

Taxonomic review of *Candalides absimilis* (C. Felder, 1862) and *C. margarita* (Semper, 1879) (Lepidoptera: Lycaenidae), with descriptions of two new subspecies

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ABSTRACT

The taxonomic status of two members of the *Candalides absimilis* (C. Felder, 1862) species group from Australia is reviewed. Two new subspecies, *C. absimilis eastwoodi* ssp. nov. from north-eastern Queensland and *C. absimilis edwardsi* ssp. nov. from south-eastern Australia, are described, diagnosed and compared with related taxa. *C. gilberti* Waterhouse, 1903 from north-western and central northern Australia is shown to comprise a geographical race of *C. margarita* (Semper, 1879) based on comparative evidence of the genitalia, adult and immature stage morphology, life history and adult behaviour, and accordingly is treated as a subspecies of that taxon. Information on the distribution, habitat, conservation status and biology are summarised for each of the three taxa, with additional notes provided on the larval food plant, behaviour and life cycle of *C. absimilis edwardsi* ssp. nov, which specialises as larvae on the flush growth of *Brachychiton populneus* (Schott and Endl.) R.Br. (Sterculiaceae) growing in eucalypt woodland. Females of both *C. absimilis edwardsi* ssp. nov. and *C. margarita gilberti* are remarkable in that they comprise the only taxa within the *C. absimilis* species group from Australia in which the white patches on the fore and hind wing are replaced with blue. A striking association between habitat (broad vegetation type) and adult female phenotype in the *C. absimilis* species group is noted, with highly contrasting 'black and white forms' occurring in closed forest and less striking 'blue forms' in open forest/woodland, and this relationship is found to extend more generally within the Australian Lycaenidae. A general hypothesis, that ambient light properties among divergent habitats or vegetation types (i.e. different light environments) is a potent selective force shaping sex-limited phenotype, is proposed for these butterflies.

KEYWORDS: ambient light environment, Australian monsoon tropics, butterfly, Candalidini, Candalides, Cape York Peninsula, Iron Range, East Gippsland, sexual dimorphism.

INTRODUCTION

The tribe Candalidini of lycaenid butterflies includes about 33 species referred to two genera, *Candalides* Hübner and *Nesolycaena* Waterhouse and Turner, both of which are endemic to the Australian Zoogeographic Region (Tite 1963; Edwards and Kerr 1978; Braby 1996, 2000; Braby and Douglas 2004). Braby (2000) and Braby and Douglas (2004), building on the foundational work of Tite (1963) and Edwards and Kerr (1978), recognised three species groups within *Candalides*, viz: the *C. absimilis* (C. Felder, 1862) species group, the *C. erinus* (Fabricius, 1775) species group, and the *C. xanthopilos* (Hübner, [1817]) species group. Phylogenetic relationships among the three species groups of *Candalides* and *Nesolycaena* are unknown at present, but each taxonomic unit is assumed to comprise a monophyletic group. By far the largest species group is the *C. absimilis* species group, containing 21 described species (Parsons 1998; Braby 2000; Tennent 2006). The group is characterised by having a comparatively long labial palpus, especially in the female; the androconial scales in

the male fore wing being concentrated into a diffuse trident-shaped patch along the basal half of veins M_3 , CuA_1 and CuA_2 , as well being distributed on the adjacent veins; and the underside pattern of the wings possessing a series of small dark markings and wavy lines but usually without terminal spots, although some species have one or more black tornal spots on the hind wing. In males, the termen of the hind wing is often produced towards the tornus, and the upperside ground colour is lustrous blue; while in females, the upperside ground colour of both wings is frequently black with a prominent white central patch. Members of this species group are distributed predominantly in rainforest habitats of mainland New Guinea and its adjacent islands and the coastal areas of eastern Australia. One species also extends across the monsoon tropics of northern Australia, while another, *C. cyprotus* (Olliff, 1886), occurs in heathland habitats in the coastal, semi-arid and arid areas of southern, central and south-western Australia (Braby 2000; Grund 2006).

In the past few decades, six species in the *Candalides absimilis* species group have been recognised from the

Australian mainland (Common and Waterhouse 1972, 1981; Edwards 1996; Braby 2000; Edwards *et al.* 2001). One of these, *C. absimilis*, shows complex geographical variation, with divergent populations at the extreme northern and southern ends of the range, and three distinct forms were recognised by Braby (2000). Another taxon, *C. margarita gilberti* Waterhouse, 1903 stat. rev. from the Kimberley and Top End of north-western and central northern Australia, has hitherto been treated as a distinct species since its description, but Braby (2000) postulated that it may be conspecific with *C. margarita* (Semper, 1879), comprising a geographical subspecies closely related to the nominate subspecies from eastern Australia. The purpose of this paper is to clarify and revise the taxonomic status of the geographical forms of *C. absimilis* and the taxonomic status of *C. margarita gilberti*. Information is also summarised on the distribution, habitat, conservation status, and biology of each species. Attention is drawn to a striking association between adult female wing colour pattern and light characteristics among divergent habitats (broad vegetation types) in *Candalides*, and this relationship is found to extend more broadly within the Australian Lycaenidae.

METHODS

The male and female genitalia of *Candalides absimilis* were dissected and examined from six populations spread across the species' latitudinal range, *viz*: Cape York Peninsula (Iron Range, Mt White Coen); Wet Tropics (Shiptons Flat, Townsville); central Queensland (Mackay, Eungella); south-eastern Queensland (Eudlo); north-eastern New South Wales (Broken Head); and eastern Victoria (Mitchell River). The male and female genitalia of *C. margarita* were examined from four populations distributed across the geographical range of the species within Australia, *viz*: Top End of the Northern Territory (Darwin, Adelaide River); Gulf Country of western Queensland (Musselbrook, near Lawn Hill National Park); Wet Tropics (Paluma Range west of Townsville); and north-eastern New South Wales (Grafton).

The size of the white central patch in female *Candalides absimilis* was analysed quantitatively across the species geographical (latitudinal) range. Specimens ($N=173$) from seven populations spread along the eastern coast, *viz*: (1) Cape York Peninsula (Iron Range); (2) Wet Tropics (Cairns-Townsville); (3) central Queensland (Mackay-Eungella); (4) south-eastern Queensland (Brisbane); (5) central New South Wales (Sydney); (6) south-eastern coastal New South Wales (Central Tilba-Bega); and (7) eastern Victoria (East Gippsland), were measured to assess the extent of geographical variation. Thirty specimens were sampled from each population, except for Cape York Peninsula and central Queensland for which only eight and 15 specimens were available respectively. The shape of the white patch on

both wings is either an ellipse or approximately circular; the area of the patch was therefore calculated using the formula $\pi r_1 r_2$, where r_1 = radius 1, and r_2 = radius 2. For the fore wing, r_1 was measured along the cubitus and vein M_3 , while r_2 was measured perpendicular to r_1 , from the mid costa to tornus; for the hind wing, r_1 was measured along vein M_2 , while r_2 was measured perpendicular to r_1 , from the apex to tornus. Radial measurements were made with vernier callipers to a precision of 0.1 mm. Fore wing length, from the base to the apex of the wing, was measured for each specimen as a proxy for body size.

The following abbreviations refer to repositories where material has been examined:

- AMS: Australian Museum, Sydney
- ANIC: Australian National Insect Collection, Canberra
- BMNH: Natural History Museum, London (formerly British Museum of Natural History)
- MCZ: Museum of Comparative Zoology, Harvard University, USA
- MFBC: private collection of Michael Braby
- MTQ: Museum of Tropical Queensland, Townsville
- NMV: Museum Victoria, Melbourne (formerly National Museum of Victoria)
- NTM: Museum and Art Gallery of the Northern Territory, Darwin (formerly Northern Territory Museum)
- SAM: South Australian Museum, Adelaide

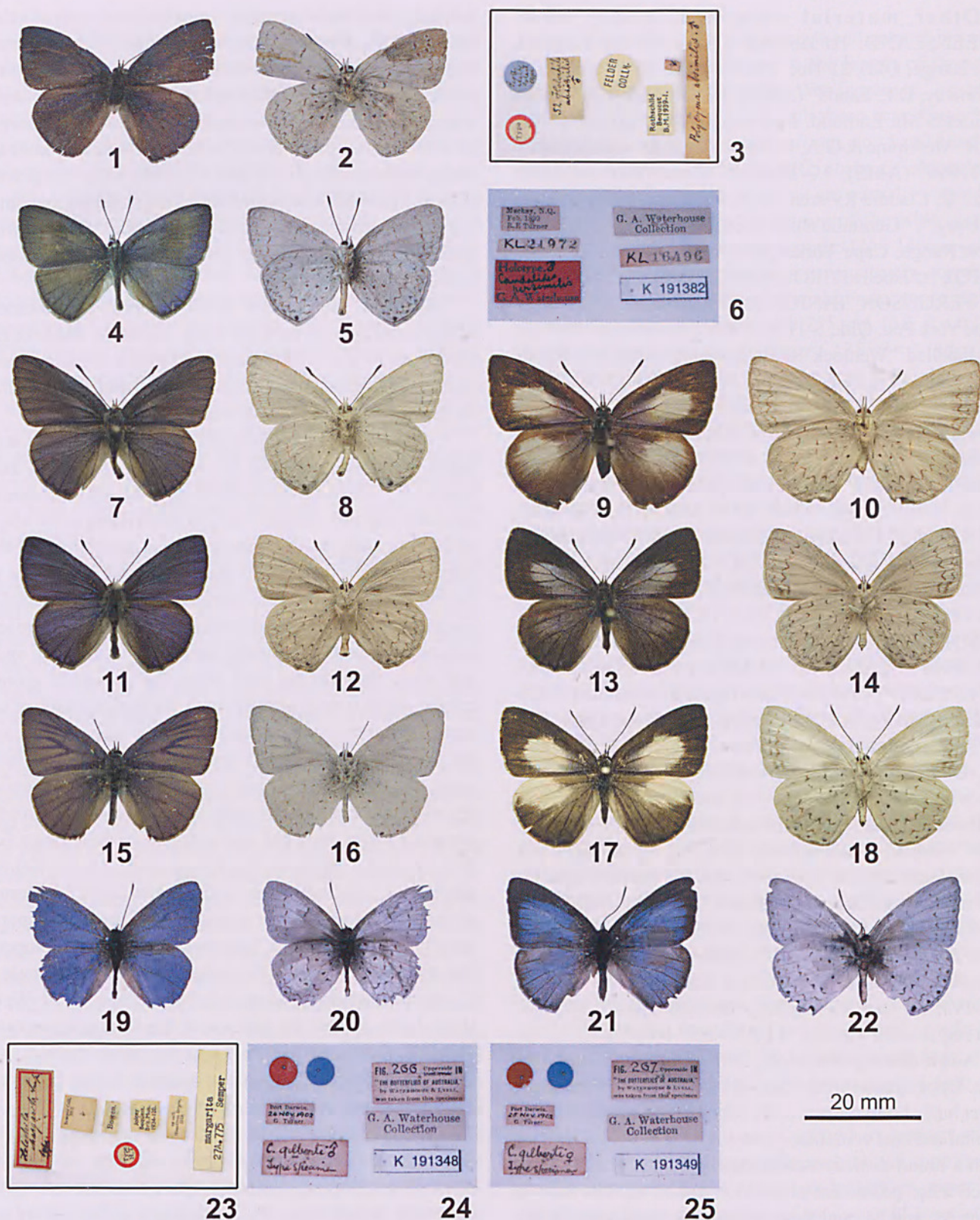
Label data of all material are given as depicted on the specimen, with quotation marks used to designate each separate label for specimens with two or more labels. The symbol "[]" is used to denote text on the reverse side of a label.

TAXONOMY

Candalides absimilis eastwoodi ssp. nov.

(Figs 7–10, 26)

Type material. HOLOTYPE – ♂ labelled "MT. WHITE, COEN, 7 JAN 1994, R. EASTWOOD" (ANIC). PARATYPES – 14♂♂, 3♀♀. QUEENSLAND: 1♀ labelled "CLAUDIE R., 29 12 13", "LEP-9841" (NMV); 1♀ labelled similarly but with date "18 2 1914", registration number "LEP-9837" (NMV); 1♀ labelled similarly but with date "5 4 14", registration number "LEP-9840" (NMV); 2♂ labelled "Claudie. R. Nth. Q., 5/16-V-61, J. Macqueen" (ANIC); 1♂ labelled "Mount White, Coen, Qld, 13°58'S 143°11'E, 29 Apr 1989, G. and A. Daniels", "G. Daniels Collection" (AMS); 4♂ labelled "Mt White, Coen, Qld, 13°58'S 143°11'E, 7 Jan 1994 447m, G. and A. Daniels", "G. Daniels Collection" (AMS); 3♂ labelled "MT. WHITE, COEN, 7 JAN 1994, R. EASTWOOD" (ANIC); 4♂ labelled similarly but with date "12 JAN 1994" (ANIC).



Figs 1-25. Type material of *Candalides absimilis* and *C. margarita*: 1-3, *Holochila absimilis* C. Felder, 1862 lectotype male from Ash Island, NSW (BMNH), showing upperside, underside and specimen labels; 4-6, *C. persimilis* Waterhouse, 1942 lectotype male from Mackay, Qld (AMS), showing upperside, underside and specimen labels; 7-8, *C. absimilis eastwoodi* ssp. nov. holotype male from Mount White, Coen, Qld (ANIC), showing upperside and underside; 9-10, *C. absimilis eastwoodi* ssp. nov. paratype female from Iron Range, Qld (NMV), showing upperside and underside; 11-12, *C. absimilis edwardsi* ssp. nov. paratype male from Mitchell River National Park, Vic. (NMV), showing upperside and underside; 13-14, *C. absimilis edwardsi* ssp. nov. holotype female from Suggan Buggan, Alpine National Park, Vic. (ANIC), showing upperside and underside; 15-16, 23, *Holochila margarita* Semper, 1879 lectotype male from Bowen, Qld (BMNH), showing upperside, underside and specimen labels; 17-18, *C. margarita margarita* female from Bluewater State Forest west of Townsville, Qld (MFBC), showing upperside and underside; 19-20, 24, *C. gilberti* Waterhouse, 1903 lectotype male from Darwin, NT (AMS), showing upperside, underside and specimen labels; 21-22, 25, *C. gilberti* paralectotype female from Darwin, NT (AMS), showing upperside, underside and specimen labels. Scale bar = 20 mm.

Other material examined. 23♂♂, 6♀♀. QUEENSLAND: 1♂ labelled "1 mile NE Mt. Lamond, Iron Range, Qld., 21 Dec. 1971", "D.K. McAlpine, G.A. Holloway, D.P. Sands" (AMS); 1♀ labelled "Claudie R., 2 miles S Mt. Lamond, Iron Range, Qld., 13 Jan. 1972", "D.K. McAlpine & G.A. Holloway", "Australian Museum K231664" (AMS); 1♀ labelled "*Candalides consimilis* toza? ♀, Claudie Rv area. N.Q., 4 January 1974, Shane F McEvey.", "Genitalia Slide M345" (ANIC); 1♂ labelled "Iron Range, Cape York. Qld, 13.xi.1991, S.J. Johnson" (MTQ); 1♂ labelled "IRON RANGE, N. Qld, 25 Nov. 1995, D J FERGUSON" (ANIC); 2♂, 1♀ labelled "Iron Range, Cape York Pen. Qld., 5-11.xii.1995, S.J. Johnson" (MTQ); 1♀ labelled "Wenlock River crossing, Coen-Iron Range road, Cape York Pen., N. Qld., 10 Sep. 1974, M.S. & B.J. Moulds", "M.S. MOULDS COLLECTION", "Australian Museum K231665" (AMS); 1♀ labelled "Rocky River (nth of Silver Plains), Qld, 13°48.415'S, 143°28.201'E, 27 Jul 2005, R.P. Field", "LEP-48088" (NMV); 1♂ labelled "Mt White, Coen, N. Qld, 5 Nov. 1979, M.S. & B.J. Moulds", "M.S. MOULDS COLLECTION" (AMS); 1♂ labelled "Mount White, Coen, Qld, 13°58'S 143°11'E, 29 Apr 1989, G. and A. Daniels", "G. Daniels Collection" (AMS); 1♂ labelled "Mt. White, Coen. Qld., 19.i.1993, S.J. Johnson" (MTQ); 1♂ labeled "Mt White, Coen, Qld, 10 Jul 1993, R.P. Field", "LEP-44854" (NMV); 1♂ labelled similarly but with date "11 Jul 1993" and registration number "LEP-44855" (NMV); 1♂, 1♀ labelled "Mt White, Coen, Qld, 13°58'S 143°11'E, 7 Jan 1994 447m, G. and A. Daniels", "G. Daniels Collection" (AMS); 1♂ labelled similarly but with date and collector "12 Jan 1994, G. Daniels R. Eastwood" (AMS); 2♂ labelled "MT. WHITE, COEN, 7 JAN 1994, R. EASTWOOD" (MCZ); 3♂ labelled "Mt. White, Coen. QLD., 27.iv.1997, S.J. JOHNSON" (MTQ); 3♂ labelled similarly but with date "9.v.1998" (MTQ); 1♂ labelled "Mt White, Coen, Qld, 13°58.035'S, 143°11.538'E, 4 Jul 2005, R.P. Field", "LEP-48086" (NMV); 1♂ labelled similarly but with registration number "LEP-48087" (NMV); 1♂ labelled similarly but with date "5 Jul 2005" and registration number "LEP-48085" (NMV).

Adult description. *Male.* Fore wing length 16.4–19.2 mm. Upperside of wings lilac-blue, with costa, termen and outer half of dorsum narrowly edged black, radial, median, cubital and anal veins black towards wing margin; fore wing with a broad distinct median patch of androconial scales, patch more prominent at anterior end of cell and base of veins M_1 and M_2 and their origin with the discocellulars, at base of veins M_3 , CuA_1 and CuA_2 and their origin with the cubital vein (Cu), and along vein $1A+2A$; hind wing with a conspicuous black tornal spot between ends of veins CuA_2 and $1A+2A$, and a smaller indistinct black terminal spot between ends of veins CuA_1 and CuA_2 . Underside of wings silvery white, with a series of small dark brown markings and a narrow dark brown termen; hind wing with a conspicuous dark brown tornal spot between ends of veins CuA_2 and $1A+2A$, and sometimes a series of four smaller

indistinct dark brown terminal spots between ends of veins M_1 and CuA_2 . *Female.* Fore wing length 17.2–19.8 mm. Upperside of wings black enclosing a large white central patch, base suffused with purplish blue scales; fore wing with purplish blue scales extending along posterior margin of white central patch above vein $1A+2A$ and sometimes along anterior margin of patch in cell; hind wing with scattered purplish blue scales bordering posterior and outer margins of white central patch. Underside of wings with ground colour and markings similar to male, but markings usually more distinct.

Variation. Males show minor variation in the extent of the tornal spot on the hind wing, and in the shape of the hind wing in which the termen and tornus are sometimes rounded. In females, the extent of the white central patch on the upperside of the hind wing varies.

Comparison. *Candalides absimilis eastwoodi* ssp. nov. males are distinct and can be readily distinguished from males of *C. absimilis absimilis* (Figs 1–6) and *C. absimilis edwardsi* ssp. nov. (Figs 11–12) by differences in the shape of the fore wing in which the termen is straighter and less convex, and the apex more sharply pointed; the shape of the hind wing in which the tornus is generally produced to a point; the extent of the underside markings, which are less conspicuous and only faintly visible, especially the spots and wavy lines on the hind wing; the upperside ground colour, which is paler purplish blue; the median patch of sex scales on the fore wing, which is more clearly visible; and the extent of the black/dark brown tornal spot on the hind wing, which is generally more prominent on the upperside and always present on the underside. *Candalides absimilis absimilis* males from the northern end of their range (i.e. Wet Tropics – between Cooktown and Townsville) are similar to *C. absimilis eastwoodi* ssp. nov. in that the tornus of the hind wing is often produced and the tornal spot is usually present (though usually not as well developed), but otherwise more closely resemble the lectotype male of *C. absimilis absimilis* from Ash Island, New South Wales (Figs 1, 2), in that the termen of the fore wing is more rounded, the underside markings are more distinct, and the upperside ground colour is brighter/deeper blue with the patch of sex scales less clearly visible.

Candalides absimilis eastwoodi ssp. nov. females differ from *C. absimilis edwardsi* ssp. nov. females by possessing a large, conspicuous white central patch on the upperside of each wing. The white patch on the fore wing is similar in size to that of *C. absimilis absimilis* populations from south of the Wet Tropics (i.e. Mackay-Sydney), but apparently smaller than those from the Wet Tropics (i.e. Cooktown-Townsville). The white patch on the hind wing of *C. absimilis eastwoodi* ssp. nov., however, is substantially larger than populations of *C. absimilis absimilis* from south of the Wet Tropics, but significantly smaller than those from the Wet Tropics (see quantitative analysis below under Remarks).

Candalides absimilis eastwoodi ssp. nov. has previously been confused with *C. consimilis* Waterhouse, 1942 (Dunn *et al.* 1994; Dunn 1995) to which it closely resembles. On Cape York Peninsula, *C. consimilis* is known only from Iron Range and has been separated as the northern subspecies *C. consimilis toza* Kerr, 1967. Dunn *et al.* (1994) initially placed material from Mount White near Coen with *C. consimilis toza*, which is known only from a few male specimens (Kerr 1967), but later considered them to belong to an undescribed subspecies of *C. consimilis* closely allied to *C. consimilis toza* (Dunn 1995). However, the valva of the male genitalia (Fig. 26) and sinus vaginalis of the female genitalia (not illustrated) clearly indicate that the population from Mount White belongs with *C. absimilis* and not with *C. consimilis*. Also, males of *C. absimilis eastwoodi* ssp. nov. are distinguished from those of *C. consimilis toza* by the absence of a conspicuous series of black terminal spots on the upperside of the fore and hind wings, particularly between the ends of veins M_1 and CuA_2 .

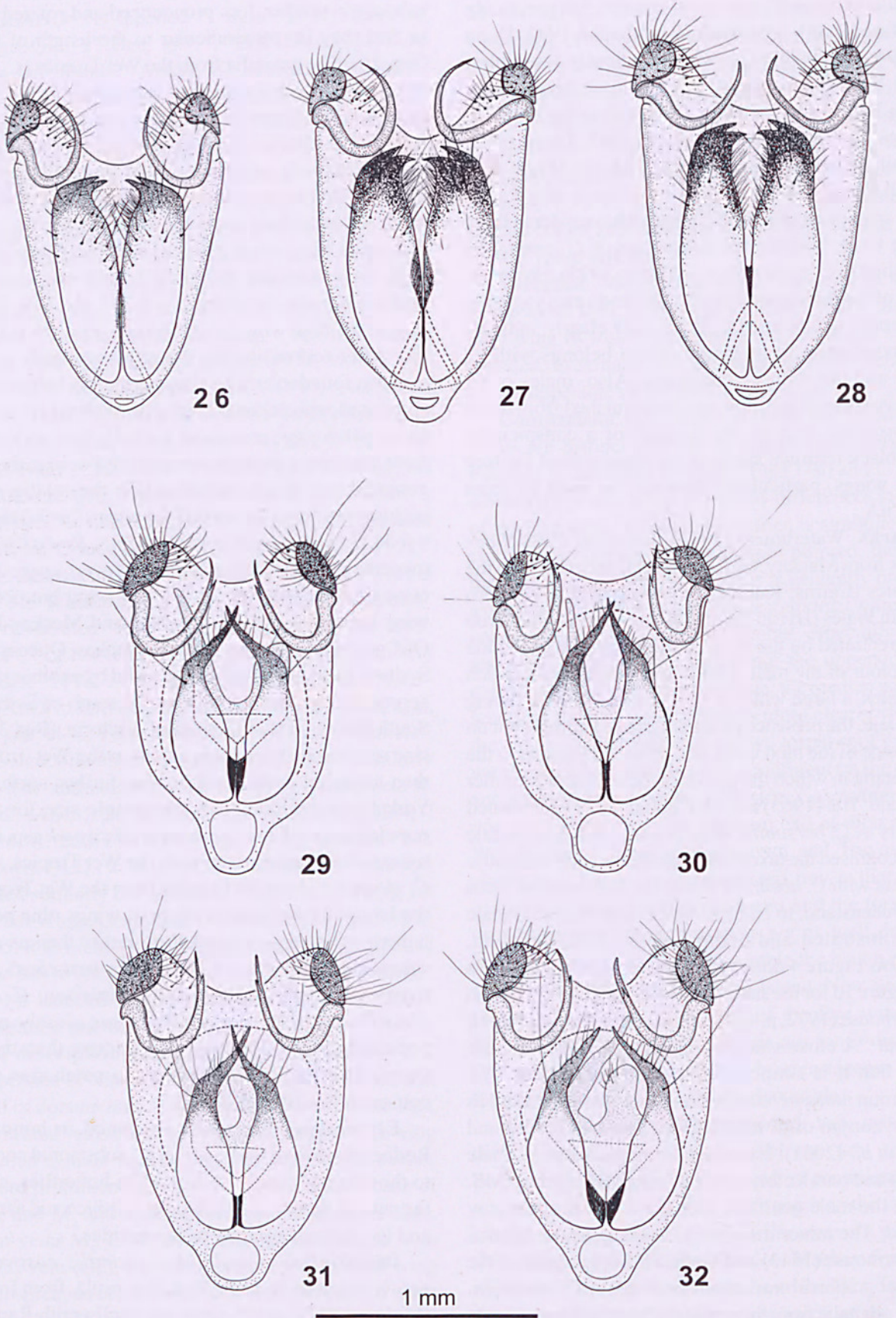
Remarks. Waterhouse (1942) described *Candalides persimilis* from Mackay, Qld, and placed material from the Wet Tropics (Cairns, Kuranda) and coastal north-eastern New South Wales (Byron Bay) with that species. The taxon was differentiated on the basis of the paler lilac upperside ground colour of the male with a more conspicuous patch of sex-scales, a large white central patch on the fore wing of the female, the presence of a distinct black tornal spot on the underside of the hind wing, and minor differences in the male genitalia in which the apices of the valvae are smaller and truncate. Tite (1963) and McCubbin (1971) questioned the validity of *C. persimilis* Waterhouse, 1942, but Tindale (1965) recognised the taxon and indicated a wide sympatric distribution with *C. absimilis* along the eastern coast, from Cairns, Queensland, to Narara, New South Wales. Tindale crudely illustrated and compared the male genitalia, although his Figure 4 does not match that of Waterhouse's (1942) Figure 1d for the same structural character. Common and Waterhouse (1972, p. 415) did not recognise the species, noting that "A close study of *C. persimilis* Waterhouse suggests that it is simply a form of *C. absimilis*." The species group name *persimilis* was subsequently treated as a junior synonym of *C. absimilis* by Edwards (1996) and Edwards *et al.* (2001). Examination of the lectotype male (Figs 4-6) and paralectotypes of *C. persimilis* in the AMS, including the male genitalia, indicate that this synonymy is justified. The minor differences in the genitalia alluded to by Waterhouse (1942) and Tindale (1965) are part of the overall geographical variation observed in *C. absimilis*. The male genitalia from three widely dispersed populations (Cape York Peninsula, south-eastern Queensland, eastern Victoria) are illustrated in Figures 26-28. The genitalia show minor geographical variation, particularly in their overall size and in the shape of the valvae. In the northernmost population (*C. absimilis eastwoodi* ssp. nov.), the genitalia are consistently smaller, and the bifurcated apices of the

valvae are smaller, less pronounced and rotated inwardly so that they lie perpendicular to the length of the valva (Fig. 26). The genitalia from the Wet Tropics (*C. absimilis absimilis*) appear transitional with those from Cape York Peninsula (*C. absimilis eastwoodi* ssp. nov.) and Mackay-Eungella in central Queensland (*C. absimilis absimilis*) in having relatively small apices that are partially rotated.

Quantitative analysis of the size of the white central patch of *Candalides absimilis* females ($N = 140$) revealed that patch size, when present, was positively correlated with body size, and this relationship was more tightly correlated in the fore wing ($r = 0.755$, d.f. 138, $P < 0.001$) than in the hind wing ($r = 0.560$, d.f. 138, $P < 0.001$) (Fig. 33). After controlling for the effects of body size, patch size was found to exhibit clinal variation, being negatively correlated with latitude (Fig. 34). Analysis of variance of mean patch size, measured for both fore and hind wing from the seven populations sampled across the species' geographical range, revealed that the relationship was highly significant for each (fore wing: $F = 7.348$, d.f. 5, $P = 0.0422$; hind wing: $F = 11.990$, d.f. 5, $P = 0.0180$). Closer inspection of the relationship, however, suggests a steep cline in this character for the hind wing but not the fore wing between Cairns-Townsville and Mackay-Eungella, Qld, negligible change between Mackay, Queensland, and Sydney, New South Wales, followed by another steep cline approaching a step for both wings south of Sydney, New South Wales, to East Gippsland, Victoria. (Fig. 34). Patch size reached its maximum extent in the Wet Tropics, and then appeared to diminish in size further north on Cape York Peninsula, although the sample size for the latter population ($n = 8$ for *C. absimilis eastwoodi* ssp. nov.) was too small for comparison with the Wet Tropics. Although *C. absimilis absimilis* females from the Wet Tropics have the largest white patches on both wings, this population is better treated as a local form rather than as a distinct subspecies until more *C. absimilis eastwoodi* ssp. nov. females become available for comparison. *C. absimilis absimilis* females from Mackay more closely resembled populations from Brisbane and Sydney than those from Cairns-Townsville with respect to patch size (see also comments by Tite 1963).

Etymology. The taxon is named in honour of Dr Rodney Eastwood who has made a substantial contribution to the scientific study of Australian butterflies, especially the natural history and ecology of ant-lycaenid associations and the phylogeography of Lycaenidae.

Distribution. *Candalides absimilis eastwoodi* ssp. nov. is restricted to Cape York Peninsula, from Iron Range (McEvey 1977) south along the McIlwraith Range to the Rocky River north of Silver Plains (R.P. Field) and Mt White near Coen, Queensland (Braby 2000) (Fig. 35). It is known from six sites (i.e. point localities > 1 km apart) representing four discrete locations (i.e. areas > 10 km apart). The subspecies is probably endemic to the mid-peninsula rainforest block (Iron Range-McIlwraith Range)



Figs. 26-32. Male genitalia of *Candalides absimilis* and *C. margarita*, showing ventral view, with aedeagus removed: 26, *C. absimilis eastwoodi* ssp. nov. from Iron Range, Qld; 27, *C. absimilis absimilis* from Eudlo, Qld; 28, *C. absimilis edwardsi* ssp. nov. from Mitchell River, Vic.; 29, *C. margarita gilberti* from Darwin, NT; 30, *C. margarita gilberti* from Musselbrook, Gulf of Carpentaria, Qld; 31, *C. margarita margarita* from the Paluma Range west of Townsville, Qld; 32, *C. margarita margarita* from Grafton, NSW. Scale bar = 1 mm.

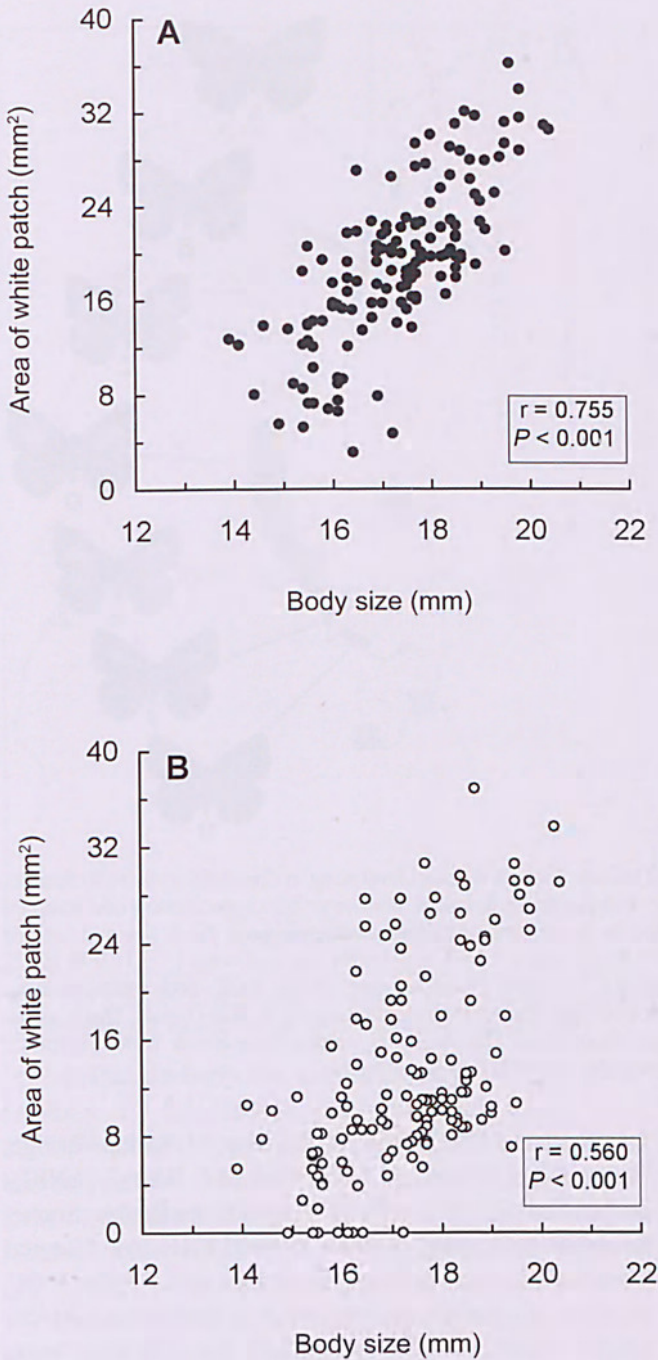


Fig. 33. Relationship between body size (measured as fore wing length) and size of white patch for each wing in *Candalides absimilis* females: A, fore wing; B, hind wing. Correlations are significant for both wings ($P < 0.001$).

of Cape York Peninsula, which is geographically separated from the Wet Tropics where the nominate subspecies *C. absimilis absimilis* reaches its northernmost limit at Cooktown, Queensland.

Despite reports to the contrary, *Candalides absimilis eastwoodi* ssp. nov. has not been recorded further north than the tip of Cape York Peninsula and the Torres Strait islands. These reports were found, on closer inspection, to be erroneous. A male labelled "Prince of Wales Is., 9 June 1908, H. Elgner.", "LEP-9890", "Seems to belong with *Candalides absimilis* Feld., det K.L. Dunn 1989" (NMV)

is considered to have been mislabelled and excluded from the material examined. Dunn and Dunn (1991) considered the record to be reliable and included Prince of Wales Island from southern Torres Strait islands in their review of the distribution of the species. A detailed chronology of Elgner's geographical movements in the Torres Strait islands and Cape York, based on insect specimens that he collected (Moulds 1977; Dunn 2007), indicate that for the period 28 April–19 July 1908, Elgner was stationed on Prince of Wales Island, so he would have had access to the island in June 1908. However, Elgner's specimen of *C. absimilis* does not agree with the characteristics of *C. absimilis eastwoodi* ssp. nov. It lacks the straight termen and pointed apex of the fore wing, paler upperside ground colour, and indistinct markings on the underside; it more closely resembles *C. absimilis absimilis* from south-eastern Queensland and New South Wales. Moreover, examination of the genitalia indicates that it conforms with typical *C. absimilis absimilis* (Fig. 27) and not to *C. absimilis eastwoodi* ssp. nov. (Fig. 26). Dunn (2007) noted a high level of accuracy in Elgner's label data; therefore, it is possible the specimen was mislabelled by subsequent curators. Two male specimens of *C. margarita margarita* in AMS labelled "Horn Is. Q., 25.6.43" and "Cape Yk. Q., 25.6.43" were found to have been misidentified as *C. absimilis* in the drawers of the main reference collection.

Biology. The early stages and larval food plants of *Candalides absimilis* have not been recorded. Adults have been collected in September, from November to February and in April, May and July, with most specimens collected during the 'build-up' and early wet season. Available data on adult phenology suggests the subspecies is on the wing throughout the year. Near Coen, males have been collected hilltopping at the summit of Mount White (R.G. Eastwood, personal communication; D.A. Lane, personal communication), a behaviour that appears to be largely absent in the two other subspecies (except for the population of *C. absimilis absimilis* in the Wet Tropics, which has been recorded hilltopping at Mt Stuart Townsville, M.F. Braby unpublished data).

Conservation status. *Candalides absimilis eastwoodi* ssp. nov. has a narrow geographical range, with an estimated extent of occurrence of 4,500 km². Available data suggests the subspecies is restricted to tropical forest of the mid-peninsula rainforest block of Cape York Peninsula (i.e. Iron Range–McIlwraith Range), most of which is now protected in the Iron Range and McIlwraith National Parks. There is no information on population trends, fragmentation of populations, or immediate threatening processes impacting on the known sites, and the ecology of the subspecies is very poorly known. Although the range of the taxon is suspected to be relatively circumscribed, there is inadequate information to make a direct assessment of the risk of threat. Its conservation status should therefore be regarded as Data Deficient (DD) according to IUCN criteria.

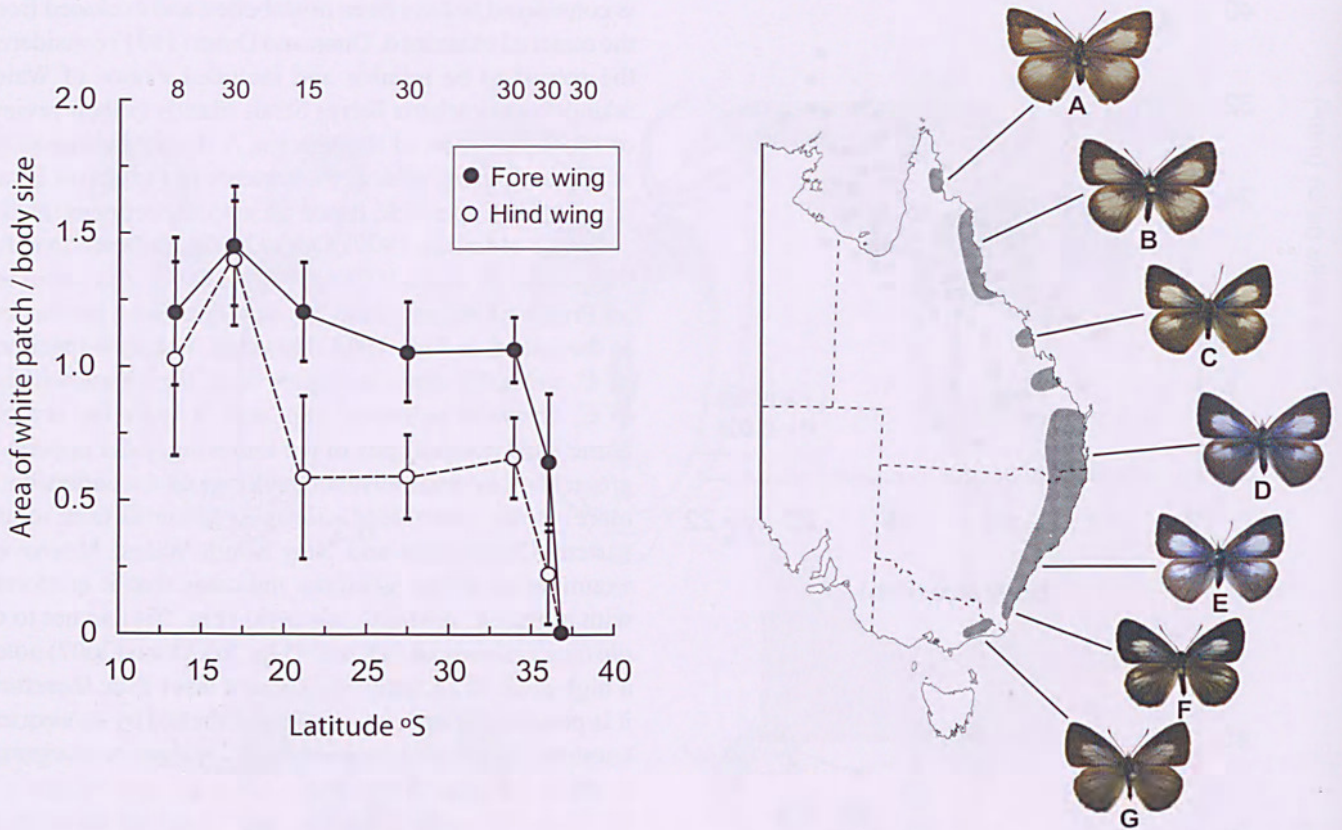


Fig. 34. Relationship between size of white patch divided by body size and latitude for both fore and hind wing in *Candalides absimilis* females sampled from seven populations across the species' geographical range. Points are mean values with error bars representing one standard deviation. Sample sizes are shown above graph. Regression equations for the significant relationship between mean patch size and latitude are as follows: $y = 1.984 - 0.0388x$ for fore wing ($F = 7.348$, $d.f. 5$, $P = 0.0422$), and $y = 1.733 - 0.0409x$ for hind wing ($F = 11.990$, $d.f. 5$, $P = 0.0180$). Accompanying map of eastern Australia shows distribution of *C. absimilis* (modified from Braby 2000), with examples from each of the seven geographical areas, as follows: A, Cape York Peninsula, Qld (Iron Range-McIlwraith Range); B, Wet Tropics, Qld (Cairns-Townsville); C, central Queensland (Mackay-Eungella); D, south-eastern Queensland (Brisbane); E, central New South Wales (Sydney); F, south-eastern coastal New South Wales (Central Tilba-Bega); and G, eastern Victoria (East Gippsland).

***Candalides absimilis edwardsi* ssp. nov.**

(Figs 11-14, 28)

Type material. HOLOTYPE – ♀ labelled “36°56’S, 148°21’E; 600m, 7 km N Suggan Buggan (by rd), Alpine NP, VIC., emg. 6 JAN. 2003, M.F. Braby & L.J. Aitchison”, “Reared from larva on *Brachychiton populneus*, coll. 8-9 DEC. 2002, pupated 25 DEC. 2002” (ANIC). PARATYPES – 15♂♂, 14♀♀. NEW SOUTH WALES: 1♀ labelled “36°45’S, 148°25’E; 300m, 18 km N Willis (by road), Kosciuszko NP, NSW; emg. 13 JAN. 2003, M.F. Braby & L.J. Aitchison”, “Reared from larva on *Brachychiton populneus*, coll. 10 DEC. 2002, pupated 2 JAN. 2003” (AMS). VICTORIA: 1♀ labelled “36°56’S, 148°21’E; 600m, 7 km N Suggan Buggan (by rd), Alpine NP, VIC., emg. 4 JAN. 2003, M.F. Braby & L.J. Aitchison”, “Reared from larva on *Brachychiton populneus*, coll. 8-9 DEC. 2002, pupated 23 DEC. 2002” (NMV); 1♂ labelled similarly but with dates “emg. 5 JAN. 2003”, “pupated 22 DEC. 2002” (AMS); 1♀ labelled similarly but with dates “emg. 12 JAN. 2003”, “pupated 31 DEC. 2002” (AMS); 1♂ labelled similarly but with dates “emg. 15 FEB. 2003”, “pupated 29 DEC. 2002” (NMV); 1♂ labelled similarly but with dates “emg. 17 OCT. 2003”, “pupated 30 DEC. 2002” (ANIC);

1♂ labelled “37°05’S, 148°24’E; 200m, McKillops Bridge, Snowy River NP, VIC., 3 JAN. 2004, M.F. Braby” (ANIC); 1♂ labelled “37°05’S, 148°24’E, McKillops Bridge, Snowy River NP, VIC., emg. 23 JAN. 2004, M.F. Braby”, “Reared from larva on *Brachychiton populneus*, coll. 3 JAN. 2004” (NMV); 1♂ labelled similarly but with date “emg. 27 JAN. 2004” (AMS); 1♂ labelled similarly but with date “emg. 28 JAN. 2004” (AMS); 1♀ labelled similarly in NMV; 1♂, 1♀ labelled but with date “emg. 29 JAN. 2004” (ANIC); 1♂ labelled similarly in NMV; 1♀ labelled similarly in AMS; 1♂ labelled “37°29’S, 148°09’E, Buchan Caves Reserve, VIC; 100m, emg. 10 JAN. 2004, M.F. Braby”, “Reared from larva on *Brachychiton populneus*, coll. 19-21 DEC. 2003” (ANIC); 1♂ labelled similarly but with date “emg. 12 JAN. 2004” (AMS); 1♀ labelled similarly in NMV; 1♂ labelled similarly but with date “emg. 15 JAN. 2004” (NMV); 1♀ labelled similarly but with date “emg. 16 JAN. 2004” (ANIC); 1♀ labelled “37°42’S, 147°21’E, Den of Nargun, Mitchell River NP, VIC., emg. 7 JAN. 2003, M.F. Braby & L.J. Aitchison”, “Reared from egg on *Brachychiton populneus*, coll. 6-7 DEC. 2002, pupated 24 DEC. 2002” (ANIC); 1♂ labelled similarly but with dates “emg. 9 JAN. 2003”, “pupated 28 DEC. 2002” (NMV);

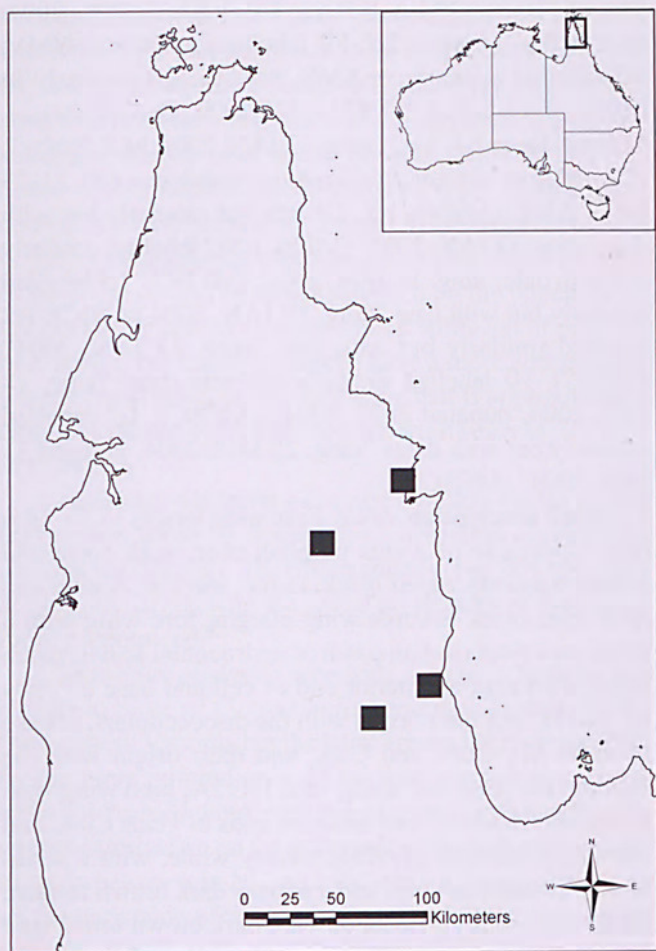


Fig. 35. Map of Cape York Peninsula showing geographical distribution of *Candalides absimilis eastwoodi* ssp. nov. (■).

1♂ labelled similarly but with date "emg. 10 JAN. 2003" (ANIC); 1♀ labelled similarly but with dates "emg. 12 JAN. 2003", "pupated 30 DEC. 2002" (AMS); 1♀ labelled similarly but with date "pupated 31 DEC. 2002" (NMV); 1♀ labelled "37°42'S, 147°21'E, Den of Nargun, Mitchell River NP, VIC., 23 DEC. 2003, M.F. Braby & L.J. Aitchison" (ANIC); 1♀ labelled similarly in AMS; 1♀ labelled "37°42'S, 147°21'E, Den of Nargun, Mitchell River NP, VIC., emg. 15 JAN. 2004, M.F. Braby", "Reared from larva on *Brachychiton populneus*, coll. 21-23 DEC. 2003" (NMV); 1♂ labelled similarly but with date "emg. 19 JAN. 2004" (AMS).

Other material examined. 61♂♂, 32♀♀. NEW SOUTH WALES: 1♂ labelled "36°45'S, 148°25'E; 300m, 18 km N Willis (by road), Kosciuszko NP, NSW; 10 DEC. 2002, M.F. Braby & L.J. Aitchison" (ANIC); 1♂ labelled similarly in NMV; 1♂ labelled similarly in AMS; 1♂ labelled "36°45'S, 148°25'E; 300m, 18 km N. Willis, Kosciuszko NP, NSW; emg. 3 MAR. 2003, M.F. Braby", "Reared from larva on *Brachychiton populneus*, coll. 10 DEC. 2002, pupated 2 JAN. 2003" (MFBC). VICTORIA: 1♂ labelled "36°56'S, 148°21'E; 600m, 7 km N Suggan Buggan (by rd), Alpine NP, VIC., emg. 4 JAN. 2003, M.F. Braby & L.J. Aitchison", "Reared from larva on *Brachychiton populneus*, coll. 8-9 DEC. 2002, pupated 22 DEC. 2002" (MFBC); 1♀ labelled

similarly but with date "pupated 23 DEC. 2002" (MFBC); 1♀ labelled "37°05'S, 148°24'E, McKillops Bridge, Snowy River NP, VIC., emg. 29 JAN. 2004, M.F. Braby", "Reared from larva on *Brachychiton populneus*, coll. 3 JAN. 2004," (MFBC); 1♂ labelled similarly but with date "emg. 30 JAN. 2004" (MFBC); 1♀ labelled similarly but with dates "emg. 30 AUG. 2004, pupated late JAN. 2004" (MFBC); 1♀ labelled similarly but with date "emg. 10 SEP. 2004" (NMV); 1♂ labelled "Buchan Caves, Buchan, Vic, 37°30.16'S, 148°9.51'E, 11 Jan 2003, R.P. Field", "LEP-46133" (NMV); 1♂ labelled similarly but with registration number "LEP-46134" (NMV); 1♂ labelled similarly but with registration number "LEP-46135" (NMV); 1♀ labelled "Buchan Caves, Buchan, Vic, 37°29.63'S, 148°10.08'E, 13 Dec 2003, R.P. Field", "LEP-46197" (NMV); 1♀ labelled similarly but with date "17 Jan 2004" and registration number "LEP-46201" (NMV); 1♀ labelled similarly but with date "em 20 Feb 2004" and registration number "LEP-46202" (NMV); 1♀ labelled similarly but with date "em 27 Feb 2004" and registration number "LEP-46203" (NMV); 1♂ labelled similarly but with registration number "LEP-46204" (NMV); 1♂ labelled similarly but with date "em 22 Sept 2004" and registration number "LEP-46789" (NMV); 1♂ labelled similarly but with registration number "LEP-46790" (NMV); 1♂ labelled similarly but with date "em 29 Sept 2004" and registration number "LEP-46785" (NMV); 1♂ labelled similarly but with registration number "LEP-46786" (NMV); 1♂ labelled similarly but with date "em 5 Jan 2005" and registration number "LEP-46799" (NMV); 1♂ labelled similarly but with registration number "LEP-46800" (NMV); 1♂ labelled similarly but with date "em 25 Jan 2005" and registration number "LEP-46903" (NMV); 1♂ labelled similarly but with registration number "LEP-46904" (NMV); 1♂ labelled similarly but with registration number "LEP-46905" (NMV); 1♂ labelled similarly but with registration number "LEP-46906" (NMV); 1♀ labelled similarly but with date "em 26 Jan 2005" and registration number "LEP-46901" (NMV); 1♀ labelled similarly but with registration number "LEP-46902" (NMV); 1♂ labelled similarly but with date "em 27 Jan 2005" and registration number "LEP-46897" (NMV); 1♂ labelled similarly but with registration number "LEP-46898" (NMV); 1♂ labelled similarly but with registration number "LEP-46899" (NMV); 1♀ labelled similarly but with registration number "LEP-46900" (NMV); 1♀ labelled similarly but with date "em 28 Jan 2005" and registration number "LEP-47218" (NMV); 1♀ labelled similarly but with registration number "LEP-47219" (NMV); 1♀ labelled similarly but with date "em 29 Jan 2005" and registration number "LEP-47220" (NMV); 1♀ labelled similarly but with date "em 30 Jan 2005" and registration number "LEP-47221" (NMV); 1♀ labelled similarly but with registration number "LEP-47222" (NMV); 1♀ labelled "37°29'S, 148°09'E, Buchan Caves Reserve, VIC; 100m, emg. 11 JAN. 2004, M.F. Braby", "Reared from larva on *Brachychiton populneus*, coll. 19-21 DEC. 2003" (MFBC); 1♀ labelled similarly but with

date "emg. 12 JAN. 2004" (MFBC); 1♂ labelled similarly but with date "emg. 17 JAN. 2004" (MFBC); 1♂ labelled similarly but with dates "emg. 17 FEB. 2004, pupated DEC. 2003" (MFBC); 1♂ labelled similarly but with dates "emg. 10 JUL. 2004, pupated JAN. 2004" (MFBC); 1♂ labelled similarly but with dates "emg. 12 SEP. 2004, pupated late DEC. 2003" (MFBC); 1♂ labelled "VIC Den of Nargun, 40 km NE Stratford, 37°42'S 147°21'E, 7 December 1977, Shane F. McEvey", "S.F. McEvey B1000♂" (AMS); 1♂ labelled similarly but with registration number "S.F. McEvey B1001♂" (AMS); 1♂ labelled similarly but with registration number "S.F. McEvey B1002♂" (AMS); 1♂ labelled "VIC The Amphitheatre, Billy Goat Bend, Mitchell River, 37°40'S 147°22'E, 8.xii.1977 S.F. McEvey", "S.F. McEvey B1008♂" (AMS); 1♂ labelled similarly but with registration number "S.F. McEvey B1009♂" (AMS); 1♂ labelled similarly but with registration number "S.F. McEvey B1010♂" (AMS); 1♂ labelled similarly but with registration numbers "S.F. McEvey B1011♂", "Australian Museum K233023" (AMS); 1♀ labelled similarly but with registration numbers "S.F. McEvey B1006♀", "Australian Museum K233021" (AMS); 1♀ labelled "VIC 1km upriver from The Amphitheatre on Billy Goat Bend, Mitchell River, 37°39'S 147°21'E, 9.xii.1977 S.F. McEvey", "S.F. McEvey B1020♀", "Australian Museum K233024" (AMS); 1♂ labelled similarly but with registration number "S.F. McEvey B1021♂" (AMS); 1♂, 2♀ labelled "DEN OF NARGUN, Mitchell River, Vic., 17 Dec. 1989, K.L. Dunn, J.M. Dunn" (ANIC), ♂ with additional label "ANIC genitalia slide No. 3183 ♂" and genitalia preparation "LYC 3183, *Candalides absimilis* (Feld.), AUST. ENT. INS. COLL. Slide E.D. Edwards 1990", ♀ with additional label "Holotype, *Candalides pseudogoodingi*"; 1♂, 1♀ labelled "VIC., Den of Nargun, Mitchell River N.P., 17 Dec. 1989, K.L. & J.M. Dunn", "*Candalides absimilis*, det KL Dunn 1989", "Reference: DUNN 1990, *Victorian Entomologist* 20: 49-53" (ANIC); 1♀ labelled similarly in SAM; 1♂ labelled similarly but with registration number "LEP-9732" (NMV); 1♂ labelled similarly but with registration number "LEP-9733" (NMV); 1♀ labelled similarly but with registration number "LEP-9754" (NMV); 1♀ labelled similarly but with registration number "LEP-9734" (NMV); 1♂ labelled "DEN OF NARGUN. V., MITCHELL R. N.P., 21 FEB. 1991, D.F. CROSBY" (ANIC); 1♂ labelled "37°42'S, 147°21'E, Den of Nargun, Mitchell River NP, VIC., emg. 1 JAN. 2003, M.F. Braby & L.J. Aitchison", "Reared from larva on *Brachychiton populneus*, coll. 6-7 DEC. 2002, pupated 19 DEC. 2002" (MFBC); 1♀ labelled similarly but with dates "emg. 5 JAN. 2003, pupated 22 DEC. 2002" (MFBC); 1♂ labelled similarly but with date "pupated 23 DEC. 2002" (MFBC); 1♂ labelled similarly but with dates "emg. 7 JAN. 2003, pupated 24 DEC. 2002" (AMS); 1♂ labelled similarly but with dates "emg. 8 JAN. 2003, pupated 25 DEC. 2002" (MFBC); 1♀ labelled similarly but with dates "emg. 10 JAN. 2003, pupated 30 DEC. 2002" (MFBC); 1♂, 1♀ labelled "37°42'S, 147°21'E,

Den of Nargun, Mitchell River NP, VIC., 2 JAN. 2004, M.F. Braby" (ANIC); 2♂, 1♀ labelled similarly in NMV; 4♂ labelled similarly in AMS; 3♂ labelled similarly in MFBC; 1♂ labelled "37°42'S, 147°21'E, Den of Nargun, Mitchell River NP, VIC., emg. 12 JAN. 2004, M.F. Braby", "Reared from larva on *Brachychiton populneus*, coll. 21-23 DEC. 2003" (NMV); 1♂, 1♀ labelled similarly but with date "emg. 13 JAN. 2004" (MFBC); 2♂ labelled similarly but with date "emg. 14 JAN. 2004" (MFBC); 1♂ labelled similarly but with date "emg. 19 JAN. 2004 (ANIC); 1♂ labelled similarly but with date "emg. 23 JAN. 2004" (MFBC); 1♀ labelled similarly but with dates "emg. 18 SEP. 2004, pupated JAN. 2004" (MFBC); 1♂ labelled similarly but with dates "emg. 23 SEP. 2004, pupated 11 JAN. 2004" (MFBC).

Adult description. *Male.* Fore wing length 15.5–16.6 mm. Upperside of wings purplish blue, with costa and termen narrowly edged black, radial, median, cubital and anal veins black towards wing margin; fore wing with a broad indistinct median patch of androconial scales, patch more prominent at anterior end of cell and base of veins M_1 and M_2 and their origin with the discocellulars, at base of veins M_3 , CuA_1 and CuA_2 and their origin with the cubital vein (Cu), and along vein $1A+2A$; hind wing with a small black tornal spot between ends of veins CuA_2 and $1A+2A$. Underside of wings silvery white, with a series of dark brown markings and a narrow dark brown termen; hind wing usually with an obscure dark brown tornal spot between ends of veins CuA_2 and $1A+2A$, and a series of smaller indistinct dark brown terminal spots between ends of veins Rs and CuA_2 .

Female. Fore wing length 15.3–16.9 mm. Upperside of wings with costa, termen and outer half of dorsum broadly black enclosing a large purplish blue central patch which extends from base and inner half of dorsum to postmedian area; fore wing usually with a small postmedian patch or suffusion of pale whitish blue scales distal to discocellulars between veins M_2 and CuA_1 or CuA_2 . Underside of wings with ground colour and markings similar to male.

Variation. The brightness of the upperside purplish blue ground colour varies in males. In females, the purplish blue central patch on the upperside occasionally extends narrowly as a suffusion of purplish blue scales to the costa between veins R_1 and R_2 and to the subterminal area between veins CuA_2 and $1A+2A$ on the fore wing, and more broadly to the termen between veins M_3 and $1A+2A$ on the hind wing. The upperside of the hind wing very occasionally possesses a small subapical patch or suffusion of pale whitish blue scales between veins Rs and M_2 or M_3 .

Comparison. *Candalides absimilis edwardsi* ssp. nov. females are distinguished from females of *C. absimilis absimilis* and *C. absimilis eastwoodi* ssp. nov. by pronounced differences in the extent of the white central patch on the upperside. In *C. absimilis edwardsi* ssp. nov., the white patch on the fore wing is absent, being replaced with a small postmedian patch of pale whitish blue scales

between veins M_2 and CuA_2 ; occasionally this patch is restricted to a narrow postmedian streak between veins M_2 and M_3 distal to the discal cell. The white patch is also absent on the hind wing, but occasionally there is a narrow subapical whitish blue streak between veins R_s and M_1 . Some *C. absimilis absimilis* females from south-eastern coastal New South Wales (Central Tilba-Bega) approach *C. absimilis edwardsi* ssp. nov. in having much reduced or no white central or subapical patch on the upperside of the hind wing and an extensive basal suffusion of purplish blue scales, but these specimens have a more conspicuous white central patch on the fore wing that is approximately circular in shape and which extends from veins M_2 to CuA_1 or CuA_2 .

Candalides absimilis edwardsi ssp. nov. males do not differ from those of nominate *C. absimilis absimilis* in external morphology. The male genitalia (Fig. 28), however, are slightly larger, with the apical projections of the valvae more pronounced.

Candalides absimilis edwardsi ssp. nov. females are similar to those of *C. consimilis goodingi* (Tindale, 1965) from eastern Victoria, but the latter are readily distinguished by the more pointed apex of the fore wing, less rounded tornus of the hind wing, presence of a small but conspicuous white central patch on the upperside of the fore wing which extends below vein M_3 , and the well-defined basal spots on the underside of the hind wing. In addition, the central iridescent area in *C. consimilis goodingi* is a brighter, richer blue, whereas in *C. absimilis edwardsi* ssp. nov. it is purplish blue. The two species also differ significantly in their genitalia (see Waterhouse 1942; Tite 1963).

Remarks. *Candalides absimilis edwardsi* ssp. nov. was previously regarded as a distinct local form that was believed to be restricted to the Mitchell River National Park of East Gippsland (Dunn 1990; Dunn and Dunn 1991; Dunn *et al.* 1994). Dunn and Dunn (1991, p. 391) concluded that in relation to the white central patch of females "This Victorian population represents the opposite extreme of the continuum ... at the subspecific level this population would be considered a poorly differentiated taxon". However, quantitative analysis of this character over the broad geographical range of the species (Fig. 34) indicates negligible variation between Mackay-Eungella, Queensland, and Sydney, New South Wales, but a steep cline approaching a step between Sydney, New South Wales, and East Gippsland, Victoria. *C. absimilis edwardsi* ssp. nov. lies at the southernmost limit of the species' geographical range and represents the extreme end of variation in the extent of the white patch. Its disjunct distribution, together with a broader geographical range than hitherto believed, and the striking female phenotypic divergence in which the reduced white patch comprises a consistent and diagnosable character state that lies at the end of a step or steep latitudinal cline, indicate that the known populations warrant formal recognition at the subspecific level.

Examination of label data of museum material of *Candalides absimilis edwardsi* ssp. nov. revealed several inconsistencies. The original Dunn material comprised 10 specimens (4♂, 6♀) collected from Den of Nargun on 17 December 1989. Most specimens have an additional label "*Candalides absimilis*, det KL Dunn 1989"; however, one female in the ANIC is labelled in Dunn's original handwriting "Holotype" and a manuscript name of Dunn's is associated with it. Because this name was never formally published, neither the specimen nor the name carry any nomenclatural validity. A male sent to the ANIC for taxonomic identification (see Dunn 1990) has its accompanying genitalia slide labelled "LYC 3183, *Candalides absimilis* (Feld.), Den of Nargun, Mitchell River, Vic., 17 Dec. 1989, K.L. Dunn & J.M. Dunn, AUST. ENT. INS. COLL. Slide E.D. Edwards 1990", indicating that correct taxonomic diagnosis of the species was not made until 1990.

Etymology. The taxon is named in honour of Mr Ted Edwards in recognition of his outstanding contribution to the study of Australian Lepidoptera, curation and development of the ANIC, and continuous support, generous help and mentoring to others, including the author, over many decades.

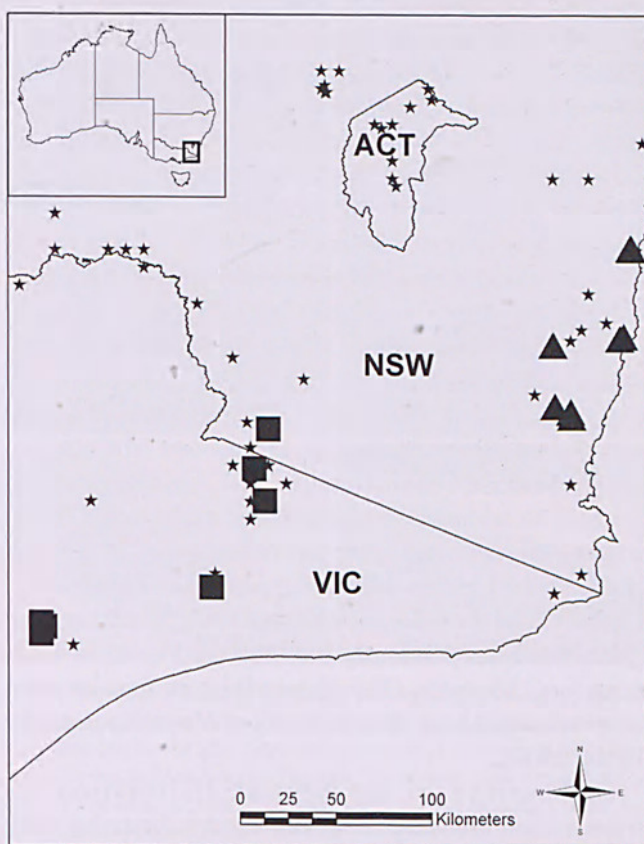


Fig. 36. Map of south-eastern Australia showing geographical distribution of *Candalides absimilis edwardsi* ssp. nov. (■) and *C. absimilis absimilis* (▲). Stars (★) indicate occurrence of the natural larval food plant, *Brachychiton populneus*, of both subspecies in the region (data based on records registered in Australia's Virtual Herbarium <http://www.cpbr.gov.au/cgi-bin/avh.cgi>).

Distribution. *Candalides absimilis edwardsi* ssp. nov. is known from a limited region in south-eastern Australia (Fig. 36). It has been recorded from three disjunct areas in south-eastern New South Wales inland of the Great Escarpment and East Gippsland of eastern Victoria at altitudes between 100–600 m. These three areas include: (1) the Upper Snowy River area on the New South Wales–Victoria border (M.F. Braby); (2) Buchan Caves Reserve (New *et al.* 2007); and (3) Mitchell River National Park (Dunn 1990). In the Upper Snowy River area, it has been recorded from three locations, viz: the southern sections of Kosciuszko National Park, New South Wales, close to the Victorian border; at Suggan Buggan and Willis in Alpine National Park, Victoria; and at McKillops Bridge in Snowy River National Park, Victoria. At Buchan Caves Reserve, it is known only from one site. In the Mitchell River National Park, it is known from three sites along the Mitchell River: 1 km upstream from The Amphitheatre on Billy Goat Bend, The Amphitheatre on Billy Goat Bend, and Den of Nargun. Thus, *C. absimilis edwardsi* ssp. nov. is known from a total of eight sites representing five locations.

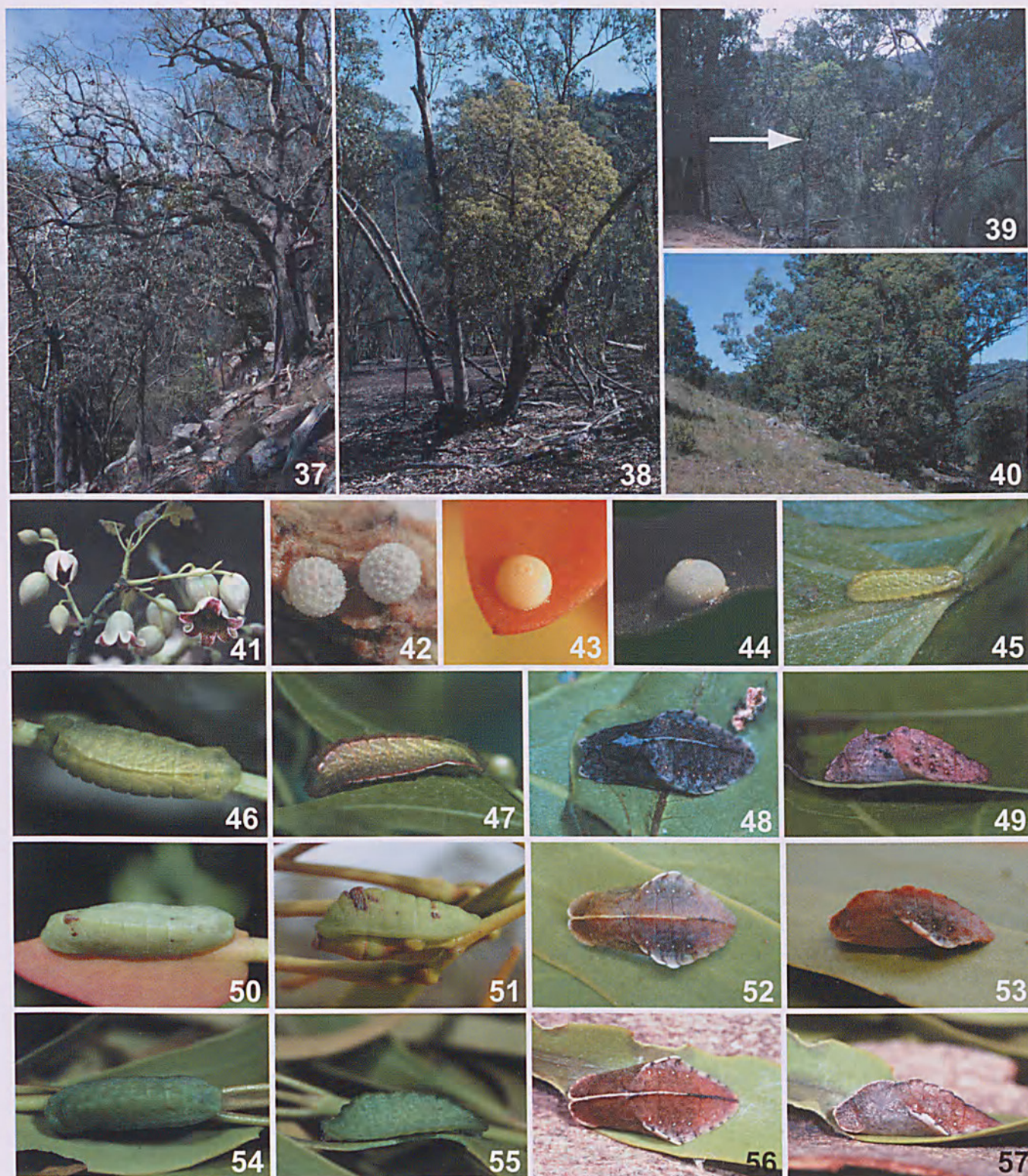
Candalides absimilis edwardsi ssp. nov. is geographically separated from *C. absimilis absimilis*, which reaches its southernmost limit in the coastal/subcoastal areas of south-eastern New South Wales (Fig. 36). *C. absimilis absimilis* was previously known as far south as Tilba Tilba, New South Wales (Braby 1998), but surveys by the author have detected the species further south near Cobargo and several sites at Bega. The two subspecies are separated by a minimum distance of 120 km in south-eastern New South Wales, but are divided by the Great Escarpment and montane plateau of the Monaro Plains. *C. absimilis absimilis* occurs east of the escarpment in moist coastal eucalypt open-forest, whereas *C. absimilis edwardsi* ssp. nov. occurs west of the escarpment in the dry box woodlands in the rain-shadow area of the Upper Snowy River south of the Great Dividing Range. The natural larval food plant of both subspecies throughout this region is *Brachychiton populneus* (Schott and Endl.) R.Br. (Braby 1998, and unpublished data), although at 13 km west of Cobargo, G. Guy (personal communication 2007) has also recorded *C. absimilis absimilis* breeding on several planted (non-indigenous) rainforest trees, viz: *Macadamia integrifolia* Maiden and Betche, *Harpullia pendula* Planchon ex F. Muell., and *Stenocarpus sinuatus* Endl. The latter two species have not previously been recorded as larval food plants for *C. absimilis*, although near Brisbane females were observed ovipositing on new shoots of *Harpullia pendula* (Braby 2000).

Comparison of the spatial distribution of *Brachychiton populneus* in south-eastern Australia with that of *C. absimilis* shows a close geographical relationship (Fig. 36). The larval food plant is apparently absent from the Monaro Plains (between Bredbo and Bombala, New South Wales) west of the Great Escarpment, suggesting that the two butterfly subspecies are indeed isolated. Searches

for *C. absimilis edwardsi* ssp. nov. by the author in the relatively dry woodland areas inland of the Great Dividing Range at Mount Majura and the Murrumbidgee River corridor, Australian Capital Territory, and the Wee Jasper district, New South Wales, where *Brachychiton populneus* grows abundantly failed to detect the butterfly. Presumably *C. absimilis edwardsi* ssp. nov. is also absent from the upper reaches of the Murray River inland of the Divide where the food plant likewise is present. Dunn and Dunn (1991) recorded *C. absimilis absimilis* from the Australian Capital Territory, based on a single female (lodged in the ANIC) collected from the Brindabella Range, but the phenotype of this specimen does not match specimens from south-eastern coastal New South Wales, suggesting the specimen is mislabelled. *C. absimilis absimilis* in south-eastern coastal New South Wales is otherwise known only from the coastal areas east of the Great Escarpment.

Four specimens of *Candalides absimilis* recorded from three localities in the outer Melbourne region (Healesville, Dandenong Ranges, Mordialloc) registered in the AMS and NMV are considered to be erroneous and accordingly their data excluded from the material examined. These specimens are labelled as follows: 1♂ “Dandenong Ranges, Victoria | 3765”, “KL16576”, “G.A. Waterhouse Collection” (AMS); 1♀ “Dandenong Ranges, Victoria | C. French, 3766”, “KL16576”, “KL22003”, “G.A. Waterhouse Collection” (AMS); 1♀ “HEALESVILLE, J.A.K.” (NMV); 1♀ “MORDIALLOC, J.A.K.” (NMV). In addition, there is a female specimen in NMV reputedly from Victoria labelled “J.A. Kershaw, Collection, PURCH JUNE 1941”. In all cases, the females resemble typical *C. absimilis absimilis* in that they have a prominent white central patch on the upperside of each wing and do agree with populations of *C. absimilis edwardsi* ssp. nov. from eastern Victoria in which the white patches are absent. Waterhouse (1942), Tindale (1965) and Dunn (1990) referred to this material in part and regarded the specimens as authentic, but Dunn and Dunn (1991) seriously questioned their validity and regarded the label data as unreliable. Dunn (1990) concluded that the specimens resulted from multiple accidental introductions to Melbourne but which failed to establish a resident breeding population, but he did not identify the mechanism or source of the introductions. However, the inadequate data on the labels and limited number of specimens suggest the material is probably mislabelled.

Crosby (1951) recorded ‘*Candalides absimilis*’ from eastern Victoria based on observations at Gypsy Point, Victoria; however, these records refer to *C. consimilis goodingi*, the species of which was not widely recognised at that time and which had previously been confused with *C. absimilis* (Waterhouse 1942). Crosby (1951) also indicated that material of ‘*C. absimilis*’ had been collected from the northern reaches of the Macalister River north of Heyfield (by V. Smith), but this material was subsequently described by Tindale (1965) as *Holochila goodingi*, with Macalister River as the type locality. McEvey (1979)



Figs 37–57. Habitat and life histories of *Candalides absimilis* and *C. margarita*: **37**, eucalypt woodland habitat of *C. absimilis edwardsi* ssp. nov. on the slopes of the Mitchell River, Vic., showing larval food plant *Brachychiton populneus* in deciduous form; **38**, eucalypt woodland habitat of *C. absimilis edwardsi* ssp. nov. at McKillops Bridge, Snowy River, Vic., showing larval food plant *Brachychiton populneus* in foreground with new flush growth; **39**, eucalypt woodland habitat of *C. absimilis edwardsi* ssp. nov. at Suggan Buggan, Vic; arrow indicates larval food plant *Brachychiton populneus* with new flush growth; **40**, open woodland habitat of *C. absimilis edwardsi* ssp. nov. at Buchan Caves, Vic., showing larval food plant *Brachychiton populneus* with mature foliage; **41**, *Brachychiton populneus* new leaf growth and flowers; **42**, egg of *C. absimilis edwardsi* ssp. nov.; **43**, egg of *C. margarita gilberti*; **44**, egg of *C. margarita margarita*; **45**, early instar larva of *C. absimilis edwardsi* ssp. nov.; **46–47**, final instar larva of *C. absimilis edwardsi* ssp. nov. showing dorsal and lateral views and colour forms; **48–49**, pupa of *C. absimilis edwardsi* ssp. nov. showing dorsal and lateral views; **50–51**, final instar larva of *C. margarita gilberti* showing dorsal and lateral views; **52–53**, pupa of *C. margarita gilberti* showing dorsal and lateral views; **54–55**, final instar larva of *C. margarita margarita* showing dorsal and lateral views; **56–57**, pupa of *C. margarita margarita* showing dorsal and lateral views.

recorded *C. consimilis goodingi* from the Mitchell River during surveys in 1977-78; however, careful examination of this material (13 specimens in AMS) indicated a mixed series comprising two species – three specimens (3♀♀) of *C. consimilis goodingi* and 10 specimens (8♂♂, 2♀♀) of *C. absimilis edwardsi* ssp. nov. McEvey surveyed three sites (Den of Nargun, The Amphitheatre on Billy Goat Bend, 1 km upstream from The Amphitheatre on Billy Goat Bend) over a three day period (7-9 December 1977). *C. absimilis edwardsi* ssp. nov. was recorded from each of these sites, but *C. consimilis goodingi* was collected only at The Amphitheatre, indicating that the two taxa occur together but presumably with limited overlap. The Mitchell River is the only known location where these two species are sympatric in Victoria. McEvey's material from the Mitchell River thus appears to represent the first genuine collection of *C. absimilis* from Victoria.

Habitat. In the Upper Snowy River area (Figs 38, 39), the breeding population occurs in dry eucalypt woodland, chiefly dominated by *Eucalyptus albens* Benth. (White Box) with some *Callitris glaucophylla* Joy Thomps. and L.A.S. Johnson (White Cypress Pine) and *Eucalyptus melliodora* A. Cunn. ex Schauer (Yellow Box) in the valley of the Snowy River, including banks of the river itself as well as gentle slopes several hundred metres above the river. In this habitat, the larval food plant is sparsely distributed over a relatively wide area, often occurring as single isolated trees, compared with those growing on the slopes of the Mitchell River (Fig. 37). The area lies in a pronounced rainfall shadow in which the mean annual rainfall (c. 800 mm) is much lower than the coastal areas of New South Wales of similar latitude further east.

At Buchan Caves Reserve (Fig. 40), the breeding population occurs in open woodland on limestone outcrops on exposed slopes with a north or west facing aspect, or along the valley floor of Fairy Creek, where the larval food plant grows. The larval food plants vary greatly in size and age, from very old large trees to young saplings only a few metres high and, within the Reserve itself, occur in relatively low density (a total of only 16 plants were located). A few scattered trees (mostly ornamental garden and street trees) also occur in residential areas of Buchan close to the Reserve where the butterfly also breeds.

At Mitchell River National Park (Fig. 37), the breeding population occurs in woodland dominated by *Brachychiton populneus* and *Eucalyptus melliodora*, with a sparse understorey of shrubs and small trees of *Acacia implexa* Benth. (Lightwood) and *A. mearnsii* De Wild. (Black Wattle), and grasses. The habitat occurs as a narrow strip on both sides of the Mitchell River in a limited zone where the larval food plant grows abundantly on steep rocky slopes between the top of escarpment and the bottom of the gorge/river valley (i.e. Mitchell River and its tributaries, such as Woolshed Creek). This habitat type is patchy in distribution because the food plants generally grow on rocky slopes with a predominantly a north to west facing aspect where

conditions are drier and more exposed. As a result, the larval food plants are more concentrated and less widely dispersed than those occurring in the Upper Snowy River area. Warm temperate rainforest dominated by *Tristaniaopsis laurina* (Sm.) Peter G. Wilson and J.T. Waterh., *Acmena smithii* (Poir.) Merr. and L.M. Perry, *Elaeocarpus reticulatus* Sm., *Pittosporum undulatum* Vent. and *Myrsine howittiana* (Mez) Jackes prevails along the gorges; however, the larval food plant does not grow, and the butterfly does not breed, in this habitat.

Biology. *Larval food plant.* *Brachychiton populneus* (Schott and Endl.) R.Br. (Sterculiaceae) (Kurrajong). The larval food plant typically grows as a tree up to 10 m in height, with a dense, dark green crown of foliage. Long-term observations made on the phenology of *Brachychiton populneus* in south-eastern Australia by the author indicated that the trees flowered and regenerated their foliage over a short interval during summer, mainly in December and January, although some trees produced new flushes of growth as late as February. Although foliage regeneration was very seasonal and occurred rapidly among individual trees, not all trees regenerated synchronously, and there was a succession of new annual leaf growth during the summer period. A proportion of trees were also deciduous (Fig. 37) – some plants dropped all of their leaves during late spring and early summer before regeneration, especially in dry years or those growing in the more exposed situations. Other trees produced new growth before shedding most of their older mature leaves, and thus remained vegetated.

Behaviour. Eggs (Fig. 42) were laid singly or sometimes in pairs, usually on the stem immediately below a terminal branchlet of new developing leaf buds, or on the new soft shoots and stipules of the young developing leaves. Many eggs were laid on individual trees, but females oviposited only on trees producing flushes of new growth or, for those trees that had shed all of their older leaves, in the early phases of regeneration; they generally did not oviposit on trees in which the leaves had reached an advanced phase of regeneration. Females were observed to oviposit on the same tree over a minimum period of 10 days. Individual trees probably remain suitable for oviposition for about two to three weeks due to the rapid growth of new foliage.

Early instar larvae (Fig. 45) fed singly on the new soft leaves (Fig. 41) at night, resting by day on the underside of the young leaves where they avoided direct sunlight. Usually only one larva occurred on a single terminal cluster of foliage, but occasionally up to four larvae were found. The later instar larvae, when not feeding, typically rested lower down on the petiole of a leaf where they remained well concealed, often in the fork between the petiole and the branchlet. Between instars, the larvae settled on the leaf petiole or further down on the thicker stems of the branchlet to moult. In the late instars (Figs 46, 47), larvae varied considerably in colour, from uniformly green to almost entirely reddish with some green at the posterior end; others were intermediate between these two phenotypic

extremes, being green with a red mid-dorsal line and a red lateral line and a slight pinkish tinge at the anterior end. Variation in larval colour was associated with the colour of juvenile foliage, which was either bright red or bright green (Fig. 41). Larvae were not observed attended by ants, despite the abundance of *Crematogaster* sp. ants on many trees.

Larvae, when reared in captivity, showed a preference to pupate in well-concealed, dark situations, such as inside rolled bark. The pupa was attached, to a silken platform spun over the substrate, by anal hooks and a silken central girdle. Pupae (Figs 48, 49) were noted to stridulate when stimulated (e.g. when gently stroked or sprayed with water). In the field, pupae were not found on the foliage, flowers or trunk and branches of the larval food plant, and it is likely that the larvae leave the food plant to pupate amongst dry leaf litter (dead leaves, bark etc) or under rocks, stones or inside rock crevices at the base of the tree.

In captivity, adults always emerged during the morning, well after sunrise, but usually before midday. After emergence, adults quickly expanded their wings and were ready for flight within 30–60 mins. In the field, males were noted to fly rapidly throughout much of the day in the mid- to upper canopy, usually between 2–8 m above the ground, around the outer foliage of larger trees of the larval food plant. They typically patrolled around a tree and then quickly flew to the next; they were also observed to fly around the outer foliage of *Pittosporum undulatum*, the leaves of which are superficially similar to *Brachychiton populneus*. Males rarely alighted to settle, especially when many individuals were present, but once settled, they usually perched for a few seconds, or sometimes for up to about 1 min, high up on horizontal leaves of the outer foliage of the larval food plant. When fewer individuals were present, males perched for longer periods on the upper foliage, especially during the late afternoon, to establish territories. In these situations, males would leave their perch briefly to patrol around the crown of the tree before settling again, usually in a different place on the tree. When settled, the wings remained closed or half opened at an angle of about 90° towards the sun. The patrolling and perching behaviour of males suggest that newly emerged females seek the mid- to upper canopy of the larval food plant for mate location.

Females were usually observed on or near the larval food plant. Their flight was considerably slower than that of males but, like males, they sometimes settled on the outer foliage of the food plant, with wings opened up to 90° towards the sun. They were observed ovipositing from late morning to early afternoon (1000–1415 hrs EST) during warm, sunny weather. Multiple females were occasionally observed to oviposit simultaneously on the same tree.

Life cycle. Adults have been collected from December to February. At several locations, early instar larvae were found in early December which, given the developmental time of the immature stages (see below), indicates that females were ovipositing in November. Thus, the putative

flight period of *Candalides absimilis edwardsi* ssp. nov. is from late November to late February, which coincides with the period of seasonal flushes of new growth of the larval food plant. In captivity, eggs hatched about a week after being laid, and the larvae completed development in about 3.5 weeks. Pupal developmental time was more variable: from a sample of 52 pupae, most (81%) reared from larvae collected in December and January developed directly, with the pupal duration lasting 11–14 days, but the others (19%) remained dormant for two months or for 6–10 months, indicating presence of a facultative diapause. The life cycle, from egg to adult for directly developing individuals, was completed in approximately six weeks. These observations suggest that most of the population of the subspecies is bivoltine, with at least two overlapping generations during the flight season.

Conservation status. *Candalides absimilis edwardsi* ssp. nov. has a narrow geographical range, with an estimated extent of occurrence of 3,200 km². It is known from eight sites (> 1 km apart) representing five locations (>10 km apart) in three disjunct areas. Although the taxon is known from a limited area, there is no evidence of decline, recent fragmentation of populations, or threatening processes impacting on the known sites or habitat, and all known populations occur in conservation reserves. Its conservation status should therefore be regarded as Least Concern (LC) according to IUCN criteria. At Buchan Caves, the low number of trees of *Brachychiton populneus* suggests the butterfly population may be small, and further planting of *B. populneus* is recommended to augment the existing population.

Dunn *et al.* (1994, pp. 236–237) provisionally regarded *Candalides absimilis edwardsi* ssp. nov. as secure on the basis that the known site was protected within a single national park, but cautioned that the population “...may become threatened because of their perching behaviour on bushes along the escarpment where adults could be taken in large numbers by hand or with a short handled net.” and that “Regular wildfires through the main breeding colony could be a threat and females appear to be associated with remnant warm temperate rainforest patches which have escaped burning.” Both of these statements in relation to threatening processes must be seriously challenged. First, the breeding area at Mitchell River, based on the extent and abundance of the larval food plant, is concentrated along the steep rocky fire-prone escarpment between the rainforest gully and woodland plateau. Moreover, not all adults perch along the escarpment, and there is little documented evidence that butterfly collecting *per se* is a threatening process, except perhaps in those situations where populations have already been substantially reduced and fragmented by habitat change (New 1991). Second, the bivoltine life cycle and behaviour of larvae, which undoubtedly leave the food plant to pupate in concealed situations near or below the ground, suggests the species would be well protected from fire.

***Candalides margarita gilberti* Waterhouse,
1903 stat. rev.**

(Figs 19–22, 24, 25, 29, 30)

Candalides gilberti Waterhouse, 1903a, p. 181; Waterhouse 1903b, p. 23; Waterhouse and Lyell 1914, pp. 78–79, pl. 15; Waterhouse 1932, p. 129, pl. 19; Common 1964, p. 122; Peters, 1971, p. 30; Common and Waterhouse 1972, p. 413, pl. 40; Common and Waterhouse 1981, pp. 527–528, pl. 47; Common and Waterhouse 1982, pp. 301–302, pl. 26; Puccetti 1991, p. 144, 146; Dunn and Dunn 1991, pp. 389–390; Samson and Wilson 1995, pp. 71–73; Edwards 1996, p. 252; Daniels and Edwards 1998, p. 90; Braby 2000, pp. 757–758, pl. 54; Edwards *et al.* 2001, p. 139; Braby 2004, p. 258; Meyer *et al.* 2006, p. 13; Franklin 2007, pp. 12–13.

Holochila gilberti (Waterhouse). – Tite 1963, p. 205; Tindale 1965, p. 173; McCubbin 1971, p. 71; D'Abrera 1971, pp. 366–367.

Comments on synonymy. *Holochila margarita* was described by Semper (1879) based on an unspecified number of specimens, but he did not designate a holotype. Gabriel (1932) gave the type locality as Bowen, Queensland, and he appears to be the first author to have referred to a type. Edwards *et al.* (2001) interpreted Gabriel's (1932) reference to a 'holotype' as a lectotype designation. The lectotype male is illustrated in Figures 15–16 and 23; a typical example of the female of *Candalides margarita margarita* (Figs 17, 18) is also illustrated for comparison. *C. margarita gilberti* was originally described as a distinct species by Waterhouse (1903a) based on a pair of specimens (Figs 19–22) collected from Darwin (given as Port Darwin), Northern Territory, by Gilbert Turner. Although both syntypes in AMS possess Waterhouse's labels indicating they are type specimens (Figs 24, 25), Waterhouse (1903a) did not designate a holotype. Both specimens were subsequently illustrated by Waterhouse and Lyell (1914, p. 79) who noted that "The figures are drawn from the types, both of which are in poor condition." Tindale (1965, p. 173) remarked that "The type is from Port Darwin...", but did not refer to a holotype. Peters (1971) referred to the syntype male as the 'holotype' and the syntype female as the 'allotype'. Edwards *et al.* (2001) interpreted Tindale's (1965) reference to a type as a lectotype designation, but this interpretation must be rejected since it is not clear which of the two syntypes Tindale was referring to. In this work, Peters (1971) incorrect reference to a holotype is regarded as a lectotype designation according to Article 74 of the ICZN (International Commission of Zoological Nomenclature 1999). In his extensive revision of the genus, Tite (1963) regarded *C. maria* Bethune-Baker, 1908 from Waigeo, Misool, Aru and mainland New Guinea to be the Papuan subspecies of *C. margarita* based on similarities in the male genitalia, and this arrangement was followed by Parsons (1998).

Waterhouse (1903a) drew attention to the distinct underside markings, especially the postmedian series, and

the reduced white areas on the upperside of the female by which *Candalides margarita gilberti* was distinguished. He considered *C. margarita gilberti* to be most closely allied to *C. absimilis*, but did not compare the taxon with *C. margarita margarita*. Tite (1963) considered *C. margarita gilberti* to be specifically distinct based on differences in the male upperside ground colour, shape of the fore wing apex, and extent of black spots on the underside of the hind wing, with *C. margarita gilberti* being pale lavender-blue, having the fore wing apex noticeably produced, and with sharp black spots on the underside. He also drew attention to the distinct upperside colouration of the female, which is pale lavender-blue with the fore wing costal margin broadly black, but without darkened veins. Tite (1963, p. 205) regarded *C. margarita gilberti* to be closely related to *C. margarita*, *C. tringa* (Grose-Smith, 1894) and *C. biaka* (Tite, 1963) on account of similarities of the male genitalia, but remarked that "Surprisingly...the male genitalia are identical with those of *margarita*." Parsons (1986), however, considered *C. margarita sensu stricto* to be closely allied to *C. afretta* Parsons, 1986 from the lowland savanna belt of the Western Province of Papua New Guinea, but he did not refer to *C. margarita gilberti*. Braby (2000, pp. 757–756) stated that "*C. gilberti* is very closely related to, and possibly conspecific with, *C. margarita*" and recommended that "Further study is needed to determine if *C. gilberti* is merely a subspecies of *C. margarita*."

Type material. LECTOTYPE – ♂ labelled "Port Darwin, 24 Nov. 1902, G. Turner | L2008", "C. gilberti ♂, Type specimen | KL21869", "G.A. Waterhouse Collection", "FIG. 266 Upperside IN 'THE BUTTERFLIES OF AUSTRALIA', by WATERHOUSE & LYELL, was taken from this specimen | KL21869", "K191348" (AMS). PARALECTOTYPE – ♀ labelled "Port Darwin, 25 Nov. 1902, G. Turner | L2009", "C. gilberti ♀, Type specimen | KL21870", "G.A. Waterhouse Collection", "FIG. 267 Upperside IN 'THE BUTTERFLIES OF AUSTRALIA', by WATERHOUSE & LYELL, was taken from this specimen | KL21870", "K191349" (AMS).

Other material examined. 58♂♂, 39♀♀. WESTERN AUSTRALIA: 1♂ labelled "16.31S 125.16E, Synnot Ck W.A., 17–20 Jun. 1988, T.A. Weir" (ANIC); 1♀ labelled "14.25S 126.38E 12 km S of Kalumburu Mission W.A., 7–11 June 1988, T.A. Weir" (ANIC). NORTHERN TERRITORY: 1♀ labelled "48 mi. SW. of Daly River, NT. 14.11S, 130.08E, 3 Sept. 1968, M. Mendum" (ANIC); 4♂♂ labelled "60 km S of Daly River N.T., 12 June 1981, D.P. Sands" (ANIC); 1♀ labelled "DALY R N.T., 30 JUNE 1969, JC LE SOUEF" (ANIC); 1♂ labelled "16°07'39"S, 130°19'00"E, Gregory NP, NT, 31 JUL. 2006, M.F. Braby", "NT Museum I004226" (NTM); 1♂ labelled "N. Territory, Burrells Trig., 13°30'S, 131°02'E, 244m, 23 July 1983, D.P. Sands" (ANIC); 1♂ labelled "Mt Burrill [sic] NT, 18 Jan 1992, R.N. STOODLEY", "L.R. Ring Collection" (ANIC); 1♂ labelled "13°29'46"S, 131°02'08"E, Burrells Trig, NT 250m, 6 MAY 2006, M.F. Braby & DA Young", "MFB

Collection 00175" (MFBC); 1♂ labelled similarly but with registration number "MFB Collection 00083" (MFBC); 3♂♂, 2♀♀ labelled "P. Darwin, F.P. Dodd | 4918-4922", "KL21874", "G.A. Waterhouse Collection" (AMS); 1♀ labelled "P. Darwin, 13 Sep. 08, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947", "LEP-9746" (NMV); 1♀ labelled "P. Darwin, Nov. 08, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947", "LEP-9745" (NMV); 1♀ labelled "P. Darwin, Bd. Nov 08, F.P. Dodd | 4349", "KL21871", "G.A. Waterhouse Collection", pupal exuvia mounted separately adjacent to specimen and labelled similarly (AMS); 1♀ labelled "P. Darwin, Bred Jan 09, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947", pupal exuvia mounted separately adjacent to specimen and labelled similarly (AMS); 1♂ labelled "P. Darwin, Jan 09, F.P. Dodd", "From F.P. Dodd, N.Q. Land, 12.12.10", "LEP-9739" (NMV); 1♂ labelled "P. Darwin, Feb. 09, F.P. Dodd", "LEP-9740" (NMV); 1♀ labelled similarly but with registration number "LEP-9743" (NMV); 1♀ labelled similarly but with registration number "LEP9-747" (NMV); 2♂♂, 1♀ labelled similarly but with additional labels "KL21872", "G.A. Waterhouse Collection" (AMS); 1♂ labelled similarly (ANIC); 1♀ labelled similarly but with additional label "Figured in "AUSTRALIAN BUTTERFLIES" Jacaranda Press, 1964, I.F.B. Common" (ANIC); 1♂ labelled "P. Darwin, Mch 09, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947" (AMS); 1♂ labelled "P. Darwin, Apr. 09, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947", "LEP-9741" (NMV); 1♀ labelled "P. Darwin, Apl 09, F.P. Dodd | 4464", "KL21873", "G.A. Waterhouse Collection" (AMS); 1♂ labelled "P. Darwin, May 09, F.P. Dodd", "Passed through C.W. Wyatt Theft-Coll. 1946-1947", "LEP-9742" (NMV); 1♂ labelled "P. Darwin, May 09, F.P. Dodd", "LEP-9737" (NMV); 1♂ labelled similarly but with registration number "LEP-9738" (NMV); 1♀ labelled similarly but with registration number "LEP-9744" (NMV); 1♀ labelled similarly but with registration number "LEP-36622", "Collection A.N. Burns" (NMV); 1♀ labelled "Darwin, Nov., Purcell", "Label data very doubtful, 22.10.68 J.V.P.", "Passed through C.W. Wyatt Theft-Coll. 1946-1947" (AMS); 1♀ labelled "Darwin NT, Jan 1949", "F.E. Parsons Collection, Donated A.N.I.C. 1967" (ANIC); 1♂ labelled "AUSTRALIA, NT DARWIN, Stuart Pk, T. FENNER ex D. Wilson", "larva on *Decaisnina signata*. em. 31 May 91" (ANIC); 1♂ labelled "Stuart Park N.T., 18 June 1991, D.N. WILSON", "NORTHERN TERRITORY MUSEUM, I003598 LYCAENIDAE, *Candalides gilberti*, Waterhouse, 1903, Det: D.N. Wilson" (NTM); 1♀ labelled "Stuart Park N.T., Ex pupa 24 June 1991, D.N. WILSON", "NORTHERN TERRITORY MUSEUM, I003599 LYCAENIDAE, *Candalides gilberti*, Waterhouse, 1903, Det: D.N. Wilson" (NTM); 1♀ labelled "Stuart Park N.T., Ex pupa 24 June 1991, D.N. Wilson", "G. Daniels Collection" (AMS); 2♀♀ labelled "Stuart Park N.T., Ex pupa 25 June 1991, D.N. Wilson" (ANIC); 1♀

labelled similarly but with additional label "Figured in *Butterflies of Australia* (1999) [sic], CSIRO Publishing, M.F. Braby" (ANIC); 1♀ labelled "Egg collected 13 May 1991, Egg hatched 15 May 1991, Larvae pupated 31 May 1991, Adult emerged 10 July 1991, Nudle Street Stuart Park N.T., D.N. WILSON", "Figured in *Butterflies of Australia* (1999) [sic], CSIRO Publishing, M.F. Braby" (ANIC); 1♂ labelled "Stuart Park NT, 07 Apr 1992, D.N. Wilson", "G. Daniels Collection" (AMS); 1♀ labelled "NIGHTCLIFF, NT, 23 AUG 92, C. MEYER XP", "G. Daniels Collection" (AMS); 1♂ labelled "NIGHTCLIFF, NT, 3 SEP 92, C. MEYER XP", "G. Daniels Collection", pupal exuvia pinned beneath specimen (AMS); 1♂ labelled "Darwin, N.T., Coconut Grove, 2 OCT. 1994 B., C. Meyer", "MFB Collection 00079", "genitalia No. 014" (MFBC); 1♂ labelled "Fannie Bay, Darwin, N.T., R.P. Weir XP, 3.8.98", "NORTHERN TERRITORY MUSEUM, I003481 LYCAENIDAE, *Candalides gilberti*, Waterhouse, 1903, Det: D.F. Trembath 16 Mar 2006" (NTM); 1♂ labelled "Darwin, NT, emg. 28 FEB. 2005, M.F. Braby & R. Weir, The Gardens", "reared from larva on flowers of *Decaisnina signata*, coll. 2 FEB. 2005", "MFB Collection 00174", "genitalia No. 023" (MFBC); 1♀ labelled "Darwin, NT, emg. 28 FEB. 2005, M.F. Braby & R. Weir, The Gardens", "reared from larva on flowers of *Decaisnina signata*, coll. 2 FEB. 2005", "MFB Collection 00176" (MFBC); 1♀ labelled similarly but with date "emg. 8 MAR. 2005" and registration number "MFB Collection 00080", pupal exuvia pinned beneath specimen (MFBC); 1♀ labelled "Stuart Park, Darwin, NT, emg. 26 MAY 2006, D.A. Young, reared from larva on *Decaisnina signata*", "MFB Collection 00178" (MFBC); 1♂ labelled similarly but with date "emg. 20 MAY 2006" and registration number "MFB Collection 00081" (MFBC); 1♂ labelled "12°22'S, 130°53'E, Leanyer, Darwin, NT, emg. 26 JUL. 2006, M.F. Braby", "reared from larva on *Decaisnina signata*, coll. JUL. 2006", "MFB Collection 00171" (MFBC); 1♀ labelled similarly but with date "emg. 31 JUL. 2006" and registration number "MFB Collection 00177" (MFBC); 1♂ labelled similarly but with registration number "MFB Collection 00082" (MFBC); 1♀ labelled similarly but with date "emg. 2 NOV. 2007", "reared from larva on foliage of *Decaisnina signata*, coll. OCT. 2007" and registration number "MFB Collection 00179" (MFBC); 1♀ labelled similarly but with date "emg. 4 NOV. 2007" and registration number "MFB Collection 00180" (MFBC); 1♂ labelled similarly but with registration number "MFB Collection 00172" (MFBC); 1♂ labelled similarly but with date "emg. 24 APR. 2008", "Reared from larva on foliage of *Decaisnina signata*, coll. APR. 2008" and registration number "MFB Collection 00187" (MFBC); 1♂ labelled "12.37308°S, 130.88657°E, Wanguri, Darwin, NT, emg. 10 FEB. 2007, M.F. Braby", "reared from egg on *Decaisnina signata*, coll. 12 JAN. 2007", "MFB Collection 00173", pupal exuvia pinned beneath specimen (MFBC); 1♀ labelled "21 August, 1970., J.V. Peters, Howard Springs, N.T., 16 mls, South Darwin." (AMS); 1♂ labelled "Tidy

Hill 233' N.T., 12°45'S. 130°54'E., 25 August 1970., J.V. Peters" (AMS); 1♂ labelled "13.21S 131.08E, Hill above Robin Falls N.T., 8 June 1993, E.D. Edwards" (ANIC); 1♀ labelled "Marrakai Rd, N.T., R.P. Weir XP, 26.10.97", "NORTHERN TERRITORY MUSEUM, I003480 LYCAENIDAE, *Candalides gilberti*, Waterhouse, 1903, Det: D.F. Trembath 16 Mar 2006" (NTM); 1♂ labelled "20 KM STH ADELAIDE R. NT., 23 FEB. 1992, RN STOODLEY", "L.R. Ring Collection" (ANIC); 1♂ labelled "30 KM STH PINE CK NT, 14 APRIL 1992, D.N. WILSON", "Figured in *Butterflies of Australia* (1999) [sic], CSIRO Publishing, M.F. Braby" (ANIC); 1♀ labelled "12.35S 131.17E, Fogg Dam N.T., 15 June 1981, D.P. Sands" (ANIC); 1♂ labelled similarly but with date "17 June 1981" (ANIC); 2♂♂ labelled "Mt. Bunday – Mary R. District. N.T., 14 May, 1972. J. Kerr" (ANIC); 1♀ labelled "11.09S 132.09E, Black Point Cobourg Pen., NT, 26 Jan. 1977, E.D. Edwards" (ANIC); 1♀ labelled "3 mi. S. of Oenpelli, NT., 11 Dec. 1970, W. Omer Cooper" (AMS); 1♂ labelled "South Alligator River N.T., 15 May 1981, D.P. Sands" (ANIC); 1♂ labelled "Little Menagerie Rock, N.T., 16 May 1981, D.P. Sands" (ANIC); 1♂ labelled "12.48S 132.42E, Nourlangie Creek, 8 km N of Mt. Cahill, N.T., 19 Nov. 1972, E.D. Edwards & M.S. Upton" (ANIC); 1♂ labelled "12.50S 132.51E, 15km NE of Mt. Cahill, N.T., 23 May 1973, E.D. Edwards & M.S. Upton" (ANIC); 1♂ labelled "12.86488°S, 132.70468°E, Mt Cahill (Mirrai lookout) Kakadu NP, NT, 3 MAY 2008, MF Braby & LJ Aitchison", registration number "MFB Collection 00186" (MFBC); 1♂ labelled 12°39'19"S, 135°51'31"E, Dhamiyaka outstation, NE Arnhem Land, NT, 14 AUG. 2007, M.F. Braby & I. Morris", "NT MUSEUM I004303" (NTM); 1♂ labelled "Hideway Motel, Gove, 17.iv.1976, A.J. Dartnell", "NORTHERN TERRITORY MUSEUM, I003479 LYCAENIDAE, *Candalides gilberti*, Waterhouse, 1903, Det: DF Trembath 16 Mar 2006" (NTM); 1♀ labelled "12°10'41"S, 136°47'01"E, Nhulunbuy, NT, emg. 12 FEB. 2008, MF Braby & LJ Aitchison", "Reared from larva on *Decaisnina signata*, coll. 27 JAN. 2008"; "MFB Collection 00181", pupal exuvia pinned beneath specimen (MFBC). QUEENSLAND: 3♂♂, 2♀♀ labelled "18.35S 138.03E, Murray's Spring 8 km W by N of Musselbrook Camp Q, 9 May 1995 GPS, E.D. Edwards" (ANIC); 3♂♂ labelled similarly but with date "11 May 1995" (ANIC); 1♂ labelled "18.38S 138.08E, Gorge 2 km S of Musselbrook Camp Q, 20 May 1995 GPS, E.D. Edwards" (ANIC); 1♂ labelled "18.42S 138.29E, Lawn Hill Ck, Q, 17 May 1995 GPS, E.D. Edwards" (ANIC).

Comparison. Adults of *Candalides margarita gilberti* are very similar to those of *C. margarita margarita* in wing shape and pattern, although in *C. margarita gilberti* the underside markings are more distinct, and the fore wing has a straighter termen with the apex more pointed. The upperside ground colour of males of the two subspecies is similar, but in *C. margarita gilberti* the colouration is somewhat paler and the black margin is narrower than in

C. margarita margarita. *C. margarita gilberti* females have narrower black margins with the large white central patches on the upperside replaced with blue. A characteristic feature of *C. margarita gilberti* noted by Waterhouse (1903a), that the postmedian spot between veins Rs and M₁ displaced proximally from the remainder of the postmedian series on the underside of the hind wing, is also shared with *C. margarita margarita* but not by other members of the *C. absimilis* species group from Australia.

Remarks. The structure of the male genitalia of *Candalides margarita*, which is substantially different and more complex than those of *C. absimilis*, is remarkably uniform across the species range (Figs 29–32). Although the genitalia are slightly smaller from the Top End and western Gulf Country (*C. margarita gilberti*) compared with those of from the Wet Tropics and north-eastern New South Wales (*C. margarita margarita*), there are no significant differences in the form of the valvae or brachia. The female genitalia (not illustrated) show a similar geographical pattern to that of the males.

Larvae of both *Candalides margarita gilberti* and *C. margarita margarita* specialise on loranthaceous food plants (Smales and Ledward 1943; Samson and Wilson 1995), and comparison of the immature stages of the two taxa indicate that the morphology of the egg (Figs 43, 44), final instar larva (Figs 50, 51, 54, 55) and pupa (Figs 52, 53, 56, 57) are identical. Comparison of the first instar larva of the two taxa also revealed no differences. The first instar larva is characterised by a pronounced dorsal ridge along the length of the body, which bears a series of long paired dorsal primary setae on the metathorax and abdominal segments 1–7; on each segment lies a pair of smaller setae posterior to the longer paired setae. The mesothorax also possesses a pair of long setae, but they are located dorsolaterally so that they are not as close together as the setae on the other segments. Final instar larvae of the two subspecies vary in pattern and colouration depending on the colour of the food consumed (red flowers or green leaves), although in *C. margarita gilberti* the darker patches on the body appear to be more pronounced.

In summary, evidence from the genitalia, adult and immature stage morphology, together with similarities in the life history and adult behaviour (see below), indicate that *gilberti* is conspecific with *Candalides margarita*; *gilberti* should be regarded as a geographical subspecies of that taxon on account of its disjunct distribution and morphological divergence in the adult stage. Thus, three subspecies are now recognised within *C. margarita*: *C. margarita maria* from mainland New Guinea and the nearby islands of eastern Indonesia; *C. margarita gilberti* from north-western and central northern Australia; and *C. margarita margarita* from eastern Australia (Thursday Island, Queensland, to Tuncurry, New South Wales). Presumably, *C. margarita gilberti* is sister to *C. margarita margarita* + *C. margarita maria* based on the greater phenotypic divergence of *C. margarita gilberti* and the close

similarity among the females of *C. margarita margarita* and *C. margarita maria*.

Distribution. *Candalides margarita gilberti* occurs in the monsoon tropics of north-western and central northern Australia, from the Kimberley, Western Australia, across the Top End, Northern Territory, to the Gulf Country of north-western Queensland (Braby 2000; Franklin 2007). It is allopatric from *C. margarita margarita*, the known ranges of the two subspecies in Queensland being separated by a minimum distance of about 700 km. *C. margarita gilberti* reaches its northernmost limit at Black Point on Cobourge Peninsula (Garig Gunak Barlu National Park), Northern Territory, about 550 km south-south-west of Aru Island in the Arafura Sea which supports the nearest population of *C. margarita maria*.

Habitat. *Candalides margarita gilberti*, in contrast to *C. margarita margarita*, occurs in savanna woodland and patches of monsoon forest and vine-thicket where the larval food plant grows. In Darwin, it is widespread and the early stages may be relatively common in suburban areas, parklands and areas with native vegetation where the subspecies breeds throughout the year.

Biology. The larval food plant, description of the early stages, general biology and habitat of *Candalides margarita gilberti* have been well documented (Samson and Wilson 1995; Braby 2000). The recorded larval food plant is the aerial-stem hemiparasite *Decaisnina signata* (F.Muell. ex Benth.) Tiegh. (Loranthaceae) (Samson and Wilson 1995), but eggs have also been found on *Decaisnina petiolata* (Barlow) Barlow at Kakadu National Park (M.F. Braby unpublished data). Although the life history was documented only relatively recently, Waterhouse and Lyell (1914, p. 79) noted earlier that "The species has since been bred by Mr. F.P. Dodd..." Examination of the Dodd material collected from Darwin during 1908-09 in AMS, ANIC and NMV (13♂♂, 13♀♀) revealed two reared female specimens each with their pupal exuviae mounted separately and labelled "P. Darwin, Bd. Nov 08, F.P. Dodd" (AMS) and "P. Darwin, Bred Jan 09, F.P. Dodd" (AMS); however, no information on the identity of the larval food plant was provided on the labels of these specimens.

Little has been documented on adult behaviour of *Candalides margarita gilberti*, but the following observations suggest it is similar, if not identical, to that of *C. margarita margarita* (M.F. Braby unpublished data). In the Northern Territory, *C. margarita gilberti* males regularly congregate on hilltops where they perch on foliage of trees to defend territories during the morning (from 7.45 am onwards) and the afternoon. When settled, they usually perch, with wings closed, 3–5 m above ground level. Males also establish territories along edges of gallery forest where they typically fly and perch, with wings closed and oriented head downwards towards the sunlight, on outer foliage of rainforest trees about 5–8 m above ground level during early to late afternoon. Females have been observed flying in similar places, but when settled frequently perch with

wings opened at about 90° towards the late afternoon sun. They have been observed ovipositing on the larval food plant during the early afternoon.

Conservation status. The conservation status of *Candalides margarita gilberti* should be regarded as Least Concern (LC) on account of its broad distribution and lack of threatening processes. No populations are known to have been extirpated and there is no evidence that the subspecies has declined or is in decline. However, its relative abundance in savanna woodland across the monsoon tropics of the Kimberley and Top End may have declined over the past century with changed fire regime because mistletoes, the larval food plant of the butterfly, are highly susceptible to fire (Kelly *et al.* 1997). In these fire-prone habitats, there has been a general increase in the extent, frequency and intensity of fires, in contrast to the general suppression of fire since European settlement in agricultural areas of temperate southern Australia where some mistletoe species appear to have increased in abundance (Kelly *et al.* 1997).

DISCUSSION

Geographical variation in *Candalides absimilis* males parallels that of *C. consimilis* males (Tindale 1965; Kerr 1967), both species of which are broadly sympatric along the eastern coast of Australia. Not only do these species diverge at the extreme ends of their geographical ranges, but they also exhibit similar patterns of phenotypic divergence, particularly on Cape York Peninsula where they both have narrow range endemic subspecies restricted to the mid-peninsula rainforest block (Iron Range-McIlwraith Range). Males of both *C. absimilis eastwoodi* and *C. consimilis toza*, which are superficially similar, are characterised by possessing a paler upperside purple ground colour, a straighter termen of the fore wing, a more prominent black tornal spot on the hind wing, and less distinct markings on the underside compared with their respective nominate subspecies. This suggests that the northernmost populations of the two species of *Candalides*, *C. absimilis eastwoodi* and *C. consimilis toza*, have diverged under similar selective pressures in both space and time. The mid-peninsula block of rainforest on Cape York Peninsula is well known for its high level of local endemism and insularity (Kikkawa *et al.* 1981), and the biogeographical patterns observed in the two species of *Candalides* suggest these butterflies have been subjected to the same underlying historical processes that have led to isolation and differentiation.

Interestingly, differences observed between males of the two Australian subspecies of *Candalides margarita* parallels the pattern of geographical variation observed in fore wing shape in *C. absimilis* and *C. consimilis* males in which the subspecies from the Kimberley and Top End, *C. margarita gilberti*, has the termen straighter and apex sharply pointed, similar to that observed in *C. absimilis*

eastwoodi and *C. consimilis toza*. *C. margarita gilberti* also has more prominent black tornal spots on the hind wing underside than in *C. margarita margarita*, but the underside basal spots and wavy lines are more distinct, whereas in *C. absimilis eastwoodi* and *C. consimilis toza* the underside markings are less distinct than their respective nominate subspecies. In *C. margarita*, the geographical variation is partitioned across the 'Carpentarian Gap', a barrier comprising the Gulf of Carpentaria and arid plains of the Gulf Country between the Top End and Cape York Peninsula, whereas in *C. absimilis* and *C. consimilis* geographical variation among the northernmost populations is partitioned across a putative barrier comprising the dry lowland plains south of Princess Charlotte Bay of Cape York Peninsula (i.e. between Iron Range-McIlwraith Range and the Wet Tropics).

Although the blue colouration differs between females of *Candalides absimilis edwardsi* and *C. margarita gilberti*, the upperside pattern of these two subspecies is broadly similar in that the white central patches are absent and the basal and central areas of both wings are broadly blue. Indeed, these two subspecies are remarkable in that they comprise the only taxa in the *C. absimilis* species group in Australia in which the white patches are replaced with blue. The only other species in the *C. absimilis* species group that possess this trait are *C. riuensis* (Tite, 1963) from Tagula (Sudest) Island, *C. lamia* (Grose-Smith, 1897) from the D'Entrecasteaux Islands, and *C. coeruleus* (Röber, 1886) from Aru Island and the lowland areas (< 200 m) of mainland New Guinea (Parsons 1998). These taxa, together with *C. cyprotus*, are exceptional as females of most members of the *C. absimilis* species group have the upperside ground colour black with contrasting patches of white in the central areas of the wings, and their morphological pattern poses interesting questions as to how this character may have evolved, its functional significance and whether the 'blue form' represents a plesiomorphic (ancestral) or apomorphic (derived) state. Answers to such questions may come from comparative analysis of female phenotype in relation to the species' ecology and phylogenetic history of the genus. For instance, among the Australian taxa, both *C. absimilis edwardsi* and *C. margarita gilberti* are associated mainly with habitats comprising eucalypt woodland, open woodland and savanna woodland (i.e. vegetation types in which the projective foliage cover < 30%), whereas *C. absimilis absimilis*, *C. absimilis eastwoodi*, *C. margarita margarita*, *C. helenita* (Semper, [1879]), *C. consimilis consimilis* and *C. consimilis toza* are associated primarily with closed forest habitats, particularly rainforest (i.e. vegetation types in which the projective foliage cover > 70%) (Braby 2000). Although *C. margarita gilberti* also occurs in dry rainforest (monsoon forest), this vegetation type in the Kimberley and Top End, compared with the evergreen tropical forests of eastern Australia, occurs as a vast network of smaller patches (mostly < 5 ha in extent) that is naturally fragmented

throughout the extensive savanna landscape so that these habitats have greater edge effects (i.e. larger perimeter/area ratios) where the canopy is more open and, depending on water availability, the dominant canopy trees are frequently deciduous or semi-deciduous during the dry season. Thus, the 'blue forms' in female *Candalides* are primarily associated with open habitats, whereas the striking and highly contrasting 'black and white forms' are associated with closed habitats. In this context, it is noteworthy that *C. absimilis absimilis* females from the extreme southern end of its range in south-eastern coastal New South Wales (Central Tilba-Bega), where it breeds primarily in eucalypt open-forest and tall open-forest (projective foliage cover 30%-70%), have substantially reduced white patches on the wings (Fig. 34F) compared with populations further north that are mainly associated with closed forest. A similar trend also occurs in *C. consimilis goodingi* females from south-eastern Australia, which occurs primarily in eucalypt tall open-forest, in which the white patch on the fore wing is reduced in extent compared with the nominate subspecies *C. consimilis consimilis*, which occurs mainly in subtropical and warm temperate rainforest.

The association between sex-limited phenotype and habitat (i.e. broad vegetation type, measured in terms of projective foliage cover) in *Candalides* also extends to other species in the family from Australia (Table 1). Of the 49 species of Lycaenidae that occur predominantly in closed forest vegetation types, 30 (61%) have the upperside ground colour black with prominent white patches in the female sex and the sexes are frequently strongly sexually dimorphic, whereas of the 90 species that live primarily in open forest/ woodland vegetation types the proportion of 'black and white forms' among females drops to 3%. The three species in the latter category include two [*Hypolycaena phorbas* (Fabricius, 1793), *Erysichton palmyra* (C. Felder, 1860)] which also occur in rainforest and one [*Leptotes plinius* (Fabricius, 1793)] in which the white patches are very obscure. Differences in the frequencies of adult female forms among the two broad vegetation types tabulated in Table 1 are significant ($\chi^2 = 55.8$, d.f. 1, $P < 0.001$), supporting

Table 1. Associations between female phenotype (upperside wing pattern) and habitat (broad vegetation type) among Australian Lycaenidae (data compiled from Braby 2000). Differences in frequency of female forms among the two vegetation types are highly significant ($P < 0.001$).

Habitat	Phenotype		Total
	Ground colour black, with white patches present*	Ground colour variable, but white patches absent†	
Closed forest	30	19	49
Open forest/ woodland	3	87	90
Total	33	106	139

* white patches may have some traces of blue pigmentation.

† ground colour frequently brown or blue.

the hypothesis that habitat characteristics affects female wing phenotype in *Candalides*, at least in terms of the visible spectrum. Further analysis is needed to establish if other factors, such as phylogenetic history and mate location or ovipositing behaviour, are correlated with the observed pattern, and if the relationship also holds in the non-visible spectrum such as ultraviolet light, which butterflies frequently use for mate recognition. Female wing pattern does not appear to be explained by shared ancestry because the trend for habitat associated sex-limited phenotype among the Australian Lycaenidae also occurs in *Jamides* and *Nacaduba*, two genera which occur in both open and closed forest.

The evolutionary forces that may have selected for female wing pattern among *Candalides*, and the Australian Lycaenidae in general, have not been established, but since the two habitats (broad vegetation types) analysed differ greatly in projective foliage cover and therefore their light environment, differences in ambient light properties may be a critical factor. Closed forest environments are optically complex, varying greatly in intensity (brightness) and spectral composition (colour) under sunny conditions (Endler 1992, 1993). Therefore, selection is expected to favour phenotypes that are more striking to maximise brightness contrast and conspicuousness among conspecifics or potential mates. A recent study (Douglas *et al.* 2007) has demonstrated that nymphalid butterflies inhabiting understorey microhabitats of tropical forest, in which light intensity is very low, are more likely to exploit polarised light as a signal for communication than related species occupying open habitats. In contrast, in open forest/woodland habitats or seasonally deciduous monsoon forests, Endler (1992) predicted that selection should favour exploitation of the shorter wavelengths (ultraviolet, blue, green) for visual signals in these 'woodland shade' light environments. These findings suggest that a more general hypothesis may be proposed, namely that ambient light characteristics among divergent habitats or vegetation types (i.e. different light environments) is a potent selective force in shaping sex-limited phenotype among Australian lycaenid butterflies.

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