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Taxonomy of the genus *Udara* (Lepidoptera: Lycaenidae) in New Caledonia and the Wet Tropics of Australia, with a review of butterfly endemism in these regions

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Abstract The lycaenid genus *Udara* Toxopeus is recorded for the first time from New Caledonia where it is represented by the newly described species *U. renevieri* sp. nov. The species is figured, the male genitalia are illustrated, and the taxon is compared with *U. cardia* (C. Felder, 1860) (from Maluku through New Guinea to the Solomon Islands and Australia) to which it appears to be most closely related. The taxonomic status of *U. cardia tenella* syn. nov. and stat. nov. from the Wet Tropics biome of north-east Australia is revised and treated as a subspecies of *U. cardia* based on comparative evidence of the morphology of the male genitalia and wing colour pattern elements. The holotypes of both *Lycaena cardia* C. Felder, 1860 and *Lycaena tenella* Miskin, 1891 are illustrated. Patterns of butterfly endemism in New Caledonia-Loyalty Islands and the Wet Tropics are discussed in relation to the conservation importance of these biodiversity hot spots. Estimated levels of endemism are 21% for New Caledonia and 5% (17% if subspecies are included) for the rainforest component of the Wet Tropics.

Key words biogeography, *Celastrina*, endemic species, *Lycaenopsis* group, new species, Polyommatinae.

INTRODUCTION

New Caledonia in the Coral Sea of the South Pacific Ocean and the Wet Tropics World Heritage Area of north-east Australia are both areas that support high levels of biological diversity and endemism (Myers *et al*. 2000; Crisp *et al*. 2001). Available data on the Lepidoptera indicate that the butterfly (Papilionoidea) faunas of these regions are also particularly rich (Holloway & Peters 1976; Kitching 1981; Kitching & Dunn 1999), although patterns of endemism within this group of insects have rarely been investigated. While the taxonomic inventory of butterflies is closer to completion compared with most other superfamilies of Lepidoptera, Tennent (2005) concluded that the inventory of New Caledonia was incomplete and that additional species of butterflies almost certainly remain to be discovered.

The lycaenid genus *Udara* Toxopeus, 1928 (Polyommatinae: Polyommatini) occurs widely in the Oriental and Australian Regions, from India and Sri Lanka to southern Japan, through South-East Asia to mainland New Guinea and its adjacent islands, north-east Australia, the Solomon Islands and Hawaii (Eliot 1973; Eliot & Kawazoé 1983). It includes more than 37 species and was placed by Eliot and Kawazoé (1983) in the *Lycaenopsis* group. *Udara* is closely related to *Celastrina* Tutt, 1906, from which it differs primarily in the morphology of the male genitalia, particularly the form of the sociuncus and valva. Morphological features of these two genera include the presence of spade- or paddle-shaped androconia (with 12–15 ridges) on the upperside of the wings of the male, a rounded termen of the hindwing without a tail or filament, the forewing discal cell being slightly longer than half the wing, veins Sc and R_1 of the forewing being well separated, eyes hairy, and a sexually dimorphic colour pattern on the upperside (Eliot & Kawazoé 1983).

Only a single species, *U. cardia* (C. Felder, 1860), has been recorded from the Solomon Islands Archipelago (Parsons 1998; Tennent 2002), which represents the most south-eastern extent of the genus. The taxon *U. cardia tenella* (Miskin, 1891) syn. nov. and stat. nov., which occurs in north-east Australia (Braby 2000), represents the southern-most extent of *Udara*. Recently, specimens of *Udara* were recorded from the island of New Caledonia, some 1500 km SSE of Guadalcanal and approximately 2000 km ESE of Cairns, QLD, by Alain Renevier-Faure. Close examination of this material and comparison with *U. cardia* and other species of the genus indicate that it comprises a hitherto undescribed species according to criteria of the general lineage species concept (de Queiroz 1998, 2007). The species is here described, figured, diagnosed

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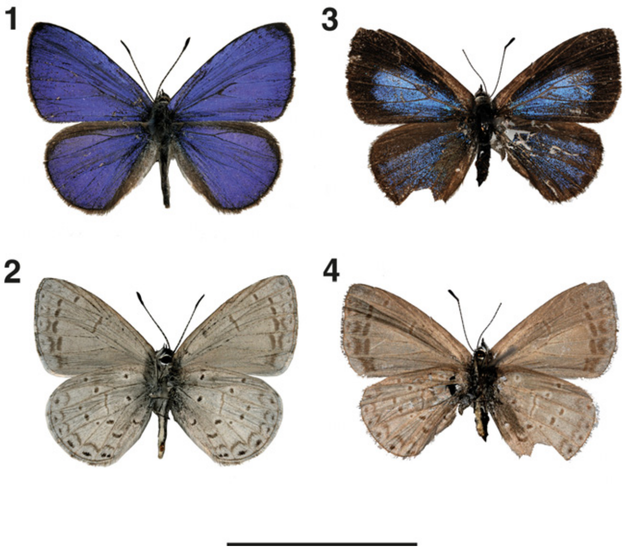
and compared with *U. cardia* from New Guinea and Australia. Recognition of this taxon has necessitated closer scrutiny of the taxonomy of *U. cardia* from the Wet Tropics of Australia, which is also revised.



Figs 1–4. *Udara renevieri* sp. nov.: (**1–2**) holotype male showing upper- and underside, (**3–4**) paratype female showing upper- and underside. Scale bar = 20 mm.

MATERIALS AND METHODS

Type material has been examined and lodged in the following repositories:

QM	Queensland Museum, Brisbane, Australia
BMNH	Natural History Museum, London, United Kingdom
MNHN	Muséum National d'Histoire Naturelle, Paris

The male genitalia of two specimens of each of *Udara renevieri* sp. nov. (from Mont Do, South Province, 1020 m, New Caledonia) and *U. cardia cardia* (from Wau, Morobe Province, 1200 m, Papua New Guinea; and Whiteman Range, West New Britain Province, 1050 m, Papua New Guinea) and a single specimen of *U. cardia tenella* (from Mt Misery, QLD, 850 m, Australia) were dissected and compared. Terminology for the morphological structure of the genitalia follows Eliot and Kawazoé (1983).

SYSTEMATICS

Udara renevieri sp. nov. (Figs 1–9)

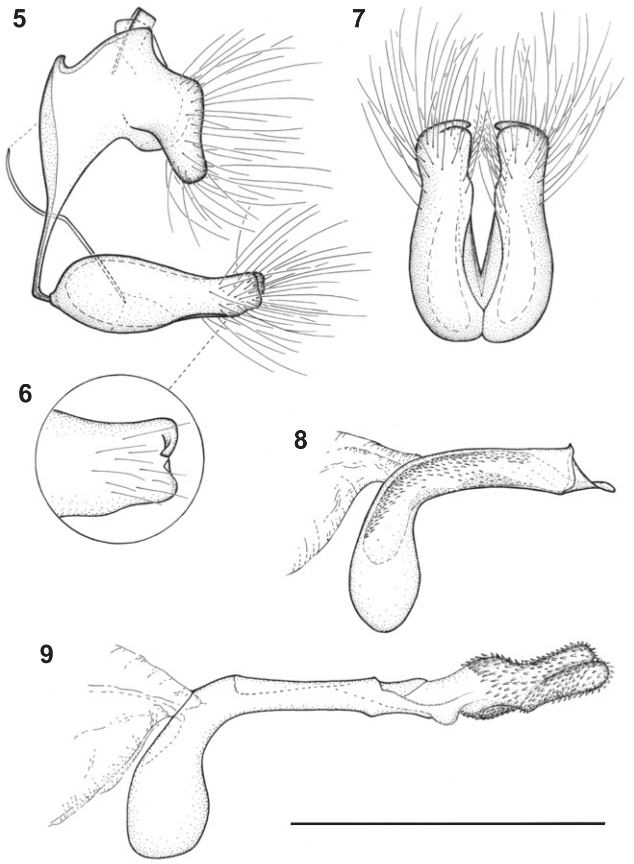
http://zoobank.org/urn:lsid:zoobank.org:act:4D413625-B1E4-4EBD-9330-094105426202

Type material

Holotype: ♂ labelled 'NEW CALEDONIA, Mont Do, Boulouparis, Sth Province, 1020 m, 12 JAN. 2013, Alain Renevier-Faure', 'Registration number T183493' (QM). *Paratypes*: 5♂, 1♀ as follows: 1♂ labelled 'NEW CALEDONIA, Mont Do, Boulouparis, Sth Province, 1020 m, 12 DEC. 2009, Alain Renevier-Faure', 'Registration number T183494' (QM); 1♂ labelled similarly but with date '31 OCT. 2011', 'Registration number T183495' (QM); 1♀ labelled similarly but with date '31 OCT. 2011', 'Registration number T183496' (QM); 2♂ labelled similarly but with date '12 JAN. 2013' (BMNH); 1♂ labelled similarly but with date '12 DEC. 2009' (MNHN). *Other material examined*: 10♂, 1♀ as follows: 3♂ labelled 'NEW CALEDONIA, Mont Do, Boulouparis, Sth Province, 1020 m, 12 DEC. 2009, Alain Renevier-Faure' (QM); 7♂, 1♀ labelled similarly in private collection of Alain Renevier-Faure.

Adult description

Male (Figs 1,2). *Head*: eyes black with fine brown hairs; frons white with black central patch; labial palp black and white with black piliform scales on ventral surface; antenna 7.5 mm long, flagellum black, shaft ringed with about 16–17 narrow white bands, club spatulate with 14 ventral bands each with a row of bristles. *Thorax*: black with grey piliform scales on dorsal surface, white piliform scales on ventral surface; legs white; forewing 16 mm long (from base to costa), upperside iridescent purple with costa and termen narrowly black extending proximally along outer veins, cilia (scale-fringe) black tipped white in ventral half, numerous paddle-shaped androconia in basal half; underside ground colour pale grey with a series of darker greyish-brown markings, a transverse bar along the discocellulars at end of discal cell, a postmedian band comprising a broken series of six broad streaks between each major vein, that nearest the costa between veins R$_5$ and M$_1$ displaced proximally, a subterminal band of five obscure streaks extending from veins M$_1$ to 1A + 2A, a series of five obscure terminal spots between each major vein (except between CuA$_2$ and 1A + 2A where the spot is absent), a narrow dark brown terminal line, followed by grey cilia tipped brown; hindwing upperside iridescent purple with costa and dorsum broadly black, termen narrowly black extending proximally along veins, cilia black tipped white, base to submedian region below radial sector with numerous white piliform scales, numerous paddle-shaped androconia in basal half; underside ground colour pale grey with a series of darker greyish-brown markings, basal region with scattered black scales especially towards dorsum, base to submedian region with scattered white piliform scales especially towards dorsum and tornus, two dark subbasal spots, a dark submedian spot between the anal veins, a narrow transverse bar or streak along the discocellulars at end of discal cell, a series of seven postmedian spots between each major vein, those between veins Rs and M$_1$, and veins CuA$_1$ and CuA$_2$ displaced proximally, a subterminal band comprising six obscure crescent-shaped streaks extending from veins Rs to 1A + 2A, which enclose a series of seven dark terminal spots, one between each major vein except between veins CuA$_2$ and 1A + 2A in which there are two spots, a narrow dark brown terminal line, followed by grey cilia tipped brown then white.



Figs 5–9. Male genitalia of *Udara renevieri* sp. nov. from Mont Do, New Caledonia: (**5**) lateral view with aedeagus removed; (**6**) interior view of apex of right valva (enlarged); (**7**) valvae ventral view; (**8**) aedeagus lateral view; (**9**) aedeagus with vesica everted lateral view. Scale bar = 1.0 mm.

Abdomen: upperside black; underside white. *Genitalia*: (Figs 5–9) sociuncus broad, with anterior lobes substantially extended posteroventrally and broadly rounded at their apex; vinculum very narrow, especially below juxta and tapering posteriorly; valva lozenge-shaped, apex obtuse, with a short, yet prominent, sharp apical process folded interiorly, juxta Y-shaped; aedeagus stout and bent at right angles at ductus, with coecum long and 'swollen' and vesica bearing numerous spine-like cornuti.

Female (Figs 3,4). *Head*: similar to male. *Thorax*: forewing 15 mm long; upperside iridescent blue with costa, tornus and dorsum broadly black, central blue area extends to dorsum in subbasal region; underside colour pattern similar to male except ground colour brownish-grey; hindwing upperside iridescent blue with costa and dorsum broadly black, termen narrowly black; underside colour pattern similar to male except ground colour brownish-grey. *Abdomen*: similar to male.

Variation

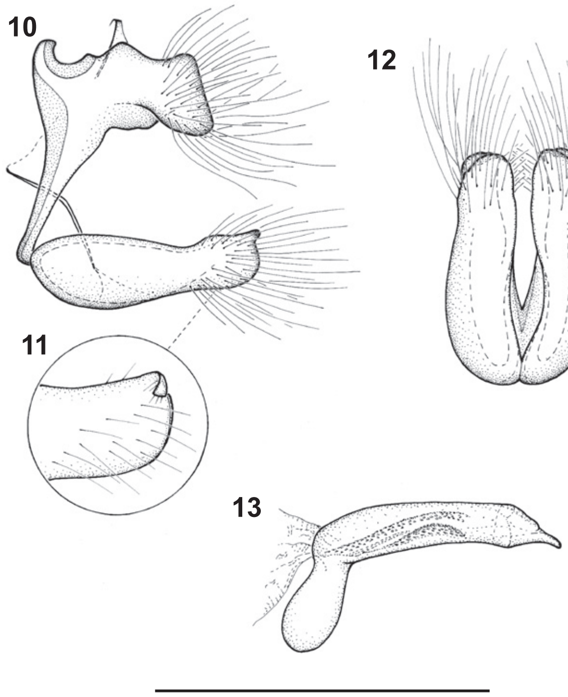
The species shows little phenotypic variation. Among the 16 males from the type locality available for study, there were minor differences in the size and clarity of the underside markings, with some specimens having the spots and marks more pronounced compared with the holotype.

Only two worn females were available for study. Apparent differences in the underside ground colour between the sexes may be real or due to an age effect. In older, worn males, the ground colour is brownish-grey (similar to the female) rather than pale grey typical of males in fresh condition, suggesting that the underside colour changes with age.

Diagnosis

This species is distinguished from all other members of *Udara* by the series of broad postmedian and subterminal brown markings on the underside of the forewing. In *U. renevieri*, these markings are more pronounced and appear as a series of rectangular streaks or bars, especially the postmedian series between veins M_1 and 1A + 2A. Furthermore, the postmedian and subterminal markings between veins M_3 and 1A + 2A are almost confluent with each other so that they appear as a double row, comprising three sets of two conspicuous streaks that converge posteriorly. It differs from *U. cardia* by six additional characters as follows: (1) in *U. renevieri* the underside ground colour is pale grey (male) or pale brownish-grey (female), whereas in *U. cardia* it is silvery-grey or silvery-white; (2) in *U. renevieri*, the terminal spots on the underside of the hindwing are obscure, whereas in *U. cardia*, they are distinct and more conspicuous; (3) on the underside of the hindwing, there are only three dark spots near the base (two subbasal, one submedian) that form a straight line in *U. renevieri*, whereas there are four or five dark spots near the base (three or four subbasal, one submedian) in *U. cardia*; (4) the upperside colour of the male is darker purple without white patches in *U. renevieri*, whereas it is paler shining blue usually with one or two black tornal spots on the hindwing and often with small whitish patches discally on the forewing and subapically on the hindwing in *U. cardia*; (5) the central blue area on the upperside in the female is less extensive with no whitish median patches on both wings in *U. renevieri*, whereas the blue area is more extensive, especially on the forewing in which it extends broadly to the dorsum in *U. cardia*; and (6) in *U. renevieri*, the upperside of the hindwing in the female is devoid of black terminal spots, but in *U. cardia*, there is a series of up to five conspicuous black terminal spots.

There are also comparative differences in the male genitalia between *U. renevieri* (Figs 5–9) and *U. cardia* (Figs 10–17). In *U. renevieri*, the sociuncus, in lateral view (Fig. 5), is shorter in length, broader in width and the lobes are more elongated, extending posteroventrally compared with *U. cardia* (Fig. 10). The ventral portion of the vinculum between the juxta and base of the valva is much narrower in *U. renevieri*, being about half as wide as that of *U. cardia*. In *U. renevieri*, the valva, in lateral view, is narrower towards the apex, which is comparatively square-shaped, and the apical process is more pronounced and of a different configuration (Fig. 6); the apical portion of the valva, in dorsal view (Fig. 7), is broader with the inner and outer walls distinctly concave compared with *U. cardia* (Fig. 12). The aedeagus in



Figs 10–13. Male genitalia of *Udara cardia cardia* from Wau, Papua New Guinea (MF Braby collection): (**10**) lateral view with aedeagus removed; (**11**) interior view of apex of right valva (enlarged); (**12**) valvae ventral view; (**13**), aedeagus lateral view. Scale bar = 1.0 mm.

U. renevieri (Figs 8,9) has the vesica longer and extending well past the ductus into the coecum, which is also larger than in *U. cardia* (Fig. 13).

Etymology

This distinctive species is named in honour of Alain Renevier-Faure of Nouméa, New Caledonia who discovered the butterfly and who has made a significant contribution to the knowledge of the butterfly fauna of the island in the past few decades.

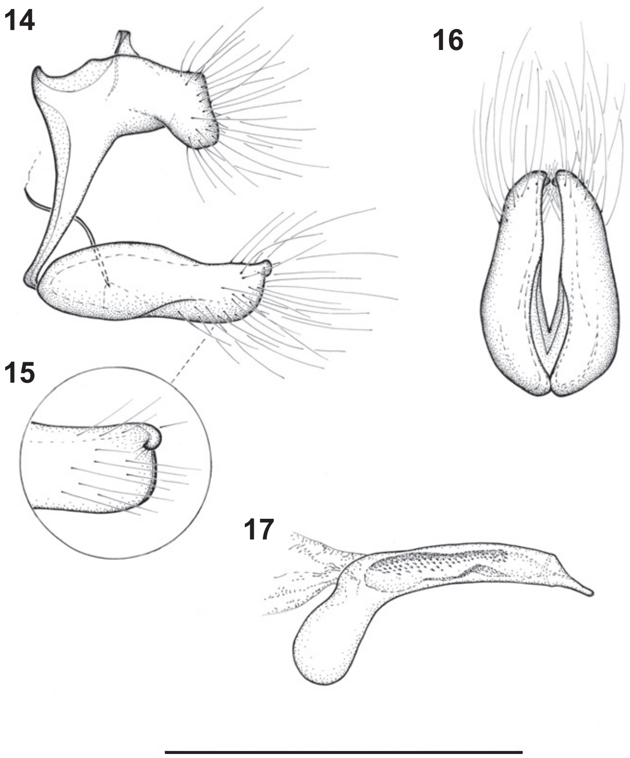
Distribution

The species is known only from a limited area on New Caledonia. To date, all material has been collected from the montane areas of Mont Do (c. 1000 m) on ultramafic soils (Fig. 18) during the warmer months from October to January. The males have a fast and erratic flight, and they avidly feed on flowers of *Geniostoma densiflorum* (Loganiaceae) and *Guioa villosa* (Sapindaceae) (A Renevier-Faure pers. comm. 2013). Very few females have been observed, and only two have been collected.

Udara cardia tenella (Miskin, 1891) syn. nov. and stat. nov.

Lycaena tenella Miskin, 1891, p. 63.

Cyaniris tenella (Miskin). — Waterhouse 1903a, pp. 144–146, pl. ii, fig. 11; Waterhouse 1903b, p. 20; Waterhouse and Lyell 1914, p. 75, figs 168–170.

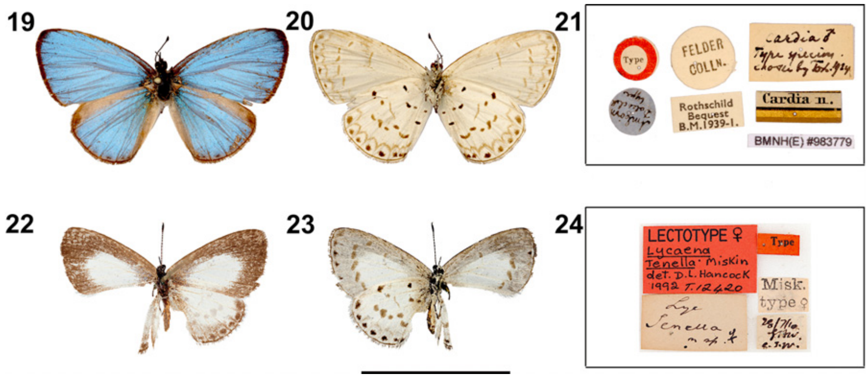


Figs 14–17. Male genitalia of *Udara cardia tenella* from Mt Misery, north-east Australia (CJ Müller collection): (**14**) lateral view with aedeagus removed; (**15**) interior view of apex of right valva (enlarged); (**16**) valvae ventral view; (**17**) aedeagus lateral view. Scale bar = 1.0 mm.

Fig. 18. Mont Do, type locality of *Udara renevieri* sp. nov. Photo A Renevier-Faure.

Lycaenopsis tenella (Miskin). — Chapman 1909, p. 464; Fruhstorfer 1922, p. 866; Waterhouse 1932, p. 141, pl. XX; Barrett and Burns 1951, p. 150; Common 1964, p. 124, fig. 503; McCubbin 1971, p. 73; Common and Waterhouse 1972, p. 428, pl. 41.

Celastrina tenella (Miskin). — D'Abrera 1971, pp. 382–383; Common and Waterhouse 1981, p. 590, pl. 39; Common and Waterhouse 1982, p. 342, pl. 22; Valentine 1988, p. 6; Dunn and Dunn 1991, p. 423.



Figs 19–24. Type specimens of *Udara cardia*: (**19–21**) holotype male of *Lycaena cardia* C. Felder (BMNH) from Ambon, southern Maluku, showing upper-, underside and label data; (**22–24**) holotype female of *Lycaena tenella* Miskin (QM) from Cairns, Australia, showing upper-, underside and label data. Scale bar = 20 mm.

Udara tenella (Miskin). — D'Abrera 1977, pp. 382–383; Eliot and Kawazoé 1983, p. 101, figs. 63, 64; D'Abrera 1990, pp. 387–388; Hancock 1995, p. 525; Edwards 1996, p. 254; Edwards *et al*. 2001, pp. 192–193; Braby 2000, p. 849, pl. 62; Braby 2004, pp. 298–299; Braby 2010, p. 76; Orr and Kitching 2010, p. 280.

Type material

Holotype: ♀ (Figs 22–24) labelled '*Lyc tenella* n sp.', 'Misk. Type ♀, 28/7/10, GAW | CJW', 'Type' [on red card], 'LECTOTYPE ♀, Lycaena tenella Miskin, det. D.L. Hancock, 1992 T.12420' [on red card] (QM).

Comments on type specimen

Miskin (1891) described *Lycaena tenella* as a distinct species based on material from Cairns, QLD, Australia, lodged in the QM. Miskin (1891) did not indicate the number of specimens before him, nor he did designate a type in the original description, although internal evidence from his publication suggests that he only had a single specimen – he described the female sex only, which was followed by the single-size measurement of 23 mm for expanse. Subsequently, Waterhouse (1903a) provided a more detailed description of the species, including a complete description of the male, which he illustrated. Waterhouse (1903a, pp. 145–146) referred to a type by stating 'Type specimen (♀) in Queensland Museum' and noted that 'Miskin described the female only, and a not too fresh specimen', implying that Miskin's description was based on a single specimen. G.A. Waterhouse subsequently labelled this specimen (Figs 22–24) as the type in 1910 so that it corresponded with his fixation of Miskin's nominal species-group name *tenella* 7 years earlier in 1903. Eliot and Kawazoé (1983) referred to this female as the holotype. Hancock (1995, p. 525) located the female specimen in the QM but interpreted Eliot and Kawazoé's (1983) type designation as a lectotype designation because he claimed that their designation was a 'lectotype by inference of holotype'. He added a lectotype label to the specimen a few years prior to his publication in 1992. Hancock's (1995) action presumably was in accordance with Recommendation 73F (avoidance of assumption of holotype) and Article 74(b) (designation of lectotype by inference of holotype) of the third edition of the International Commission on Zoological Nomenclature (ICZN) (1985, p. 74) in which it is stated that 'when it cannot be determined that a nominal species-group taxon was established on a single specimen and when a holotype was not designated, the first subsequent author to have published the inference that one original specimen is the "holotype", or the "type", is deemed, should another syntype or syntypes be discovered, to have designated a lectotype.' Hancock (1995, p. 525) noted that Miskin's species was 'described from (probably one) female collected by J. Wild at Cairns', but he did not list or provide data of any additional syntypes. Edwards *et al*. (2001) followed Hancock's (1995) action and referred to Miskin's type as a lectotype; however, both Hancock (1995) and Edwards *et al*. (2001) appear to have been unaware of Waterhouse's (1903a) earlier fixation of Miskin's syntype. Examination of material in the QM, Miskin's notes on the species and an old register in the QM indicate only a single type (G Thompson pers. comm. 2013). These facts agree with evidence implied in the original publication and Waterhouse's (1903a) action noted earlier that the nominal species-group taxon was based on a single specimen. Hence, under Article 73.1.2 of the most recent edition of the ICZN (1999), Miskin's type is the holotype by monotypy; it cannot be a lectotype.

Comments on synonymy and change of status

Fruhstorfer (1922, p. 866) drew attention to the close relationship, and likely synonymy, of *Lycaenopsis cardia* and *Lycaenopsis tenella*, noting that 'The clasping-organs of this species [*Lycaenopsis tenella*] in their contours resemble those of *Lycaenopsis cardia*, but the valve is shorter, growing broader, the terminal tooth being stunted . . . We may even consider *tenella* to be only a strongly modified form of *Lycaenopsis cardia*, so that *tenella* would replace the Indo-Malayan *Lycaenopsis cardia* in New Guinea and Australia. This matter will be cleared up, when the larva and perhaps also the androconia will be known.' The male *U. tenella* illustrated by Fruhstorfer in plate 152, figure IXg is actually *U. cardia* from montane New Guinea, which he refers to as *Lycaenopsis tenella parvipuncta*.

In their monograph of the *Lycaenopsis* group, Eliot and Kawazoé (1983) recognised two subspecies of *U. cardia*: the nominate subspecies *U. cardia cardia* (C. Felder, 1860), which occurs widely from southern Maluku (Buru, Serang, Ambon), the Kai and Aru Islands, through mainland New Guinea and its adjacent islands to the Solomon Islands, and *U. cardia miyashitai* Eliot & Kawazoé, 1983, which is restricted to northern Maluku (Ternate, Batjan). The type specimen of *Lycaena cardia* C. Felder from Ambon, Maluku, is illustrated in Figures 19–21. Eliot and Kawazoé (1983) provisionally treated *U. tenella* from north-east Australia (which lies in proximity to the geographical range of *U. cardia cardia*) as a distinct allopatric species on the basis of phenotypic differences in colour pattern; however, they suggested that it is probably conspecific with *U. cardia* and drew attention to similarities in the underside pattern and the upperside shining blue colour of the male; they also illustrated the male and female genitalia and showed that several components, namely the morphology of the sociuncus, valva, juxta and aedeagus of the male, were more or less identical. For the past 120 years, the taxon *Lycaena tenella* has been treated as a full species under at least five different generic combinations.

The taxa included under the genus *Udara*, and their species boundaries, as circumscribed by Eliot and Kawazoé (1983), differ fundamentally in the comparative morphology of the male and female genitalia, the underside wing pattern elements (extent, distribution and shape of the spots), the upperside colour pattern and sometimes in the degree of sexual dimorphism. Braby *et al*. (2012) recommended that the null hypothesis of a single species, with two or more subspecies, should only be rejected if evidence from multiple properties (colour pattern, morphology, behaviour or ecology) shows that a set of allopatric populations differ in all three character types (with a total of four to six characters). In this context, it is noteworthy that *U. tenella* possesses many characters that are shared with *U. cardia* but only differs in one diagnosable character type, namely colour pattern. Moreover, these phenotypic differences are relatively trivial (minor). The chief points of difference concern: (1) the extent of the white patches on the upperside of the forewing and hindwing in the male – in all three subspecies, the upperside colour is shining blue, but in *U. cardia tenella*, there is a prominent white central patch on the forewing and a large white subapical patch on the hindwing, whereas in *U. cardia cardia* and *U. cardia miyashitai*, these patches are reduced and usually absent on the forewing; (2) the extent of white on the upperside of the forewing and hindwing in the female – in *U. cardia tenella*, the upperside is predominantly white with the shining blue areas restricted to the basal region, whereas in *U. cardia cardia*, the shining blue areas are more extensive with the white areas restricted to a central patch beyond the discal cell on the forewing and sometimes present as a subapical patch on the hindwing; (3) the presence of black terminal spots on the upperside of the hindwing in the male – in *U. cardia tenella*, there is a series of five or six spots narrowly ringed with white, whereas in *U. cardia cardia*, these spots, unlike the female, are reduced to one or two tornal spots; and (4) the extent of the subterminal band of crescent-shaped streaks enclosing the terminal spots on the underside – in *U. cardia tenella*, these markings diminish in intensity towards the apex, especially on the forewing where they may be absent, whereas in *U. cardia, cardia* the markings are more pronounced. The width of the black terminal band on the upperside in male *U. cardia tenella* (2.0 mm) is much broader than in male *U. cardia cardia* (0.5 mm), but this character state is also broad in male *U. cardia miyashitai* (2.0 mm) (Eliot & Kawazoé 1983); hence, it is not unique to *U. cardia tenella*. Eliot and Kawazoé (1983) drew attention to the presence of a 'subbasal spot' near the dorsum between the anal veins 1A + 2A and 3A on the underside of the hindwing as a diagnostic character of *U. cardia*, and this feature is also present in *U. cardia tenella*.

Examination of the male genitalia revealed no striking morphological differences between *U. cardia cardia* (Figs 10–13) and *U. cardia tenella* (Figs 14–17). Overall, the genitalia of *U. cardia tenella* are smaller, but the small difference in size is undoubtedly a reflection of the fact that *U. cardia tenella* is a slightly smaller butterfly (by 1–2 mm) than *U. cardia cardia*. Fruhstorfer (1922) noted that the valva of *U. cardia tenella* is slightly shorter and the apical tooth less pronounced than in *U. cardia cardia*, and this difference is evident in the material we have examined. The apical portion of the valvae, in dorsal view, of *U. cardia tenella* appears narrower (Fig. 16), but this is largely due to their orientation in which each valva was rotated closer together in the dissected specimen prepared. There are minor differences in the shape of the sociuncus between the two taxa, but these are not of the same magnitude seen in *U. renevieri* and are considered to fall within the expected variation among allopatric populations distributed over the species' geographical range.

Given the four minor colour pattern differences, lack of substantial morphological differences in the male genitalia, and striking similarities in underside markings (between the respective sexes) and the similar upperside shining blue colouration between *U. tenella* and *U. cardia*, subspecific status for *U. tenella* seems more appropriate. Additional evidence from other sources of data, including ecology, behaviour and population genetics, is needed to test this hypothesis. The ecology and biology of the immature stages are presently unknown, but both subspecies occur in tropical forest, especially in montane areas (Parsons 1998; Braby 2000, 2004; Tennent 2002).

DISCUSSION

The presence of *Udara* on New Caledonia is intriguing biogeographically. The species *U. renevieri* represents a substantial extension to the known geographical range of the genus; previously, *Udara* was known no further south than the Wet Tropics of north-east Australia and no further east than the Solomon Islands (Braby 2000; Tennent 2002). *U. renevieri* is almost certainly endemic to New Caledonia where it is possibly restricted to montane areas, and further field studies are needed to determine the full extent of its spatial distribution, habitat preference and larval food plant specificity. In contrast, *U. cardia cardia* occurs widely in the Australian Region, from Maluku, the Kai and Aru Islands, through mainland New

Table 1 Species of butterflies endemic to New Caledonia and the Loyalty Islands (compiled from data in Holloway & Peters (1976) and Tennent (2005, 2006, 2008))

Family	Species
Papilionidae	*Graphium gelon* (Boisduval, 1859)
	Papilio montrouzieri Boisduval, 1859
Pieridae	*Elodina signata* Wallace, 1867
	Delias ellipsis de Joannis, 1901
Nymphalidae	*Euploea helcita* Boisduval, 1859
	Paratisiphone lyrnessa Hewitson, 1872
	Austroypthima petersi Holloway, 1974
	Charaxes gamma Lathy, 1898
	Charaxes clitarchus Hewitson, 1874
Lycaenidae	*Deudorix pewcaecus* Tennent, 2008
	Nacaduba deplorans (Butler, 1875)
	Psychonotis purpurea Druce, 1902
	Theclinesthes petersi Tennent, 2005
	Udara renevieri

Guinea and its adjacent islands to the Solomon Islands (Eliot & Kawazoé 1983; Parsons 1998), whereas *U. cardia tenella* is endemic to north-east Australia. Very few specimens of *U. cardia cardia* have been recorded from the Solomon Islands Archipelago, where it is known only from Bougainville (politically part of PNG), Guadalcanal and Rendova (Tennent 2002), and *U. cardia tenella* is also generally rare.

New Caledonia has been identified as one of the world's biodiversity hot spots, with high levels of diversity and endemism coupled with substantial threats with many taxa facing extinction (Myers *et al*. 2000). The island supports more than 2500 species of endemic vascular plants (representing 76% of the island's flora) and 84 species of endemic vertebrates (representing 44% of the islands vertebrate fauna), and estimates of habitat loss of the original extent of primary vegetation are around 72% (Myers *et al*. 2000). Recognition of *U. renevieri* as a distinct endemic species emphasises the peculiarity of the island's unique Lepidoptera (Holloway 1974, 1979; Holloway & Peters 1976; Tennent 2005).

In their detailed review of the butterflies of New Caledonia and the adjacent Loyalty Islands, Holloway and Peters (1976) recorded 67 species, of which two genera (*Paratisiphone, Austroypthima*) and 11 species were considered to be endemic to the area. A more recent review by Tennent (2005, 2006) indicates that 72 species of butterflies have been recorded from the New Caledonia-Loyalty Islands group, of which 12 are endemic to New Caledonia (Table 1). Tennent (2008) subsequently described a new species of *Deudorix*, which was previously listed under the name *D. epijarbas* (Moore, 1858) (Holloway & Peters 1976), and this species is also endemic to New Caledonia. More recently, A Renevier-Faure (pers. comm. 2013) has added *Eurema smilax* (Donovan, 1805), *Famegana alsulus* (Herrich-Schäffer, 1869) and the new species of *Udara* from New Caledonia.

Of the 75 species of butterflies recorded from the New Caledonian island group, two (*Eurema candida* (Cramer, 1782) and *Hemiargus isola* (Reakirt, 1867)) are considered very doubtful (i.e. incorrectly labelled), three (*Papilio anactus* Macleay, 1826, *Pieris rapae* (Linnaeus, 1758) and *Danaus plexippus* (Linneaus, 1758)) have been introduced, and two (*Vanessa itea* (Fabricius, 1775) and *V. kershawi* (McCoy, 1868)) are rare vagrants from Australia and therefore non-resident (Holloway & Peters 1976; Tennent 2005, 2006). *Papilio anactus*, otherwise endemic to Australia, is thought to have been introduced to New Caledonia (JV Peters in Braby 2000). It was first recorded from Népoui and Pouémbout in early 1972 (Holloway & Peters 1976) and subsequently from Bourail in March 1974, but it now appears to be resident on the west coast (Pouembout, Koné, Témala, Poum) where it breeds on cultivated *Citrus* (A Renevier-Faure pers. comm. 2013). Similarly, *E. smilax*, also endemic to Australia, is now locally common on the west coast of New Caledonia (Pouembout, Poum, Poya, Bourail, Moindou) where it breeds on *Cassia tora* (A Renevier-Faure pers. comm. 2013), but it is not certain how it became established. An additional two species (*Euploea sylvester tristis* (Butler, 1866) and *E. treitschkei* Boisduval, 1832) are very poorly known, being based on a few historic specimens from the 19th century, and their presence on the island seems doubtful and requires confirmation (A Renevier-Faure pers. comm. 2013).

The remaining 65 species are considered to comprise the indigenous resident fauna. Thus, with the addition of *U. renevieri*, the number of butterflies endemic to New Caledonia is 14 species (Table 1), which represents 21% of the island's indigenous butterfly fauna. This is a remarkable level of endemism given that remote oceanic islands in the South Pacific are typically characterised by an impoverished butterfly fauna consisting mostly of widespread and highly dispersive elements (Patrick & Patrick 2012). Tennent (2005) concluded that additional species of butterflies undoubtedly remain to be discovered, noting that several genera (e.g. *Ionolyce*, *Petrelaea*) have been recorded both in Australia and Vanuatu but not from New Caledonia, suggesting that the level of endemism may even be higher.

The distinct Lepidoptera fauna of New Caledonia no doubt reflects the geological and evolutionary history of the island and its geographical isolation. New Caledonia is geologically older than neighbouring island groups such as Vanuatu and the Solomons, and together with New Zealand and Lord Howe Island, it makes up the Gondwanan continental block Tasmantis, which separated from the east margin of Gondwana 90–80 Ma (Swenson *et al*. 2001). New Caledonia is composed of several allochthonous terranes that formed in the pre-Pacific Ocean (Heads 2008) during the Late Jurassic to Early Cretaceous (Pelletier 2007). However, modern Tertiary geological models of the region do not imply the existence of direct land connections of New Caledonia with any other units of the Tasmantis block, or with Australia or Outer Melanesian Arc islands (Smith *et al*. 2007). Geological evidence indicates that the island was completely submerged for about 20 Ma (from 65–45 Ma), and land did not become available for colonisation until the Late Eocene (c. 37 Ma) (Pelletier 2007). That is, New Caledonia likely endured several catastrophic events during the Tertiary, including mass extinctions, such that much of the biotic diversification is relatively recent (Murienne *et al*.

Table 2 Butterfly species and subspecies endemic to the Wet Tropics biome of north-east Australia (compiled from data in Braby (2000))

Family	Species	Subspecies
Papilionidae	†*Ornithoptera euphorion* (Gray, [1853])	†*Papilio ambrax egipius* Miskin, 1876
Hesperiidae	*Chaetocneme porphyropis* (Meyrick & Lower, 1902)	†*Euschemon rafflesia alba* Mabille, 1903
Hesperiidae	*Toxidia melania* (Waterhouse, 1903)	*Toxidia rietmanni parasema* (Lower, 1908)
Hesperiidae		*Sabera fuliginosa fuliginosa* (Miskin, 1889)
Pieridae	*Appias melania* (Fabricius, 1775)	*Delias ennia nigidius* Miskin, 1884
Nymphalidae	*Tisiphone helena* (Olliff, 1888)	*Tellervo zoilus zoilus* (Fabricius, 1775)
Lycaenidae		*Hypochrysops apollo apollo* Miskin, 1891
Lycaenidae		*Hypochrysops pythias euclides* Miskin, 1889
Lycaenidae		*Philiris diana diana* Waterhouse & Lyell, 1914
Lycaenidae		*Philiris nitens nitens* (Grose-Smith, 1898)
Lycaenidae		*Philiris sappheira manskiei* Ring & Olive, 1997
Lycaenidae		*Danis danis serapis* Miskin, 1891
Lycaenidae		*Jamides aleuas coelestis* (Miskin, 1891)
Lycaenidae		*Udara cardia tenella* (Miskin, 1891)

†, Taxon extends marginally outside biome with a disjunct population in the Mackay district.

2005). Indeed, most phylogenetic studies and lineage through time plots have rejected vicariant hypotheses for a Gondwanan origin of its distinct biodiversity (e.g. Smith *et al.* 2007; Espeland & Murienne 2011). Swenson *et al.* (2001) found a connection with New Guinea based on a phylogeny of *Nothofagus*, attributed to long-distance dispersal and mass extinctions. In contrast, Ladiges and Cantrill (2007) suggested that parts of the New Caledonian archipelago might have remained subaerial back into the Cenozoic that possibly allowed old biota to persist.

As noted by Holloway and Peters (1976), the butterflies endemic to New Caledonia comprise a taxonomically isolated group, and their origin may date back to multiple dispersal events during the Miocene. Moreover, there is no evidence of radiation in the butterfly fauna. Braby and Pierce (2007) and Müller *et al.* (2013) concluded that the ancestor of *Delias ellipsis* de Joannis, 1901 (endemic to New Caledonia) colonised the island via long-distance dispersal via stepping stones from mainland Australia, or from mainland New Guinea and the Bismarck Archipelago via the Inner Melanesian Arc or possibly via the Solomons Archipelago during the late Pliocene. Further systematic analyses of the genus *Udara* are needed to establish the phylogenetic relationships of *U. renevieri* and *U. cardia*, and to estimate their divergence times in relation to past geological events. Such an analysis would elucidate historical processes of vicariance or dispersal in facilitating speciation among these two allopatric butterflies.

The Wet Tropics biome of north-east Australia, stretching from Cooktown to Townsville and including the Atherton Tableland, QLD, is renowned for its unique lowland and upland rainforests, and is similarly a major centre of endemism on the Australian continent, especially for vascular plants (Crisp *et al.* 2001). It is also a region of high species diversity. *Udara cardia* is one of 10 species of butterflies that is within Australian limits restricted to, or largely restricted to, this biome (Table 2). Five of these species are narrow-range endemics, while the five others (*Papilio ambrax*, *Sabera fuliginosa*, *Hypochrysops pythias*, *Philiris sappheira*, *Udara cardia*) occur more widely outside the continent in mainland New Guinea and often its adjacent islands, but each is represented by subspecies that are endemic to the Wet Tropics (Table 2). The lycaenid *Jamides aleuas* (C. & R. Felder, 1865) was within the Australian continent previously believed to be restricted to the Wet Tropics, where it is represented by the endemic subspecies *J. aleuas coelestis* (Miskin, 1891); however, the species was recently found to also occur on Cape York Peninsula, where it is represented by the subspecies *J. aleuas pholes* Fruhstorfer, 1915 (Brown *et al*. 2011). An additional eight subspecies of butterflies are endemic to the Wet Tropics (Table 2).

Udara cardia tenella is thus one of a set of 19 Australian butterfly taxa (5 species, 14 subspecies), all of which are distantly related, that is endemic to the Wet Tropics, emphasising the biogeographical and conservation importance of this biome. All but one of these taxa are restricted to rainforest habitats: the exception is *Hypochrysops apollo apollo* Miskin, 1891, which occurs in coastal paperbark woodlands and mangroves. Synoptic distribution maps and habitat data in Braby (2000) indicate that 225 species of butterflies have been recorded from the Wet Tropics (including the adjacent montane open forests and woodlands, and lowland paperbark swamps and mangroves), of which 103 species occur primarily in rainforest. Thus, the level of endemism for the rainforest component of this relatively small area is 4.8% (or 17.5% if subspecies are included). The Wet Tropics has been identified as an area of exceptionally high butterfly species richness (Kitching 1981; Kitching & Dunn 1999), but its importance as an area of endemism appears to have been overlooked. An immediate question arises: why is the Wet Tropics an area of endemism for rainforest butterflies? Is it because these species/subspecies share a similar biogeographical history of range contraction, vicariance and speciation in isolation, or did their ancestors enter the biome relatively recently over different time intervals via dispersal and then the populations diverged allopatrically, or have the taxa evolved adaptively to a unique combination of ecological factors restricting their ranges? Further studies examining the evolutionary history of the lineages to which these taxa belong would be most rewarding in terms of answering these questions and understanding their patterns of differentiation.

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