise allopatric, morphologically distinct according to wing colour pattern and male genitalia (total of five character state differences), and do not share mtDNA haplotypes. The lack of clear phylogenetic structure between *O. arcana arcana* and *O. arcana sublustris* is possibly due to a relatively recent divergence, incomplete lineage sorting or historical gene flow. Schmidt et al. (2014) argued that these taxa may be at an 'intermediate' state of genetic divergence in that the speciation process is not yet completed. Therefore, under the general lineage species concept and criteria for delineating species and subspecies in butterflies (Braby et al. 2012) we recognise two species in the *O. otares* complex and two subspecies within *O. arcana*. Similarly, in this work we treat *O. halmaturia waterhouseri* as a subspecies of *O. halmaturia* given that all mainland populations of this species from Victoria and South Australia are sufficiently and consistently distinct from material of *O. halmaturia halmaturia* from Kangaroo Island, SA, a fact first pointed out 100 years ago by Tindale (1923). There are fewer morphological character state differences (a total of seven) between these two allopatric populations than between known sister species within the *O. idmo* species group. Additionally, there are currently no known biological differences between the mainland and Kangaroo Island populations; therefore, subspecific rank for *waterhouseri* is more appropriate than species-level designation.

The *Ogyris idmo* species group has undergone two significant host shifts away from aerial Lorantheae, onto root-parasitic Santalaceae and a presumed further shift to entomophagy. The exact nature of this entomophagy, whether ant brood predation (myrmecophagy), brood parasitism (trophallaxis), or predation or parasitism of other ant nest residents, is unconfirmed due to the concealed nature of the subterranean larvae. The obligate association with the largely terrestrial-nesting *Camponotus* ants may have encouraged the foliage-dwelling ancestors of this clade to live in galleries or shelter at the entrances of ant nests, as is still

**Table 2.** Revised classification of the *Ogyris idmo* species group in relation to the occurrence and conservation status according to various conservation schedules and other published sources.

| Taxon                                           | Occurrence   | International (IUCN) | National (EPBC) | State (FFG, BC) | Comments                                                                                                                                                |
|-------------------------------------------------|--------------|----------------------|-----------------|-----------------|---------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Ogyris otanes</i>                            | NSW, VIC, SA |                      |                 | CR (VIC: FFG)   | Considered to be EX in NSW, EN in VIC and possibly VU in SA ( <a href="#">Sands and New 2002</a> )                                                      |
| <i>Ogyris arcana</i> stat. rev.                 | WA           |                      |                 |                 | Western coastal population considered to be Thr nationally                                                                                              |
| <i>Ogyris arcana arcana</i> comb. nov.          | WA           |                      |                 |                 | No conservation significance                                                                                                                            |
| <i>Ogyris arcana sublustris</i> comb. nov.      | WA           |                      |                 |                 | Considered to be Thr nationally ( <a href="#">Geyle et al. 2021</a> )                                                                                   |
| <i>Ogyris halmaturia</i>                        | VIC, SA      | EN                   |                 |                 | Considered to be EN internationally ( <a href="#">Young et al. 2021</a> )                                                                               |
| <i>Ogyris halmaturia halmaturia</i>             | SA           |                      |                 |                 | Previously considered to be EX ( <a href="#">Field 1997</a> ; <a href="#">Braby and Douglas 2008</a> ) but now most likely CR since rediscovery in 2014 |
| <i>Ogyris halmaturia waterhousei</i> stat. rev. | VIC, SA      |                      |                 | CR (VIC: FFG)   | Considered to be EX in VIC and EN in SA ( <a href="#">Sands and New 2002</a> ; <a href="#">Braby and Douglas 2008</a> )                                 |
| <i>Ogyris idmo</i>                              | WA           |                      |                 |                 | No conservation significance, but current taxonomy is uncertain and range is highly fragmented ( <a href="#">Williams et al. 2020</a> )                 |
| <i>Ogyris subterrestris</i>                     | NSW, VIC, SA |                      |                 | EN (VIC: FFG)   | Considered to be EX in NSW, EN in VIC and VU in SA ( <a href="#">Field 1997</a> ; <a href="#">Sands and New 2002</a> ; <a href="#">Douglas 2012</a> )   |
| <i>Ogyris petrina</i> stat. rev.                | WA           |                      | CR              | CR (WA: BC)     | Considered to be CR nationally ( <a href="#">Geyle et al. 2021</a> )                                                                                    |

EX, Extinct in the wild; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; Thr, Threatened; IUCN, International Union for Conservation of Nature Red List Categories; EPBC, *Environmental Protection and Biodiversity Act 1999*; FFG, *Flora and Fauna Guarantee Act 1988*; BC, *Biodiversity Conservation Act 2016*; NSW, New South Wales; VIC, Victoria, SA, South Australia; WA, Western Australia.

seen in *O. otales* and *O. arcana*, and in the nearest relatives of the *O. idmo* species group, *O. zosine* and *O. genoveva*. This shelter is particularly important for *O. otales* and *O. arcana*, as no loose bark or cracks are usually present on the Santalaceae shrub hosts. A concealed, underground lifestyle is likely to add further protection within the fire-prone environments of southern and south-western Australia. The close cohabitation of lycaenid larvae within the ant nests may have been a driver for the suspected entomophagous behaviour exhibited by some species (Fig. 1). Species diversification in the Theclinae-Polyommata assemblage is known to be correlated with ant entomophagy (Pierce et al. 2002; Pierce and Dankowicz 2022a). Among the non-monophyletic Theclinae, the *Ogyris idmo* species group is one of only two lineages to have undergone significant diversification that is correlated with entomophagy (Fig. 1), the other lineage being the genus *Acrodipsas* Sands, 1980 that is also endemic to Australia. Generally, other thecline genera are phytophagous, with only a single or very few species that are predatory, with species richness decreasing as obligate interactions increase (Pierce and Dankowicz 2022b). The diversity of species adopting an entomophagous larval feeding strategy in this small section of the Australian Theclinae resembles that of the host strategies adopted by the Miletinae elsewhere. The dynamics of the asymmetrical relationship between ant and butterfly in the *O. idmo* species group require further study, although the larvae are likely to be entomophagous (*sensu* Pierce et al. 2002). Lycaenids that engage in entomophagy are known to be morphologically conservative (Heath 1997), a condition apparent in the *O. idmo* group. Curiously, the four suspected entomophagous *Ogyris* species associate with only a single ant species, *Camponotus terebrans*, although *C. terebrans* very likely represents a complex of similar species (R. G. Eastwood, pers. comm.). Additionally, the evolution of the *O. idmo* species group was influenced by biogeographic factors (Schmidt et al. 2014), however this may not be truly independent of ant association if these factors have also affected the host ants.

Entomophagous relationships within Lycaenidae are always unidirectional and the highly specialised lifestyle has ultimately left these taxa more vulnerable to extinction. Indeed, butterflies in the *Ogyris idmo* species group are among the most threatened Australian Lepidoptera – our revised taxonomic classification of the group, together with the conservation status, is summarised in Table 2. Six (75%) of the eight recognised taxa are considered to be threatened, either nationally or regionally (state level). However, only one species (*Ogyris petrina*) is listed nationally under federal legislation (EPBC Act) and only one (*Ogyris halmaturia*) is listed internationally under the IUCN Red List categories, highlighting the disparity between conservation need and current listing. Clearly, there is an urgent need for re-assessment of conservation status at the national and international levels and nomination for

protective legislation for all taxa. Like other lycaenids with obligate ant interactions, these butterflies require a very high density of the associated host species within the environment. This is a biological strategy that can fail if the environment is altered by extensive habitat loss or fragmentation so as to be unfavourable for supporting high densities of host ant colonies. This risk is increased due to the species generally being highly localised. Accordingly, the species in this group are primarily threatened by widespread habitat loss and fragmentation by way of land clearing for agriculture and mining activities (Sands and New 2002).

## Supplementary material

GenBank Accession Numbers and general locality information for the molecular component of this study are included in Supplementary Table S1. Supplementary material is available [online](#).

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**Data availability.** Molecular data for this project can be found on GenBank, see Supplementary Table S1 for GenBank accession numbers. Author ZooBank numbers are as follows: Ethan Beaver, [urn:lsid:zoobank.org:author:E85BA5D9-54F9-4920-9D2A-DC7262F44BBC](https://zoobank.org/author:E85BA5D9-54F9-4920-9D2A-DC7262F44BBC); Michael Braby, [urn:lsid:zoobank.org:author:4D3A7605-EBD0-40F6-A5F2-7F67F59E3D60](https://zoobank.org/author:4D3A7605-EBD0-40F6-A5F2-7F67F59E3D60); Richard V. Glatz, [urn:lsid:zoobank.org:author:EB9E57BA-0B47-4302-8D4E-848789AA3B27](https://zoobank.org/author:EB9E57BA-0B47-4302-8D4E-848789AA3B27).

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