



<http://dx.doi.org/10.11646/zootaxa.3949.4.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:B3123099-882F-4C42-B83B-2BA1C2906F65>

Revision of the Sundaland species of the genus *Dysphaea* Selys, 1853 using molecular and morphological methods, with notes on allied species (Odonata: Euphaeidae)

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Abstract

The Sundaland species of the genus *Dysphaea* were studied using molecular and morphological methods. Four species are recognized: *D. dimidiata* Selys, *D. lugens* Selys, *D. ulu spec. nov.* (holotype ♂, from Borneo, Sarawak, Miri division, Upper Baram, Sungai Pejalai, Ulu Moh, 24 viii 2014; deposited in RMNH) and *D. vanida spec. nov.* (holotype ♂, from Thailand, Ranong province, Khlong Nakha, Khlong Bang Man, 12–13 v 1999; deposited in RMNH). The four species are described and illustrated for both sexes, with keys provided. The type specimens of the four *Dysphaea* taxa named by E. de Selys Longchamps, i.e. *dimidiata*, *limbata*, *semilimbata* and *lugens*, were studied and their taxonomic status is discussed. Lectotypes are designated for *D. dimidiata* and *D. limbata*. *D. dimidiata* is recorded from Palawan (the Philippines) for the first time. A molecular analysis using three markers (COI, 16S and 28S) is presented. This includes specimens of three Sundaland species of the genus (*D. lugens* missing) and two congeners from other regions (*D. basitincta* and *D. gloriosa*). Notes and photographs of the male holotype of *D. walli* Fraser (from Maymyo, Burma) are provided.

Key words: Odonata, Euphaeidae, *Dysphaea*, new species, Sundaland, COI, 16S, 28S

Introduction

Dysphaea Selys, 1853 is a small oriental genus of the family Euphaeidae with seven species recognized at present (Table 1). The distribution of the genus extends from southwestern India in the west to Java and Borneo in the east and to Yunnan, Guangxi and Guizhou in the north.

The genus-group name *Dysphaea* was introduced by Selys Longchamps (1853) as one of the four subgenera of the genus *Euphaea* [Selys, 1840] within the “Legion Euphaea”, which corresponds to the present family Euphaeidae. Later Selys Longchamps (1873) divided “Legion Euphaea” into three genera (*Epallage* [Charpentier, 1840], *Anisopleura* [Selys, 1853] and *Euphaea* [Selys, 1840]), but still ranked *Dysphaea* as a subgenus of *Euphaea*. Kirby (1890) listed *Dysphaea* as a full genus, as he did for all other Selysian subgenera.

Selys Longchamps introduced four species-group names in *Dysphaea*, all being from Sundaland. *D. dimidiata* Selys, 1853 (the type species of the genus) was described from a series of male specimens from Java (Selys Longchamps 1853). *D. limbata* Selys, 1859 was named as a ‘race of *dimidiata*’ based on male and female specimens from Mt Ophir (Johor, Malay Peninsula), Singapore, and Sarawak in Borneo (Selys Longchamps 1859). *D. lugens* Selys, 1873 was described from a single male specimen from ‘South Borneo’ and ranked as a ‘race of *dimidiata*?’ (Selys Longchamps 1873). *D. semilimbata* Selys, 1873 was described from a single male from Labuan, Borneo and was ranked as ‘variety or race of *dimidiata*?’ (Selys Longchamps 1873).

The relative status of these taxa obviously puzzled Selys Longchamps; in 1869 he upgraded *limbata* to the rank of full species (Selys Longchamps 1869), but 10 years later he reconsidered and recognised only a single species in the genus *Dysphaea* (= *dimidiata*) (Selys Longchamps 1879). In Selys Longchamps (1889) he retained this view and listed *lugens*, *semilimbata* (misspelled as *sublimbata*) and *limbata* as ‘forms’ or ‘races’ of *dimidiata*. The taxonomic status of these Sundaland taxa has been treated in different ways by various later authors. Kirby (1890)

listed these taxa as four distinct species. Laidlaw (1902) used the species name *D. limbata* for specimens collected by himself in Kelantan. Williamson (1904) and Ris (1911) identified a male from Trang (Lower Siam) and Ain Durian (Malacca), respectively, as *D. limbata*. Later, Laidlaw (1924, 1931a) called the Peninsular Malaysian taxon *D. dimidiata*, but in his lists of the Bornean Odonata, Laidlaw (1920, 1931b) listed two species from Borneo: *D. lugens* and *D. limbata*. Kimmins (1936) identified specimens from Mt Dulit (Sarawak) as *D. dimidiata* race *semilimbata* (actually these specimens are *D. lugens*, see below). Based on a study of a series of Sumatran specimens, Lieftinck (1935) concluded that *D. limbata* and *D. dimidiata* could not be separate species. In Lieftinck (1949) *limbata* was ranked as subspecies of *dimidiata*, but in his annotated catalogue of Sundaland Odonata, Lieftinck (1954) listed both *limbata* and *semilimbata* as synonyms of *dimidiata*. This interpretation has been followed by all later authors.

TABLE 1. List of the known species of the genus *Dysphaea* Selys, 1853 with data on distribution. The species are arranged in chronological order.

Species	Distribution
<i>Dysphaea dimidiata</i> Selys, 1853	Java, Sumatra, Billiton, Borneo, Palawan, Peninsular Malaysia, southernmost Thailand northwards to Songkhla and Trang provinces; see Fig. 83.
<i>Dysphaea lugens</i> Selys, 1873	Borneo; see Fig. 84.
<i>Dysphaea basitincta</i> Martin, 1904	Northern Vietnam (Ninh Binh, Hoa Binh, Lang Son and Bac Can provinces); southern China (Yunnan, Guangxi, Hainan).
<i>Dysphaea ethela</i> Fraser, 1924	Southern India (Karnataka, Kerala and Tamil Nadu States).
<i>Dysphaea walli</i> Fraser, 1927	Burma (Maymyo in Mandalay division).
<i>Dysphaea gloriosa</i> Fraser, 1938	Central and northern Thailand, Cambodia, Laos, southern Vietnam (Lam Dong, Dong Nai, Ho Chi Minh), northern Vietnam (Hoa Binh), northern India (Assam, Meghalaya), southern China (Yunnan, Hainan).
<i>Dysphaea haomiao</i> Hämäläinen, 2012	Southern China (Guizhou, Yunnan and Guangxi), northern and central Vietnam (Cao Bang, Quang Binh).
<i>Dysphaea ulu</i> spec. nov.	Northern Borneo (Brunei, Sarawak and Sabah); see Fig. 85.
<i>Dysphaea vanida</i> spec. nov.	Southern and western Thailand; see Fig. 86.

Since Lieftinck (1954), only two good species, *dimidiata* and *lugens*, have been listed from Borneo (e.g. Orr 2001, 2003). During extensive molecular work on Odonata, especially the suborder Zygoptera, carried out at Naturalis Biodiversity Center in Leiden (cf. Dijkstra & al. 2014), a number of samples of *Dysphaea*, many of them from northern Borneo, were analysed. In studies with the DNA Barcoding marker COI, and COI in combination with the more conserved 16S and 28S markers (see Figs. 1–4) one of the analysed north Bornean taxa appears as the sister of all other taxa studied, including among others *D. dimidiata* from Peninsular Malaysia and Borneo, *D. gloriosa* Fraser, 1938 (specimen from Hainan) and *D. basitincta* Martin, 1904 (specimens from Hainan). This led us to reconsider the status, based on morphological evidence, of all Sundaland *Dysphaea* material available to us, to study the type specimens of all *Dysphaea* taxa introduced by Selys Longchamps, and to expand the molecular analysis. Rather surprisingly, this revealed three structurally distinct species from Borneo, one of them being an undescribed species. We present a molecular analysis using the markers COI, 16S and 28S, based on samples of five species, including all but one of those occurring in Sundaland. In this paper we also name and describe the rather distinct looking taxon from Thailand, which was briefly characterized and illustrated as '*Dysphaea dimidiata* Selys forma (?)' by Asahina (1985) and as *D. dimidiata* by Asahina (1990). This brings the total number of known species in the genus to 9. We also designate lectotypes of both *Dysphaea* taxa named by Selys Longchamps from more than a single specimen and discuss briefly the other known species of the genus.

Material and methods

DNA extraction and amplification. Genomic DNA was extracted from legs using a NucleoMag 96 Tissue kit (Macherey-Nagel GmbH & Co.) on a KingFisher Flex magnetic particle processor (Thermo Scientific). A volume

of 150 µl was used for elution. Fragments of the nuclear 28S rRNA gene (1428–1435 bp) and the mitochondrial 16S rRNA (522–524 bp) and COI genes (613 and 658 bp) were amplified using primer combinations provided in Table 2. Several *Dysphaea* specimens from Thailand produced a COI fragment containing a stop-codon and an 18 base pair gap (position 20–37) when using the conventional primers, therefore a different forward primer DysF 5'-GCATGGGCAGGAATAGTAGGAAC-3' was developed for these samples with its primer site starting within the gap (position 23–45). Twenty-five microlitres of PCR reaction mixes for 16S and COI contained 5 µL of 5x Phire II Reaction Buffer (Thermo Scientific), 1 µL of each primer (10 pM), 0.5 µL of Phire Hot Start II DNA Polymerase (Thermo Scientific), 0.5 µL of dNTPs and 1 µL of DNA template. Five microlitres of Q- solution (Qiagen) were added to the reaction mix for 28S. The amplification protocol consisted of 30 sec at 98° C followed by 40 cycles of 5 s at 98° C, 5 s at 50° C and 15 s at 72° C, and a final 5 min at 72° C. Bi-directional Sanger sequencing was performed at BaseClear, Leiden, The Netherlands.

TABLE 2. Primer combinations used for amplification of 28S, 16S and COI.

Primer name	Target	Direction	Sequence (5' to 3')	Reference
ODO_28S_f2_2	28S	F	CCCGGCCGGGTCCCCGACGGT	Dijkstra <i>et al.</i> 2014
ODO_28S_r2_p3	28S	R	TTACACACTCCTTAGCGGATTC	Dijkstra <i>et al.</i> 2014
ODO_28S_f3	28S	F	ACCATGAAAGGTGTTGGTTG	Dijkstra <i>et al.</i> 2014
ODO_28S_r3_p3	28S	R	ATCTCCCTGCGAGAGGATTC	Dijkstra <i>et al.</i> 2014
ODO_12852F	16S	F	AGAAACCGACCTGGCTTAAA	Dijkstra <i>et al.</i> 2014
ODO_13393R	16S	R	CGCCTGTTTATCAAAAACAT	Dijkstra <i>et al.</i> 2014
ODO_LCO1490d	COI	F	TTTCTACWAACCAYAAAGATATTGG	Dijkstra <i>et al.</i> 2014
ODO_HCO2198d	COI	R	TAAACTTCWGGRTGTCCAAARAATCA	Dijkstra <i>et al.</i> 2014
LepF1	COI	F	ATTCAACCAATCATAAAGATATTGG	Hebert <i>et al.</i> 2004a
LepR1	COI	R	TAAACTTCTGGATGTCCAAAAAATCA	Hebert <i>et al.</i> 2004a
LCO1490	COI	F	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> 1994
HCO2198	COI	R	TAAACTTCAGGGTGACCAAAAAAATCA	Folmer <i>et al.</i> 1994
DysF	COI	F	GCATGGGCAGGAATAGTAGGAAC	This paper

Sequences were edited with Sequencher 4.10.1 (Gene Codes Corporation) and appended in BioEdit 7.2.5 (Hall 1999). COI sequences were checked for stop-codons using the invertebrate mitochondrial genetic code in Geneious pro 6.1.8 (Kearse & al. 2012). All sequence data and additional geographic and ecological data as well as photographs of the specimens were uploaded to the Barcode of Life Data System (BOLD; Ratnasingham & Hebert 2007). Sequences were also deposited in GenBank. GenBank accession numbers are provided in Table 3.

Phylogenetic analyses. Multiple sequence alignments were performed using MAFFT version 7 (Katoh & al. 2009) under default parameters. Maximum likelihood (ML) and Bayesian inference (BI) analyses were performed on the individual datasets as well as the combined 28S + 16S and 28S + 16S + COI datasets. ML analyses were run with RAxML 8.0.24 (Stamatakis & al. 2008) using a partitioned model, the GTRGAMMA model was used for multiparametric bootstrapping according to the majority rule criterion. For the BI, the general time reversal (GTR + I + G) nucleotide substitution model (nst = 6) with a proportion of invariable sites and a gamma distribution for rates across sites (rates = invgamma) was assessed in MrModeltest 2.3 (Nylander 2004) for each of the individual fragments. For each dataset, two independent Monte Carlo Markov Chain simulations were run in MrBayes 3.2.2 (Huelsenbeck & Ronquist 2001) with three heated and one cold chain for 10,000,000 generations at a temperature of 0.05. Trees were sampled every 500 generations. The burn-in was determined from the point stationarity of an average standard deviation of split frequencies < 0.01 had been reached. The resulting trees were visualized in FigTree 1.4.2 (Rambaut 2014) and adjusted for publication in Adobe Illustrator.

Specimens studied. We studied specimens held in four major European museums: RMNH (Leiden), IRSN (Brussels), BMNH (London) and CUMZ (Cambridge) and in the private collections of Rory A. Dow, André Günther, Matti Hämäläinen, Albert G. Orr and Philip Steinhoff. For the molecular analysis a total of 34 specimens of *Dysphaea* from five species, including examples of *D. basitincta* (Hainan), *D. dimidiata* (Borneo, Sumatra,

TABLE 3. GenBank accession numbers for specimens used in the molecular analysis. The accession numbers for the outgroup (non-*Dysphaea*) taxa were previously published in Dijkstra *et al.* (2014).

Species	RMNH number	Country	Area	COI	16S	28S
<i>Dysphaea basitincta</i>	508506	China	Hainan	KP979480	KP979512	KP979561
	508575	China	Hainan	KP979481	KP979513	KP979562
<i>D. dimidiata</i>	229164	Brunei	Temburong district	KF369377	KF369707	KF370106
	500943	Malaysia	Bintulu division, Sarawak	KP979486	KP979516	KP979565
	501089	Malaysia	Pahang	KP979499	KP979523	KP979572
	501315	Malaysia	Miri division, Sarawak	KP979498		
	501316	Malaysia	Miri division, Sarawak	KP979497	KP979522	KP979571
	503913	Malaysia	Terengganu	KP979496	KP979521	KP979570
	506832	Malaysia	Johor	KP979495	KP979520	KP979569
	509664	Malaysia	Kapit division, Sarawak	KP979494	KP979519	KP979568
	509901	Malaysia	Limbang division, Sarawak	KP979493		
	509902	Malaysia	Kuching division, Sarawak	KP979492		
	509903	Malaysia	Kapit division, Sarawak	KP979491		
	509904	Malaysia	Bintulu division, Sarawak	KP979490		
	509982	Indonesia	Pasir regency, Kalimantan Timur	KP979489		
	509983	Thailand	Narathiwat	KP979488	KP979518	KP979567
	557835	Indonesia	Riau province, Sumatra	KP979485	KP979517	KP979566
	557839	Indonesia	Riau province, Sumatra	KP979484	KP979515	KP979564
	557872	Brunei	Belait district	KP979483	KP979514	KP979563
	557875	Brunei	Belait district	KP979482		
	557876	Brunei	Belait district	KP979487		
<i>D. gloriosa</i>	508577	China	Hainan	KP979500	KP979524	KP979573
<i>D. ulu</i>	503424	Malaysia	Miri division, Sarawak	KP979505		KP979575
	506336	Malaysia	Miri division, Sarawak	KP979506	KP979526	KP979576
	509905	Malaysia	Miri division, Sarawak	KP979504		
	509906	Malaysia	Miri division, Sarawak	KP979503		
	509907	Malaysia	Sri Aman division, Sarawak	KP979502		
	557687	Malaysia	Kapit division, Sarawak	KP979501	KP979525	KP979574
<i>D. vanida</i>	505749	Thailand	Ranong	KP979509	KP979529	KP979579
	505755	Thailand	Ranong	KP979508	KP979528	KP979578
	505799	Thailand	Ranong	KR095338		
	509984	Thailand	Kanchanaburi	KP979510	KP979530	KP979580
<i>Anisopleura furcata</i>	509985	Thailand	Kanchanaburi	KP979507	KP979527	KP979577
<i>Euphaea decorata</i>	505757	Thailand	Chiang Mai	KF369297	KF369617	KF370015
<i>E. superba</i>	500389	China	Guangdong	KP979511	KP979531	KP979581
<i>Cryptophaea vietnamensis</i>	229184	China	Guangxi	KF369389	KF369722	KF370121
<i>Lestes praemorsus decipiens</i>	229255	Vietnam	Northern Vietnam	KF369354	KF369682	KF370080
	503590	Malaysia	Bintulu division, Sarawak	KF369423	KF369759	KF370158

Peninsular Malaysia and southern Thailand), *D. gloriosa* (Hainan), *D. ulu* **spec. nov.** (Borneo) and *D. vanida* **spec. nov.** (Thailand), were analyzed for COI. Markers 16S and 28S were analysed for a smaller number of samples, but still including the same five species; these are listed in Table 3 and indicated in the material lists under each species (specimens with a RMNH.INS. number given). Unfortunately no material sufficiently fresh for DNA extraction by normal methods was available for *D. lugens* or Javan *D. dimidiata*. Several other members of the Euphaeidae and one *Lestes* species were included as outgroup taxa; these are also listed in Table 3.

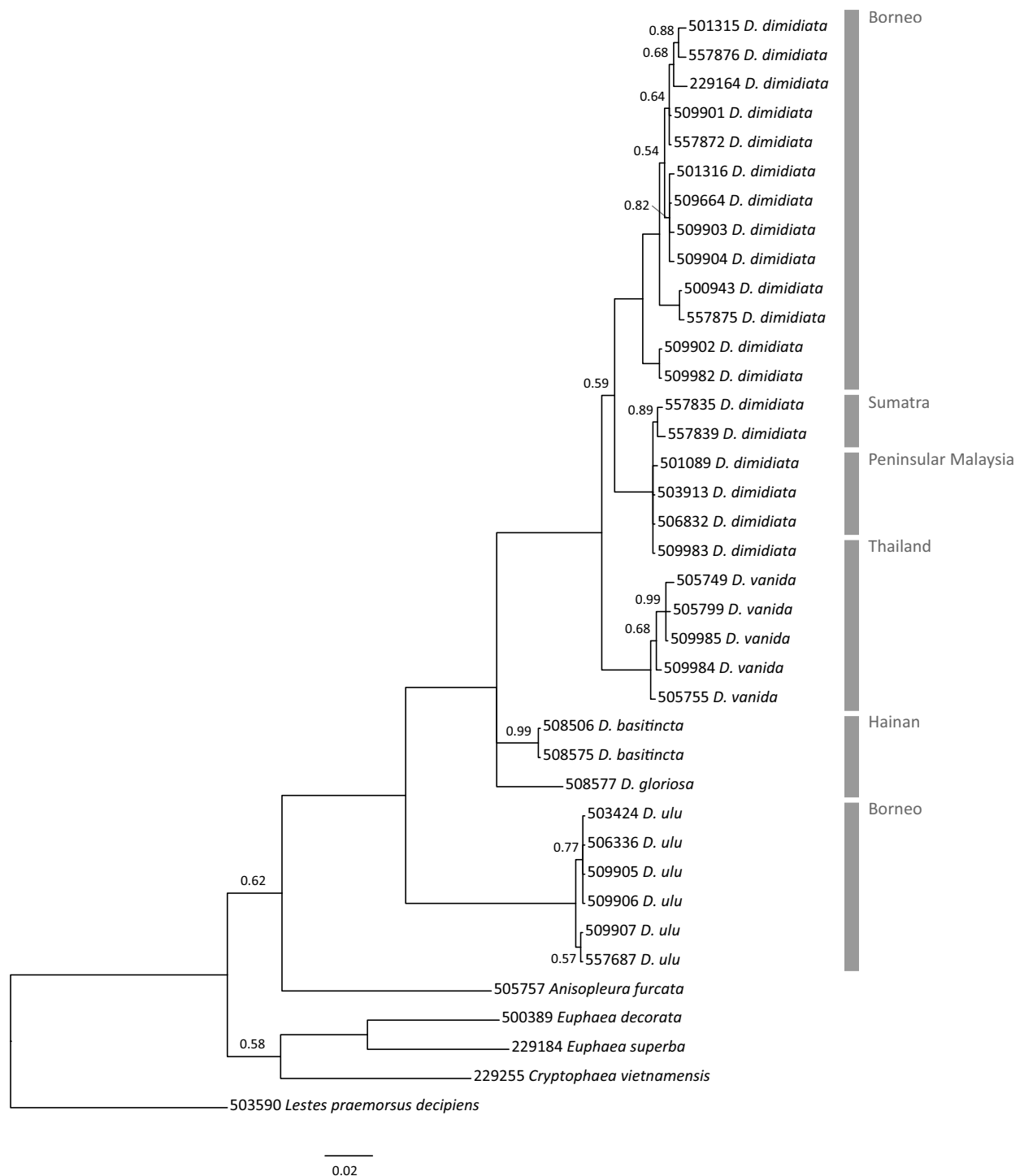


FIGURE 1. COI gene tree for 33 specimens of *Dysphaea* and five outgroup taxa, from Bayesian Inference analysis. Posterior probability values are shown (as percentages) if less than 100%. RMNH collection codes are shown for each specimen, with the RMNH.INS. prefix omitted.

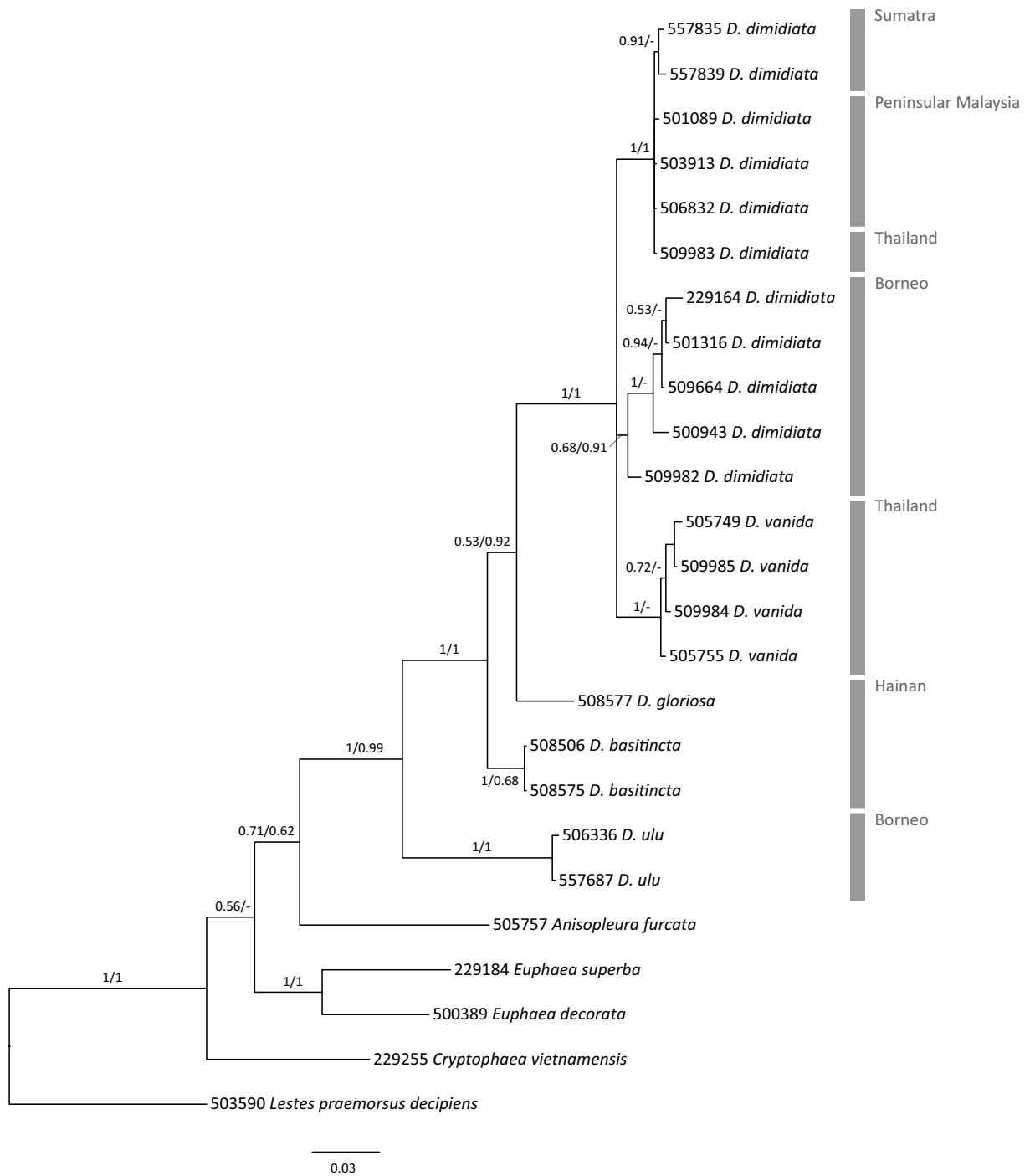


FIGURE 2. Gene tree for 20 specimens of COI and 16S for which both markers are available. Posterior probability values are shown (as percentages) if less than 100%. RMNH collection codes are shown for each specimen, with the RMNH.INS. prefix omitted.

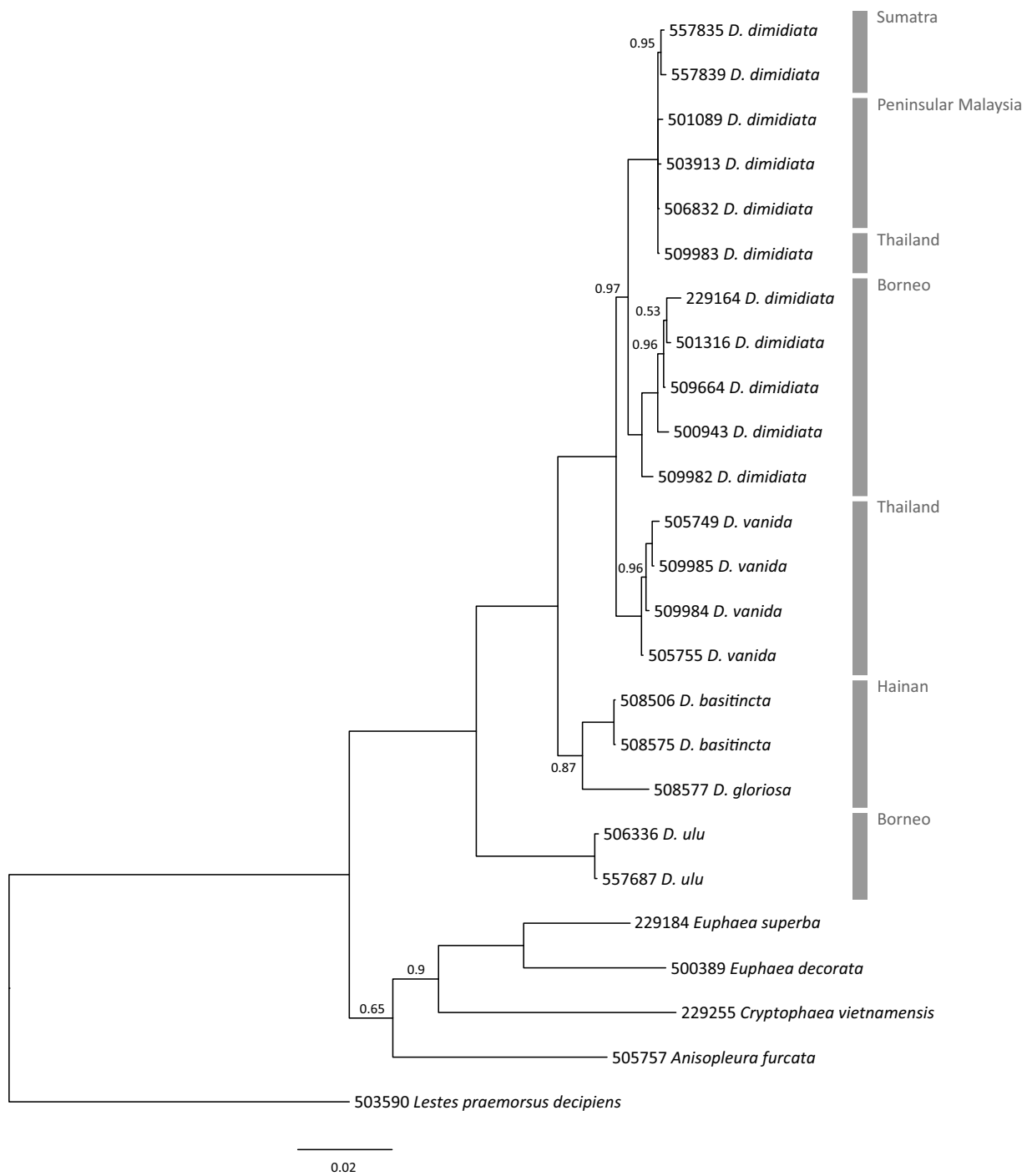


FIGURE 3. Phylogenetic reconstruction for 17 specimens of *Dysphaea* plus five outgroup taxa from the combined COI+16S+28S data from Bayesian Inference analysis. Posterior probability values are shown (as percentages) if less than 100%. RMNH collection codes are shown for each specimen, with the RMNH.INS. prefix omitted.

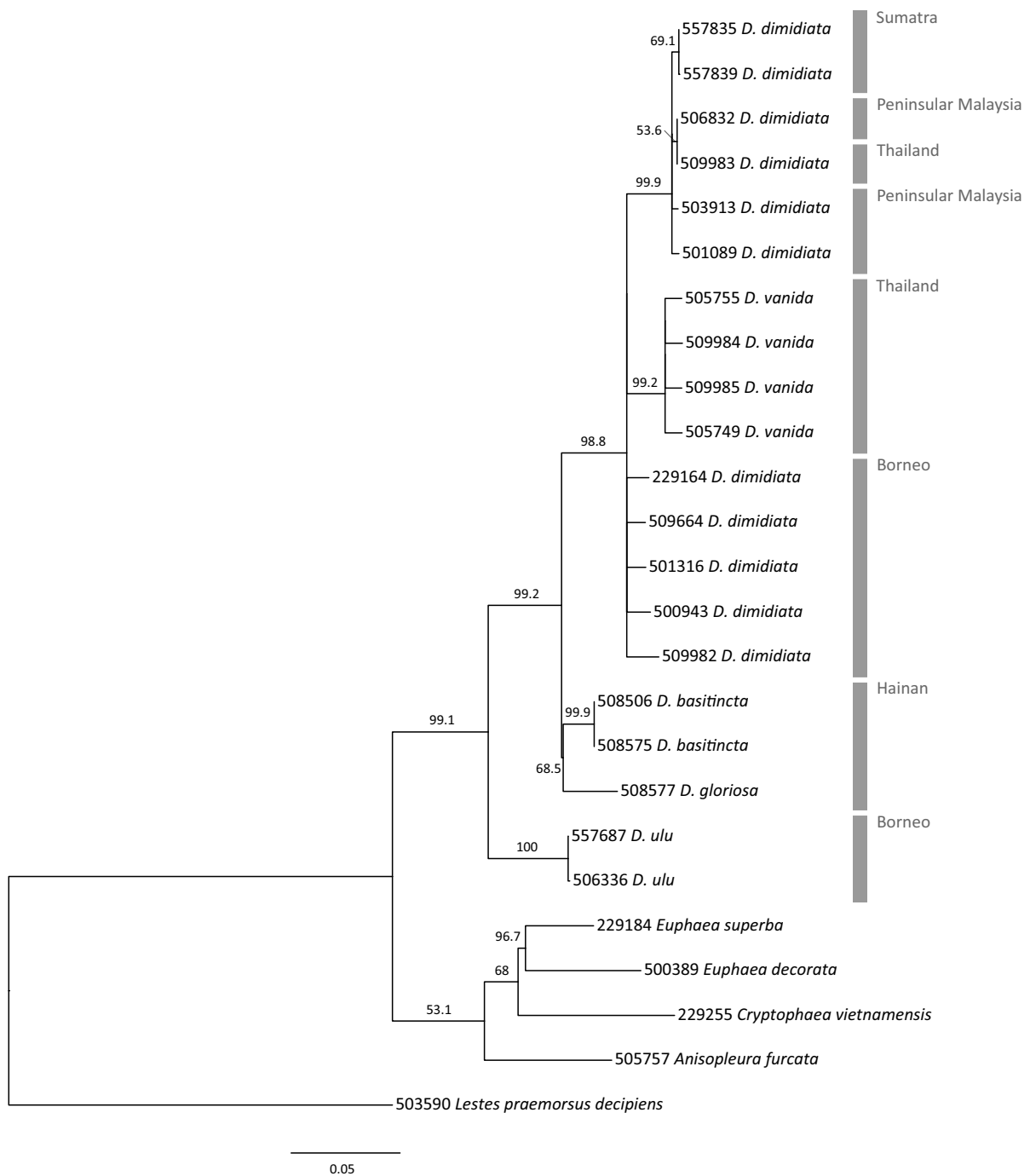


FIGURE 4. 50% majority rule consensus tree (from 1000 trees) for 17 specimens of *Dysphaea* plus five outgroup taxa from the combined COI+16S+28S data set from Maximum Likelihood analysis. Bootstrap support values are shown (as percentages) if less than 100%. RMNH collection codes are shown for each specimen, with the RMNH.INS. prefix omitted.

Sundaland species of *Dysphaea*

Molecular analysis. Fig. 1 shows the gene tree for COI resulting from Bayesian Inference (BI) analysis of 33 specimens of *Dysphaea*. Posterior probability values are shown as percentages if less than 100%. In the COI gene tree *D. dimidiata* is divided into two clades, one from Borneo and the other from Peninsular Malaysia, Sumatra and southern Thailand; however, support for this relationship is relatively low at 0.59. *Dysphaea vanida* is the sister of

D. dimidiata with complete support. The relationship of *D. basitincta* with *D. gloriosa* is not resolved, but the two are the sisters of the combined *D. dimidiata* + *D. vanida* clade with complete support. *Dysphaea ulu* is the sister of all other *Dysphaea* species included, with complete support.

Fig. 2 shows the COI gene tree from BI of a smaller data set (20 samples) for which 16S is also available, but including the same taxa and, in the case of *D. dimidiata*, including representatives from the same landmasses and countries as the analysis shown in Fig. 1. Substantially the same topology was obtained from BI analysis of the corresponding 16S data set; the support values for 16S are shown in Fig. 2, separated from those for COI by a slash (/). Here again *D. dimidiata* is divided into two clades, one consisting of specimens from Borneo, the other of the remaining specimens; *D. vanida* forms a separate clade. However the relationships of these clades to one another are not resolved. *Dysphaea gloriosa* is the sister of the combined *D. dimidiata* + *D. vanida* clade, but with substantially higher support in 16S than in COI. *Dysphaea basitincta* is the sister of *D. gloriosa* + *D. dimidiata* + *D. vanida* with complete support and, again, *D. ulu* is the sister of all analysed *Dysphaea* species with complete (COI) or very high (16S) support. The differences between the COI results in Figs. 1 and 2 indicate that the analysis is sensitive to the number of samples included.

With 28S (not illustrated), *D. basitincta*, *D. dimidiata*, *D. gloriosa* and *D. vanida* form a clade but are not distinguished from one another; this is not surprising given the highly conserved nature of 28S. However *D. ulu* is once again recovered as the sister of the other species with high support.

Fig. 3 shows the phylogenetic tree constructed using BI with the combined COI+16S+28S data set, using the 17 *Dysphaea* specimens for which all three markers are available and the same outgroup taxa. The same relationships are recovered for *D. dimidiata* (two clades, one from Borneo, the other from peninsular Malaysia, Sumatra and Thailand) and *D. vanida* (sister of *D. dimidiata*) as seen in Fig. 1, but the support is high for the relationship of the two *D. dimidiata* clades in the combined analysis. A clade consisting of *D. basitincta* + *D. gloriosa* is the sister of *D. dimidiata* + *D. vanida*, with complete support. Once again *D. ulu* is recovered as the sister of all other *Dysphaea* included, with complete support.

Fig. 4 shows the tree constructed using the same combined COI+16S+28S data set and ML analysis. In this analysis *D. vanida* and *D. dimidiata* from outside Borneo fall into distinct clades, but their relationship with *D. dimidiata* from Borneo is not resolved, although the whole set of *D. dimidiata* + *D. vanida* forms a clade. Again, a clade consisting of *D. basitincta* + *D. gloriosa* is the sister of the *D. dimidiata* + *D. vanida* clade, and *D. ulu* is recovered as the sister of all other *Dysphaea* taxa included.

Taxonomy

Dysphaea dimidiata Selys, 1853

Selected references:

Dysphaea dimidiata Selys, 1853:—Selys Longchamps (1853: 54, original description of ‘*Dysphaea dimidiata*, De Selys’, male, Java);—Selys Longchamps & Hagen (1854: 185–187, pl. 5, Fig. 4, pl. 14, Fig. 4, extended description of male, Java);—Selys Longchamps (1879: 378–379, reprint p. 32–33, description of female, Sumatra);—Albarda (1887: 6–7: pl. 2, Figs. 1–2, ♂, ♀ from C. Sumatra);—Krüger (1898: 78, Sumatra, Silago);—Laidlaw (1924: 300, Pahang);—Laidlaw (1931a: 180, Pahang);—Schmidt (1934: 330–331, S. Sumatra, Borneo);—Lieftinck (1934: 385, Java; no new records from Java);—Lieftinck (1935: 4, Sumatra);—Coomans de Ruiter (1936: 74–75, Fig. 3, W. Borneo, W. Java);—Lieftinck (1936: 109–110, Fig. 14; W. Java);—Lieftinck (1949: ix–xi, Java, notes on larva, bionomics);—Lieftinck (1950: 664–665, Java, phenology);—Lieftinck (1954: 19–20, distribution, habitat, references);—Lieftinck (1959: 101–103, notes, drawings (Figs. 4–6), behaviour of both sexes);—Furtado (1969: 866, 874, 876, habitats, Peninsular Malaysia);—Paulson (1981: 134–135, Sarawak, behaviour);—Asahina (1981: 6, South Thailand, Trang);—Asahina (1985: 31–34, Figs. 35–44, 64, S. Thailand, descriptions of both sexes);—Tsuda & Kitagawa (1988: 3, Sumatra);—Kemp & Kemp (1989: 39, Pahang);—Dunkle (1993: 75, Songkla);—Norma-Rashid (1995: 81, Perak);—Hämäläinen & al. (1996: 5, Kelantan);—Norma-Rashid & al. (1996: 134, Kelantan, Pahang);—Hämäläinen & Pinratana (1999: 29, 123, part; Thailand, records from the southernmost provinces);—Orr (2001: 178 (part, 1 male specimens from Kuala Belalong Field Studies Centre; sites 1,2); Sites 30–31, all specimens);—Norma-Rashid & al. (2001: 143, Pahang, Tasek Bera);—Orr (2003: 37, part; 58 part);—Kalkman (2004: 28, Pahang);—Cleary & al. (2004: 445);—Dow (2005: 11, Gunung Mulu N.P.);—Wilson & Gibert (2005: 27, Johor, Endau-Rompin);—Orr (2005: 26, text);—van Tol (2006: 13, East Kalimantan);—Wahizatul & al. (2006: 101, 102, 103, Terengganu);—Kitagawa & Katatani (2007: 31, Johor);—Dow & Reels (2008: 3, Gunung Mulu N.P., part);—Choong (2009: 226, Johor, Panti Forest Reserve);—Norma-Rashid (2009: 68, Negeri Sembilan);—Choong (2010: 230–

231, Fig. 2, Perak, Bintang Hijau Forest Reserve);—Dow & Reels (2010: 15, Sarawak, Kubah National Park, part);—Dow & Unggang (2010: 1353, Sarawak, Binyo Penyilam);—Tang & al. (2010: 41–42, Singapore, past records, photos of Johor specimens);—Dolný & al. (2011: 72), Kalimantan, Sg. Wain);—Choong (2011: 237, Perak, Royal Belum State Park);—Choong (2013: 207, Kelantan, Chamah Highlands);—Ng & al. (2011: 10, 11, Perak);—Choong & al. (2012: 97, Terengganu);—Ng & al. (2012: 83, Pahang);—Dow (2012: 9, Sarawak, Annah Rais);—Dow & al. (2013b: 11, record Kubah N.P.);—Bárta & Dolný (2013: 70, 138, Kalimantan, Sg. Wain).

Dysphaea dimidiata limbata Selys, 1859:—Selys Longchamps (1859: 443–444, reprint p. 9, description of male and female from Mt Ophir (Malay peninsula), Singapore and Sarawak as ‘*Dysphaea dimidiata*, De Selys; Race *Dysphaea limbata*, De Selys’);—Fraser (1942: 99, Perak, behaviour);—Lieftinck (1949: xi, *limbata* ranked as subspecies of *D. dimidiata*).

Dysphaea limbata Selys, 1859:—Selys Longchamps (1869: 660, reprint p. 16, upgraded to full species);—Selys Longchamps (1873: 487, reprint p. 23, correction of original description, discussion of variability);—Krüger (1898: 78, Sumatra, Soekaranda);—Laidlaw (1902: 88, Kelantan);—Laidlaw (1903: 194, Jalor [Yala];—Williamson (1904: 182–183, Lower Siam, Trang);—Ris (1911: 232–233, Malacca);—Laidlaw 1920: 328 (specimens from Tatau, Sarawak);—Kennedy 1920: pl. 1, Figs. 40–41, penis);—Laidlaw (1931b: 241, West Central Borneo);—Lieftinck (1935: 4, mutual status of *limbata* and *dimidiata* discussed);—Lieftinck (1954: 19–20, listed as synonym of *dimidiata*).

Dysphaea dimidiata semilimbata Selys, 1873:—Selys Longchamps (1873: 486, reprint p. 22, description of male from Labuan as ‘*Dysphaea semilimbata*, De Selys; Variété ou race de *dimidiata*?’);—Lieftinck (1954: 19–20, listed as synonym of *dimidiata*).

Dysphaea lugens [nec Selys, 1873]:—Laidlaw (1920: 327, specimens from Limbang River and Retuh);—Matsuki & Kitagawa (1993: 2, specimens from Mulu N.P. are obviously *D. dimidiata*);—Orr (2001: 178, Brunei, all specimens from sites 15, 29–31, 35);—Orr (2003: 58, part);—Dow & Reels (2008: 3, Sarawak, Gunung Mulu N.P.);—Dow (2011: 48, Sarawak Planted Forest Project).

Study of the type material. Selection of lectotype of *Dysphaea dimidiata* Selys, 1853. The type series preserved in Coll. Selys at IRSN (Brussels) consists of five pinned male specimens, all from West Java. To fix the identity of the nominal taxon *Dysphaea dimidiata* based on one specimen, we herewith designate the best preserved specimen of this series as lectotype. For the selected lectotype and its labels, see Fig. 5. The measurements of the lectotype are Hw 32 mm, abdomen (apps. excl.) 35 mm, cerci 2 mm. The ratio of the length of abdomen (apps. excl.) and Hw is 1.10. The corresponding measurements of the paralectotypes are 30–33.5 and 34–38, the ratio being 1.13–1.17.

Selection of lectotype *Dysphaea limbata* Selys, 1859. The type series of *limbata* consists of at least five pinned male specimens and one female. The males originate from Mt Ophir [Johor, Peninsular Malaysia], Singapore and Sarawak and the female specimen from Singapore, all collected by Alfred Russell Wallace (1823–1913). The specimens from Sarawak and Singapore are in Coll. Selys. There are three known male specimens from Mt Ophir, one in Coll. Selys at IRSN (Brussels), one at the Übersee-Museum Bremen (see Seehausen 2014) and one at BMNH (B.M. 1938-674; ex. coll. McLachlan); the latter bears the labels “*D. limbata*”, “Malacca”, “Paratype”. To fix the identity of the nominal taxon *Dysphaea limbata* based on one specimen, we herewith designate the male specimen from Mt Ophir, kept in Coll. Selys at IRSN (Brussels), as lectotype. The lectotype and the attached labels are presented in Fig. 6. The measurements of the lectotype are: Hw 30.5 mm, abdomen (apps. excl.) 36 mm, cerci 2 mm. The ratio of the length of abdomen (apps. excl.) and Hw is 1.18. The Hw length of the male paralectotype from Singapore is 28.5, the length of abdomen 34; the abdomen/Hw length ratio is 1.19. Corresponding figures for the Sarawak male paralectotype are 29, 34.5 and 1.19. The female paralectotype is a small broken specimen; its Fw is 29 mm.

Holotype of *Dysphaea semilimbata* Selys, 1873. Described from a single male specimen from Labuan (Fig. 8). This (pinned specimen) is preserved in Coll. Selys at IRSN (Brussels). Measurements: Hw 32, abdomen (apps. excl.) 37 mm, cerci 2 mm. Abdomen/Hw length ratio 1.16. The real type locality of *semilimbata* in Borneo is uncertain, it is possible that ‘Labuan’ [island off the west coast of Sabah] merely refers to the port from where the specimen was shipped to Europe.

Other material studied. Java.—RMNH: 39 ♂, 9 ♀, W. Java, 7 km SW of Djasinga, Tjibarembang River, alt. 150 m, leg. M.A. Lieftinck; various dates in 1935–1939, in April–June, September–February: 28 iv 1935, 30 iv 1935, 12 v 1935, 14 vi 1935, 16 x 1935, 25 x 1935, 24 xi 1935, 6 xii 1935, 8 xii 1935, 20 ix 1936, 30 ix 1936, 1 xi 1936, 15 xi 1936, 7 ii 1937, 15 i 1939, 14 xi 1939, 26 xi 1939; 1 ♂, W. Java, 10 km NW of Djasinga, Tjibeurum River, 25 x 1935, leg. M.A. Lieftinck; 1 ♂, [Java], Soerabaja [= Surabaya], D. [= Danau] Ranau, 28 x [no year, no collector].—BMNH: 3 ♂, W. Java, Djasinga, Tjibarembang River, 16 x 1935, leg. M.A. Lieftinck.

Billiton.—RMNH (all specimens in 1935–1937, leg. F.J. Kuiper unless noted otherwise): 2 ♂, Begantung, 17 iii 1936; 2 ♂, as above, 20 iv 1937; 1 ♂, as above, 27 v 1937; 1 ♂, O. Billiton, Kp. Ajer Lautjje, 21 x 1935; 2 ♂, G.

Tadjem, 20 xi 1936; 1 ♂, N.W. Billiton, Ajer Gelarak, 30 iv 1937; 1 ♂, 1 ♀, Tandjong Pandan, 7 xii 1949, leg. Cardinaal.

Sumatra.—**RMNH:** 1 ♂, [N. Sumatra], Atjeh [= Aceh], Losten, 400m, 22 v 1957, leg. A. Hoogerwerf; 1 ♂, N.E. Sumatra, Sg. Radja, 9 ix 1928, [leg. J.C.] v.d. Meer Mohr; 1 ♂, N.E. Sumatra, Deli, Dolok Ilir, Serbalawan, 20 ii 1948, leg. R. Straatman; 1 ♂, N.E. Sumatra, Serbalawan, Dolok Ilir, 90m, 15 iv 1948, leg. R. Straatman; 4 ♂, N.E. Sumatra, Tandjong Morawa, Serdang, (no date), leg. Dr B. Hagen; 2 ♂, N.E. Sumatra, Deli, Laut Tador, 5 ii & 6 v 1951, leg. R. Straatman; 2 ♂, as above, alt. 60 m, 29 iv 1948; 1 ♀, as above, alt. 90 m, 10 vii 1948; 1 ♂, as above, 24 i 1950; 1 ♂, E. Sumatra, Kampar Kanan, 22 x 1925, leg. Fulmek & Karny; 2 ♂ (RMNH.INS.557835, 557839), Riau province, Pekan Baru, Rama Rama, 18 ii 2014, leg. R.A. Dow; 4 ♂, C.W. Sumatra, Bengkulen, Ds. Bindjai, Air Musi, alt. 100 m, x 1941, leg. W.C. Verboom; 1 ♂, [C.W. Sumatra], Bengkulen, Lebong area, Air Kelemong, alt. 600m, 11 ix 1937, leg. F.W. Rappard; 1 ♀, [C.W. Sumatra], Silago, tot.12/777; 2 ♂, S. Sumatra, S.W. Lampongs, Mt Tanggamoos Giesting, Waiteboe [Wai Tebu], 29 xii 1934, leg. Lieftinck & Toxopeus; 3 ♂, S. Sumatra, Mt. Tanggamoos, Wai Tebu, 300m, 19–31 iii 1940, leg. M.A. Lieftinck; 1 ♂, S. Sumatra, Lampung distr., Borgen Est., Tg. Karang, 10 ix 1952, leg. A. Sollaart; 1 ♂, S. Sumatra, S.W. Lampongs, Terbanggi hilir (Menggala), 14 viii 1936, leg. M. Bartels.—**BMNH:** 1 ♂, W. Sumatra, Lebong Tandai, Benkoelen Residency, vii 1922, leg. C.J. Brooks; 1 ♂, as above, 1912–1919; 1 ♂, W. Sumatra, leg. C.J. Brooks; 1 ♂ Sumatra, McLachlan collection, ‘*limbata*’.—**Coll. Dow:** 2 ♂, Rama Rama, Pekan Baru, Riau province, 18 ii 2014, leg. R.A. Dow.—**Coll. Hämäläinen:** 1 ♂, Aceh, v 1990, ex. coll. Haruki Karube.

Borneo.—**IRSN:** 6 ♂, Borneo, Labuan; 3 ♂, Borneo W.[est-]K.[ust]. [= West Kalimantan]; 5 ♂, [Borneo], Sintang, Coll. Clément; N. Borneo, 1 ♂, Bukau, (Juill.).—**RMNH:** 1 ♂ (RMNH.INS.229164), Brunei Darussalam, Temburong, Belalong River at Kuala Belalong Field Studies Center, 19 xi 2004, leg. K.D.B. Dijkstra & V.J. Kalkman; 4 ♂, Brunei Darussalam, Belait River, caught from boat, 11 ix 1992, leg. D. Thompson; 1 ♂, as above, 29 ix 1992; 1 ♂, Brunei Darussalam, 15 minutes walk south of Ingei base camp, 50 m E of Ingei River, ca. 4° 09’ N, 114° 43’ E. 6 x 1992, leg. D. Thompson; 3 ♂ (RMNH.INS.557872, 557875, 557876), Brunei, Belait district, Sungai Ingei, 2 iii 2014, leg. R.A. Dow; 4 ♂, N. Borneo, E. Sabah, Lahad Datu 60 km W, Danum Valley Field Centre, Sungai Segama, 160–180 m asl., 4° 58’N, 117° 48’E, 3 v 1987, leg. J. van Tol; 1 ♂, as above, Sungai Palum Tambun, 1 v 1987; 1 ♀, as above, 17 iii 1987, leg. J. Huisman; 1 ♂ (RMNH.INS.509902), Sarawak, Kuching division, Lundu, Kampung Sebako, Sungai Sebako, 28 vii 2013, leg. R.W.J. Ngiam; 1 ♂ (RMNH.INS.509903), Sarawak, Kapit division, Lanjak Entimau Wildlife Sanctuary, Ulu Katibas, 22 viii 2013, leg. J. ak Awan & M. ak Adu; 1 ♂ (RMNH.INS.501316), Sarawak, Kapit division, stream in disturbed forest between Kapit town and the Hose Mountains, 14 v 2010, leg. G.T. Reels; 1 ♂ (RMNH.INS.509664), Sarawak, Kapit division, between Kapit town and Hose Mountains, stream on main Rimbunan Hijau logging road ca one hour from the Baleh river crossing, 18 vi 2013, leg. R.A. Dow; 1 ♂ (RMNH.INS.509904), Sarawak, Bintulu division, Bukit Sarang Proposed National Park, Sungai Sarang, 13 x 2008, leg. R.A. Dow; 1 ♂ (RMNH.INS.500943), Sarawak, Bintulu division, Sarawak Planted Forest Project, stream at Kakus acacia nursery, 12 xi 2010, leg. S. Stone; 1 ♂ (RMNH.INS.501315), Sarawak, Bintulu division, Tubau, Sarawak Planted Forest Project, stream at Kemena Camp, 11 vi 2010, leg. R.A. Dow; 1 ♂ (RMNH.INS.509901), Sarawak, Miri division, Gunung Mulu National Park, Bat Observatory stream, 5 ii 2006, leg. L. Southwell; 2 ♂, Borneo Exped. Dr Nieuwenhuis, Bloe-oe, 26 ix 1894; 10 ♂, 1 ♀, S. E. Borneo, Balikpapan, Mentawir River, 2–25 x 1950, leg. A.M.R. Wegner; 1 ♂, 1 ♀, as above, 12 xi 1950; 2 ♂, E. Borneo, Sangkoelirang, Kariorang, v 1937, leg. M.E. Walsh; 4 ♂, 1 ♀, as above, Babi Djuton, alt. 0 m, vi 1937; 1 ♂, as above, Batau Besi, v 1937; 1 ♂, E. Borneo, Tabang, Bengen River, 26 x 1956, leg. A.M.R. Wegner; 4 ♂, 1 ♀, S.E. Borneo, Moam, 12 xi 1950, leg. A.M.R. Wegner; 3 ♂, East Kalimantan, Gunung Meratus Protected Forest—ICTI, 1998–2000, leg. D.F.R. Cleary; 1 ♂, as above, 26 x 2000; 1 ♂ (RMNH.INS.509982), East Kalimantan, Pasir district, Prayan Base Camp area, Sungai Prayan, 14 xi 2005, leg. J. van Tol; 1 ♂ (RMNH.INS.509981), East Kalimantan, same area, Sungai Seranum, 20.xi.2005, leg. J. van Tol; 1 ♀, W. Borneo, Singkawang, Bengkajang Rd, 20 i 1932, leg. L. Coomans de Ruiter; 1 ♂, as above, 8 iv 1932; 1 ♂, W. Borneo, Singkawang, Penaring, 8 ii 1932, leg. L. Coomans de Ruiter; 1 ♂, W. Borneo, Singkawang, Kali Piong San, 8 xii 1931, leg. L. Coomans de Ruiter; 2 ♂, W. Borneo, Singkawang, Bengkajang, 23 ii 1934, leg. L. Coomans de Ruiter; 1 ♂, W. Borneo, Singkawang, Bakuan, 22 i 1934, leg. L. Coomans de Ruiter; 1 ♂, West Borneo, weg naar Bengkajang, 18 iii 1932, leg. L. Coomans de Ruiter; 1 ♂, 97.53.14. Kalimantan Tengah, Sangai-C92, 1998–2000, 13 vi 1997, leg. D.F.R. Cleary.—**BMNH:** 2 ♂, “SAR” [Sarawak], leg. Wallace, “Saunders 68.3”; 1 ♂, “SAR”, “57/55”; 1 ♂, Sarawak, (“D. limbata”); 2 ♂, 1 ♀, Labuan, McLachlan collection.—**CUMZ:** 1 ♂, Sabah, Maliau Basin,

tributary to Sungai Maliau near Maliau Basin Field Centre, 15 vii 2012, leg. S. Luke; 1 ♂, Brunei, SW, 23–27 vi 1995, leg. D.A.L. Davies.—**Coll. Dow:** 2 ♂ (1 ♂ in collection Hämäläinen), Sarawak, Kuching division, foot of Gunung Penrissen, Annah Rais, 19 iii 2005, leg. R.A. Dow; 1 ♂, same location, 26 i 2006, leg. G.T. Reels; 1 ♂, Sarawak, Kuching division, Kubah National Park, Matang Wildlife Centre, Sungai Rayu, 25 i 2006, leg. G.T. Reels; 1 ♂, same location, 4 i 2015, leg. R.A. Dow; 1 ♂, ♀ (in tandem), Sarawak, Kapit division, Lanjak Entimau Wildlife Sanctuary, Ulu Katibas, 22 viii 2013, leg. J. ak Awan & M. ak Adau; 1 ♂, same area as above, Sungai Katibas at mouth of Sungai Satap, 23 viii 2013, leg. J. ak Awan & M. ak Adau; 1 ♂, same area as above, Sungai Pemanca, 24 viii 2013, leg. J. ak Awan & M. ak Adau; 1 ♂, Sarawak, Bintulu division, Tatau, Anap Muput Forest Management Unit, Sungai Sawih, 17 xi 2010, leg. R.A. Dow; 1 ♂, Sarawak, Bintulu division, Samarakan area, Sarawak Planted Forests Project, small muddy stream with narrow forest buffer in acacia, 28 ii 2008, leg. R. A. Dow; 1 ♂, 1 ♀ (in tandem), same area as above, Sungai Gagak (stream with acacia to bank), 3 iii 2008, leg. R.A. Dow; 1 ♂, Sarawak, Bintulu division, Sarawak Planted Forests Project, stream with forest buffer in block T1C, 9 v 2011, leg. R.A. Dow; 1 ♂, Sarawak, Bintulu division, Binyo Penyilam Proposed National Park, Sungai Penyilam, 9 iii 2006, leg. A. Juhin; 1 ♂, Sarawak, Bintulu division, Sarawak Planted Forest Project, stream in block K2L, 23 vi 2010, leg. R.A. Dow; 1 ♂, same area as above, stream at Kakus acacia nursery, 30 vi 2010, leg. R.A. Dow; 1 ♂, ♀, same location and date as above, leg. O. Tateh; 1 ♂, Sarawak, Bintulu division, Sarawak Planted Forest Project, stream at Kapur Camp, 1 vii 2010, leg. R.A. Dow; 1 ♂, Sarawak, Bintulu division, Sarawak Planted Forest Project, Bukit Mina Wildlife Corridor, Sungai Mina, 27 iv 2011, leg. R.A. Dow; 1 ♂, same location and date, leg. O. Tateh; 1 ♂, Sarawak, Bintulu division, Tubau, Sarawak Planted Forest Project, stream at Kemena Camp, 19 i 2008, leg. R.A. Dow; 1 ♂, same location as above, 18 x 2008, leg. R.A. Dow; 1 ♂, same area as above, stream in block E2N, 16 vi 2010, leg. R.A. Dow; 2 ♂, Sarawak, Miri division, mid Baram, Sungai Suan, 11 xii 2007, leg. G.T. Reels; 1 ♂, same area, Sungai Lamah, 7 ii 2015, leg. R.A. Dow; 1 ♂, Sarawak, Miri division, Gunung Mulu National Park, Bat Observatory stream, 16 iv 2005, leg. R.A. Dow; 1 ♂, same location as above, 5 ii 2006, leg. G.T. Reels; 1 ♂, same location as above, 30 xii 2007, leg. R.A. Dow; 2 ♂, Sarawak, Limbang division, Gunung Mulu National Park, Lubang Cina, Headhunters Trail, 11 ii 2006, leg. R.A. Dow; 1 ♂, same area as above, Sungai Mentawai and tributaries, 13 ii 2006, leg. R.A. Dow; ♂, same location and date as above, leg. L. Southwell; 2 ♂, Brunei, Belait district, Sungai Ingei, 2 iii 2014, leg. R.A. Dow.—**Coll. Hämäläinen:** 3 ♂, Sabah, Danum Valley Field Centre, Sungai Palum Tambun, 150–160m, 23–28 iv 1994, leg. M. Hämäläinen; 1 ♂, Sarawak, Kuching division, foot of Gunung Penrissen, Annah Rais, 19 iii 2005, leg. R.A. Dow; 1 ♂, Sarawak, Kuching division, Kubah National Park, Matang Wildlife Centre, Sungai Rayu, 20 i 2006, leg. R.A. Dow; 1 ♂, Sarawak, Sri Aman division, Sekerang (Skrang) River, Bunu Longhouse, 1° 19.2' N, 111° 39.4 E, 11 vii 1997, leg. T. Donnelly; 1 ♂, Sarawak, Miri division, Gunung Mulu National Park, Bat Observatory stream, 16 iv 2005, leg. R.A. Dow.—**Coll. Steinhoff:** 2 ♂, Sarawak, Miri Division, Gunung Mulu National Park, stream below Kenyalong loop start and Bat Observatory, 27 iii 2014, leg. P.O.M. Steinhoff; 1 ♀, same area as above, swamp pool/stream, next to Waterfall Trail, 4 iv 2014, leg. P.O.M. Steinhoff; 1 ♂, same area as above, Sg. Melinau, up stream from [park] HQ, 20 iv 2014, leg. P.O.M. Steinhoff; 1 ♂, same area as above, Sg. Paku tributary upstream from conflux, 7 v 2014, leg. P.O.M. Steinhoff.

Palawan.—**Coll. André Günther:** 1 ♂, Philippines, South Palawan, Quezon, 14 iii 1992, A. Günther leg.

Peninsular Malaysia.—**RMNH:** 1 ♂ (RMNH.INS.503913), Terengganu, Sekayu Recreational Forest, Sungai Peres, 19 viii 2011, leg. R.A. Dow; 1 ♂, Perak, Jor Camp, alt. 1200m, leg. A. Grubauer; 2 ♂, Perak, Sg. Ternom/S. Plus, 22 vii 1961, leg. H.T. Pagden; 1 ♂, C. Perak, 10 mi N. of Ipoh, Sungai Chepor, 6 iii 1963, leg. M.A. Lieftinck; 1 ♂, C. Perak, Phu River area, Sei Chior, 7 iii 1963, leg. M.A. Lieftinck; 1 ♂, Selangor, Ampang Intake Res., 24 iv 1961, H.T. Pagden & M. ?; 2 ♂, Selangor, Ulu Gombak, alt. 200m, 16–17 iii 1963, leg. M.A. Lieftinck; 2 ♂, Selangor, Kuala Lumpur, Templer Park, 21 iii–11 iv 1963, leg. M.A. Lieftinck; 1 ♂, Pahang, Bilut Valley, 7 x 1960; 1 ♂, Pahang, 55 km N of Jerantut, surroundings of Park Headquarters of Taman Negara near village of Kuala Tahan, 13 vii 2002, leg. V.J. Kalkman; 1 ♂ (RMNH.INS.501089), Pahang, Kuala Tahan, tributary of Sungai Tembeling, 10 xii 2010, leg. R.A. Dow; 1 ♂, [Johor], Mt Ophir; 1 ♂, S. Johor, Bahru, Sei, Mapor, K. Tinggi, Mawai Rd, 17 iv 1963, leg. M.A. Lieftinck; 1 ♂ (RMNH.INS.506832), Johor, Gunung Belumut, 2 viii 2012, leg. R.A. Dow.—**BMNH:** 1 ♂, Malacca (?); 2 ♂, [Pahang], Kuala Teku, alt. 500–1500 ft., 31 vii 1905, leg. H.C. Robinson; 1 ♂, Pahang, Kuala Teku, Pahang, 7 xii 1921; 1 ♂, Pahang, Kuala Tahan, 300 ft, 22 xi 1921, leg. H.M. Pendlebury; 1 ♂, 1 ♀, Perak, Kuala Kangsar, Kenas dam, 9 i 1938.—**CUMZ:** 2 ♂, Selangor, Templer Park, 16 x 1995, (ex coll. Davies).—**Coll. Dow:** 1 ♂, Terengganu, Sekayu Recreational Forest, Sungai Peres, 19 viii 2011, leg. F-N. Yong; 1 ♂, Terengganu, Bukit Kesing Recreational Forest, 23 viii 2011, leg. R.A. Dow; 1 ♂, Perak, Kuala

Woh, 27 ix 2008, leg. R.A. Dow; 2 ♂, ♀ (in tandem with one of the males), Johor, Gunung Belumut, 4 viii 2012, leg. R.A. Dow.—**Coll. Hämäläinen:** 1 ♂, Perak, on road up to Cameron Highlands, 1986, leg. Brandstetter, ex coll. D.A.L. Davies; 6 ♂, Kelantan, Sungai Galas, 13 vi 1994, leg. Mohd. Zakaria-Ismail; 2 ♂, Kelantan, Sungai Selieh (tributary of Sg. Berok), near Kampung Selieh, 4° 42' 55"N, 101° 40' 15"E, 14 vi 1994, leg. Mohd. Zakaria-Ismail; 3 ♂, Kelantan, 31 km E of Fort Brooke, Sungai Selieh, 4°43'12"N; 101°39'22"E, alt. 365 m, 10–13 iv 1995, leg. M. Hämäläinen; 1 ♂, Kelantan, 58 km E of Fort Brooke, Sungai Lasau, 4°44'51"N; 101° 45'14"E, 10–13 iv 1995, leg. M. Hämäläinen; 2 ♂, Pahang, near Kuala Pian, Sungai Krau, 3°47'20"N; 102° 14'10"E, 22 vi 1994, leg. Mohd. Zakaria-Ismail; 1 ♂, Pahang, Sungai Krau, 3°49'20"N; 102° 13'25"E, 24 vi 1994, leg. Mohd. Zakaria-Ismail; 2 ♂, Pahang, Sungai Perlok, 3°50'45"N; 102°13' 00"E, 21 vi 1994, leg. Mohd. Zakaria-Ismail; 1 ♂, Pahang, Sungai Lompat, 3°41'40"N; 102° 12'40"E, 24 vi 1994, leg. Mohd. Zakaria-Ismail; 1 ♂, Pahang, Krau Wildlife Reserve, Kuala Lompat, Sg. Lompat, 22–27 xi 1996, leg. M. Hämäläinen & H. Olsvik; 5 ♂, 1 ♀, Pahang, Krau Wildlife Reserve, Bukit Rengit, Sg. Rengit, 18–23 iv 1995, leg. M. Hämäläinen; 3 ♂, 1 ♀, as above, 21–23 i 1996; 2 ♂, 1 ♀, as above, 15–20 xi 1996; 3 ♂, as above, 5–8 vi 1997; 1 ♂, as above, 24–27 xi 1998; 2 ♂, as above, 18–19 xii 2003; 1 ♂, as above, 7–8 ii 1997, leg. H-S. Yong; 1 ♂, Pahang, Krau Wildlife Reserve, Kuala Gandah, Sg. Gandah, 22 iv 1995, leg. M. Hämäläinen; 1 ♂, as above, 18 xi 1996; 3 ♂, Pahang, Krau Wildlife Reserve, Pos Perlok, Sg. Perlok, 28 xi 1996, leg. M. Hämäläinen & H. Olsvik; 1 ♂, Pahang, river 1 km south of main Temerloh/Kuantan road, on road to Kampung Rambai/Lake Chini, 15 ii 1988, leg. R.G. Kemp; 1 ♂, Selangor, Kerling, Bukit Tarek, Sungai Jerneh, 4 vi 1997, leg. M. Hämäläinen; 1 ♂, Johor, Panti Forest, alt. 66m, 25–26 iv 2009, leg. M. Hämäläinen.

Singapore.—**BMNH:** 1 ♂, “Singapore”, “96-163”. It is uncertain whether this specimen is part of the type series.

Thailand.—**RMNH:** 1 ♂ (RMNH.INS.509983), Narathiwat, Sungai Ko-Lok, Pru Tuh Daeng peat swamp forest, 5 vi 2003, ex. coll. Amnuay Pinratana.—**BMNH:** 1 ♂, Malacca, Mabek, Jalor [= Siam, Yala], 24.7.1901, leg. Annandale, “*D. limbata*”.—**CUMZ:** 1 ♂, Yala, 18 iii 1985. [Rest of labels illegible]. (Ex coll. D.A.L. Davies).—**Coll. Hämäläinen:** 1 ♂, Songkhla, Ton Nga Chang waterfall, 28 iii 1993, ex coll. Amnuay Pinratana; 2 ♂, as above, 25 iv 1996; 1 ♂, Songkhla, Boripat waterfall, 27 i 1995, ex coll. Amnuay Pinratana; 1 ♂, Narathiwat, Sungai Ko-Lok, Pru Tuh Daeng peat swamp forest, 5 vi 2003, ex. coll. Amnuay Pinratana.

Descriptive notes on *D. dimidiata*. Topotypical specimens from Java.

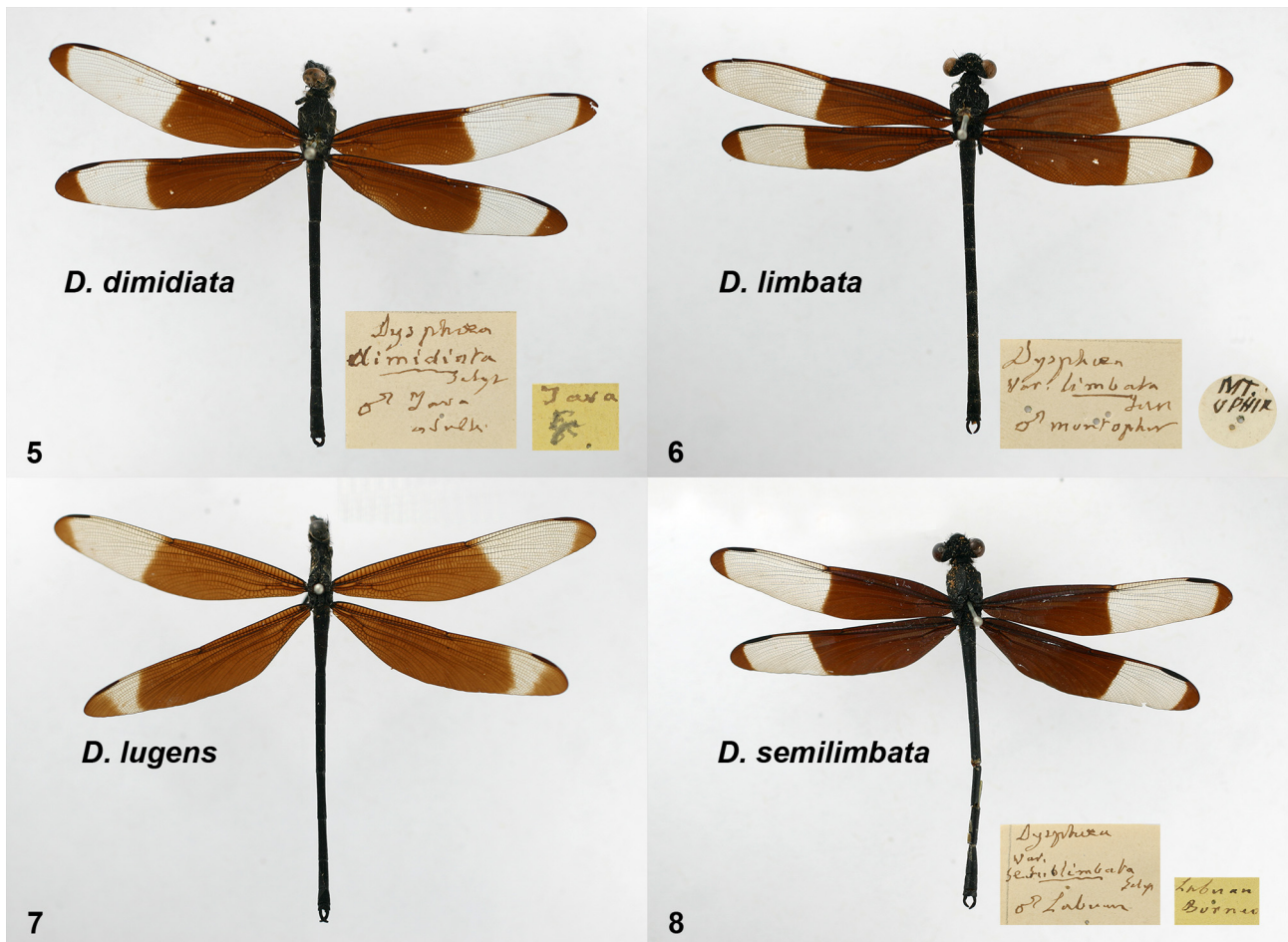
Diagnosis. Male: Black-bodied species with much of the wing surface opaque blackish; hyaline area longer in Fw. Cerci with lower border distinctly arched near base in lateral view. Terminal segment of penis with two long apical arms, appearing sub-rectangular in ventral view.

Male (for habitus see Figs. 5, 9). Head: Labrum, base of mandibles and clypeus shining black, frons and vertex matt black. Thorax: Matt black, with pale brownish stripe on mesepimeron bordering first lateral suture; much of metepisternum pale brownish; metepimeron with small apical pale brownish patch near wing base and with ventrolateral patch in the apical half of metepimeron (Fig. 13). Venter of thorax with or without sparse, tiny tubercles on metaposternum, the tubercles never as dense as in Bornean specimens (cf. Fig. 17). Legs wholly black.

Wings: Most of wing surface opaque black; extent of hyaline area between dark base and apex somewhat variable. Opaque areas of wings with a distinct bluish-violet reflections (cf. Fig. 79). In Fw of lectotype (Fig. 5) basal opaque area extends to level of nodus; in costal field one cell beyond nodus. In other specimens (Figs. 19–20) this character is somewhat variable, extending to level of 3–4 cells before or beyond nodus (rarely 5 cells before or 6–7 cells beyond); but in costal field always at least to level of nodus, although occasionally the colour is incomplete in the last 1–6 cells. In Hw of lectotype opaque area extends to level of 10 cells beyond nodus; in other specimens to level of 1/3–1/2 of distance between nodus and pterostigma. Costal field between the opaque areas is hyaline in both wings, or at most only slightly darkened at proximal and distal ends.

Abdomen: Matt black throughout in dead mature specimens, rarely with very faint and incomplete intersegmental rings on one or two segments; these more developed in living specimens. Appendages black; cerci twice as long as S10, subcylindrical, widely separated at base, hollowed out interiorly in the apical half; apices curling and meeting or overlapping (Fig. 31); in lateral view ventral margin of cercus distinctly arched near base (Fig. 37). Paraprocts very short, rounded and featureless.

Penis: Terminal segment with two long, flat, rectangular, apical arms directed straight outwards and upwards, then turned downwards towards apex (Figs. 41, 45).



FIGURES 5–8. Selysian type specimens and labels: **5)** *D. dimidiata* lectotype; **6)** *D. limbata* lectotype; **7)** *D. lugens* holotype; **8)** *D. semilimbata* holotype.

Measurements (mm): Hw 29.5–34 (in lectotype 32), abdomen (apps. excl.) 34–38 (in lectotype 35); cerci 1.5–2. Abdomen/Hw ratio 1.10–1.17.

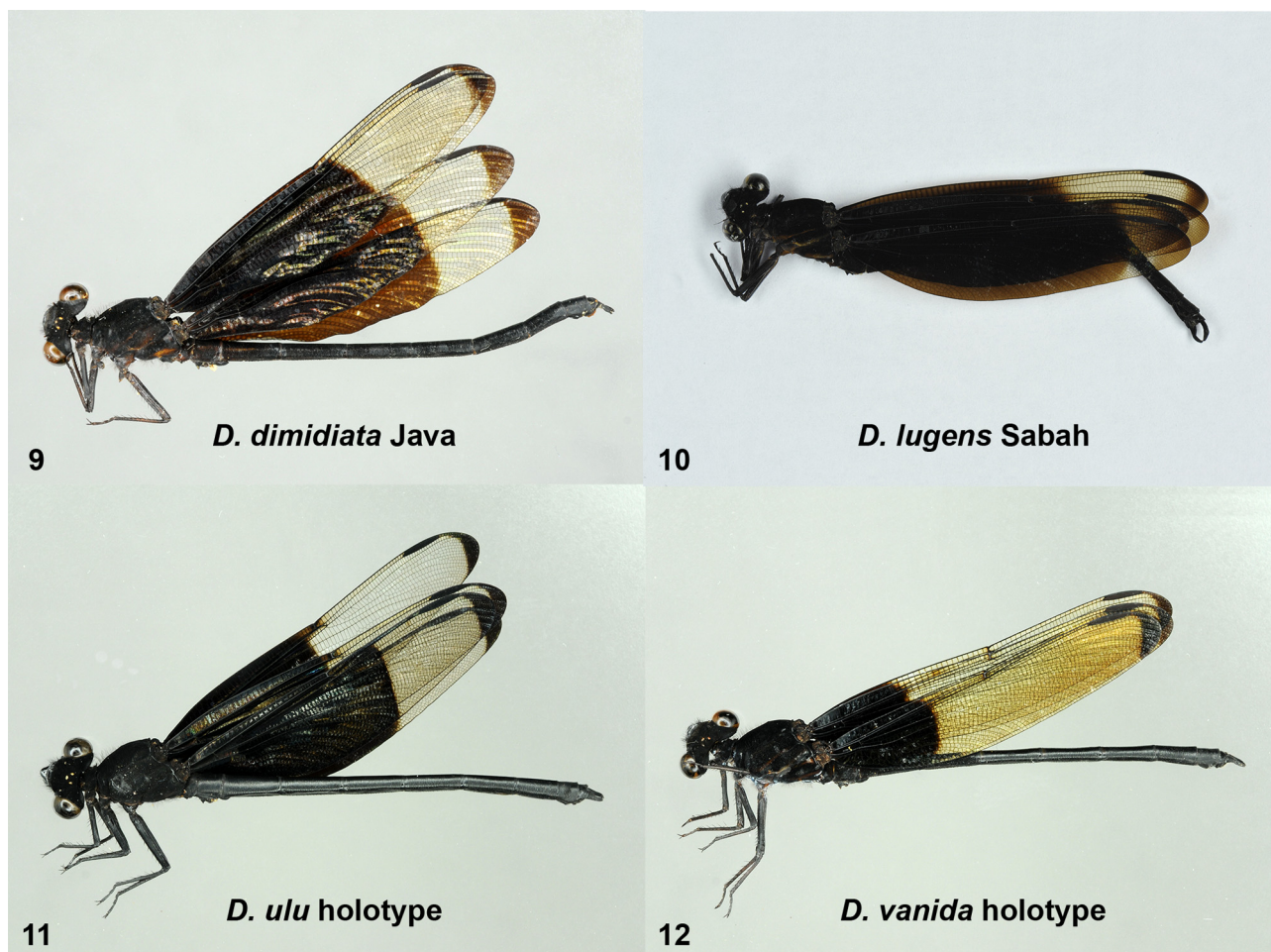
Female (for habitus see Fig. 49). Head: Labrum shining black, with broadly yellow centre, indented with black basally. Base of mandibles largely yellow with a black incomplete stripe medially. Clypeus shining black with obscure yellow stripe or marking anteriorly. Frons matt black with broad yellow stripe throughout antefrons, stripe narrower in the middle, connected to yellow genae (cf. Fig. 53). Antennae black. Vertex and occiput matt black, with two tiny yellow spots on occiput.

Thorax: Prothorax black with rounded, large yellow spots on either side of dorsum of middle lobe and with yellow spots on sides and centrally on hind lobe. Hind lobe largely black, usually with lateral ends yellow and a yellow marking medially. Posterior part of hind lobe raised obliquely upwards to form an elongate rectangular flap-like process, the lateral ends of which are often curled (Figs. 57, 63). The median part between the curled lateral parts is typically less raised, usually appearing at least slightly concave in dorsal view, occupies little more than 1/2 length of hind lobe. Synthorax matt black, with extensive yellowish markings as in Figs. 63, 69. Broad stripes on mesepisternum always forming complete loop, those on mesepimeron not joining to form loop at wing base. Metepisternum and metepimeron nearly completely yellowish, black stripe covering both sides of second lateral suture in apical half; a small black area in middle of metepimeron. Legs black, coxa broadly yellow on sides; short, basal pale stripes on flexor surface of middle and hind femora.

Wings: Hyaline, slightly brownish tint in basal half of Fw (to the level of nodus) and much more extensively on Hw, typically to level of halfway between nodus and pterostigma, occasionally almost to pterostigma. Tips of both wing tinted slightly darker brown; in Hw dark apical area larger than in Fw.

Abdomen: Matt black, with yellowish lateral markings. S1 with lateral spot covering much of segment. S2–7 with lateral stripes, rather broad on S2–3, gradually becoming narrower towards apical segments; on S3–7 pale

area projecting dorsally to form a “tooth” at base of each segment, that on S6–7 being disconnected. S8 usually with only a tiny, pale spot apically but occasionally also with a tiny basal spot, S9 with distinct lateral marking at apical half, ventrolateral edge of S8 obscurely pale at apical half to two-thirds, that of S9 typically pale at basal third, sometimes along whole segment length and occasionally fused with the lateral marking. The markings on S8 and S9 often differ between left and right sides of the same individual. Appendages black.

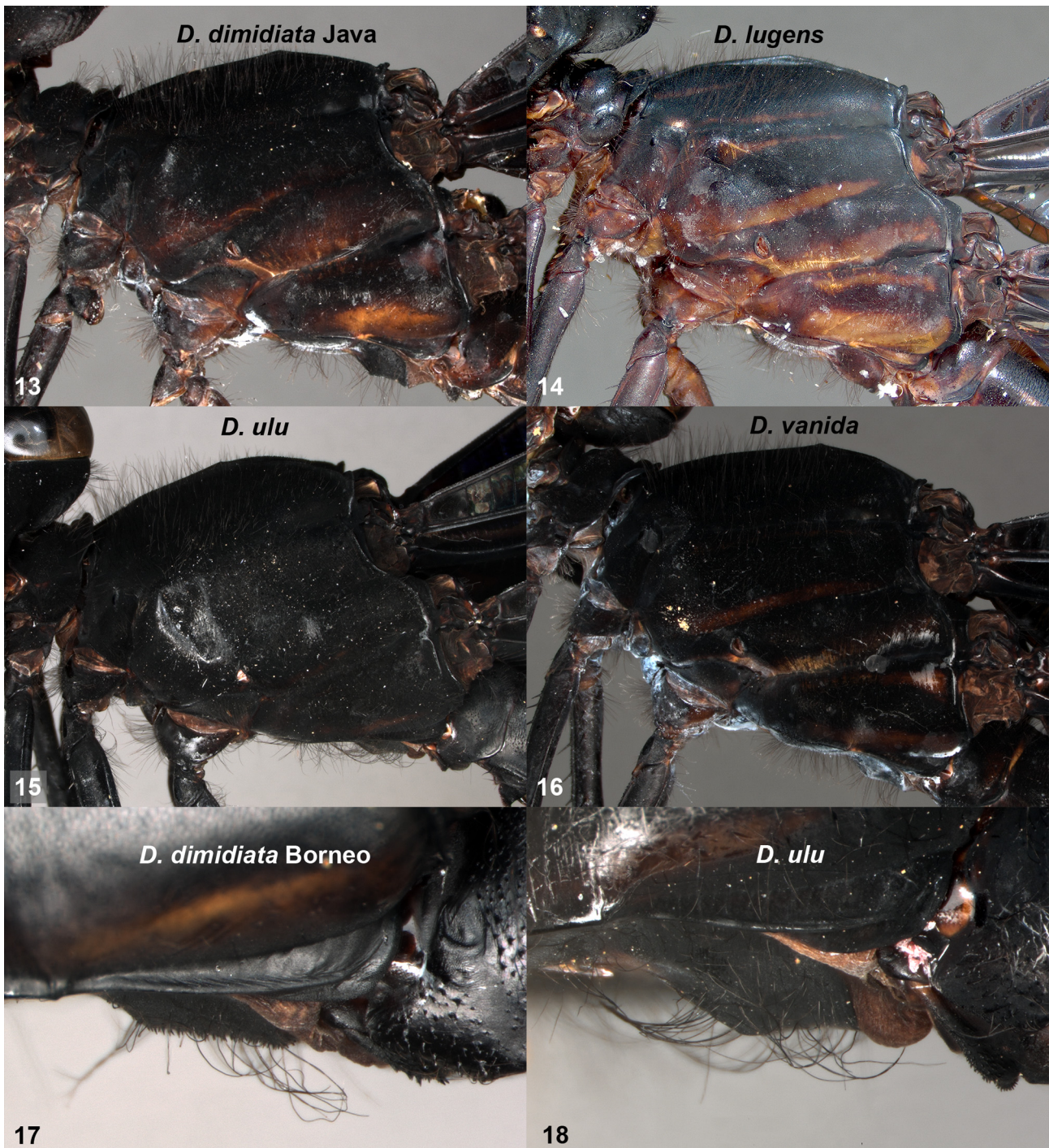


FIGURES 9–12. Habitus of male *Dysphaea*: **9)** *D. dimidiata* West Java; **10)** *D. lugens* Danum Valley, Sabah; **11)** *D. ulu* holotype (flipped horizontally); **12)** *D. vanida* holotype (flipped horizontally).

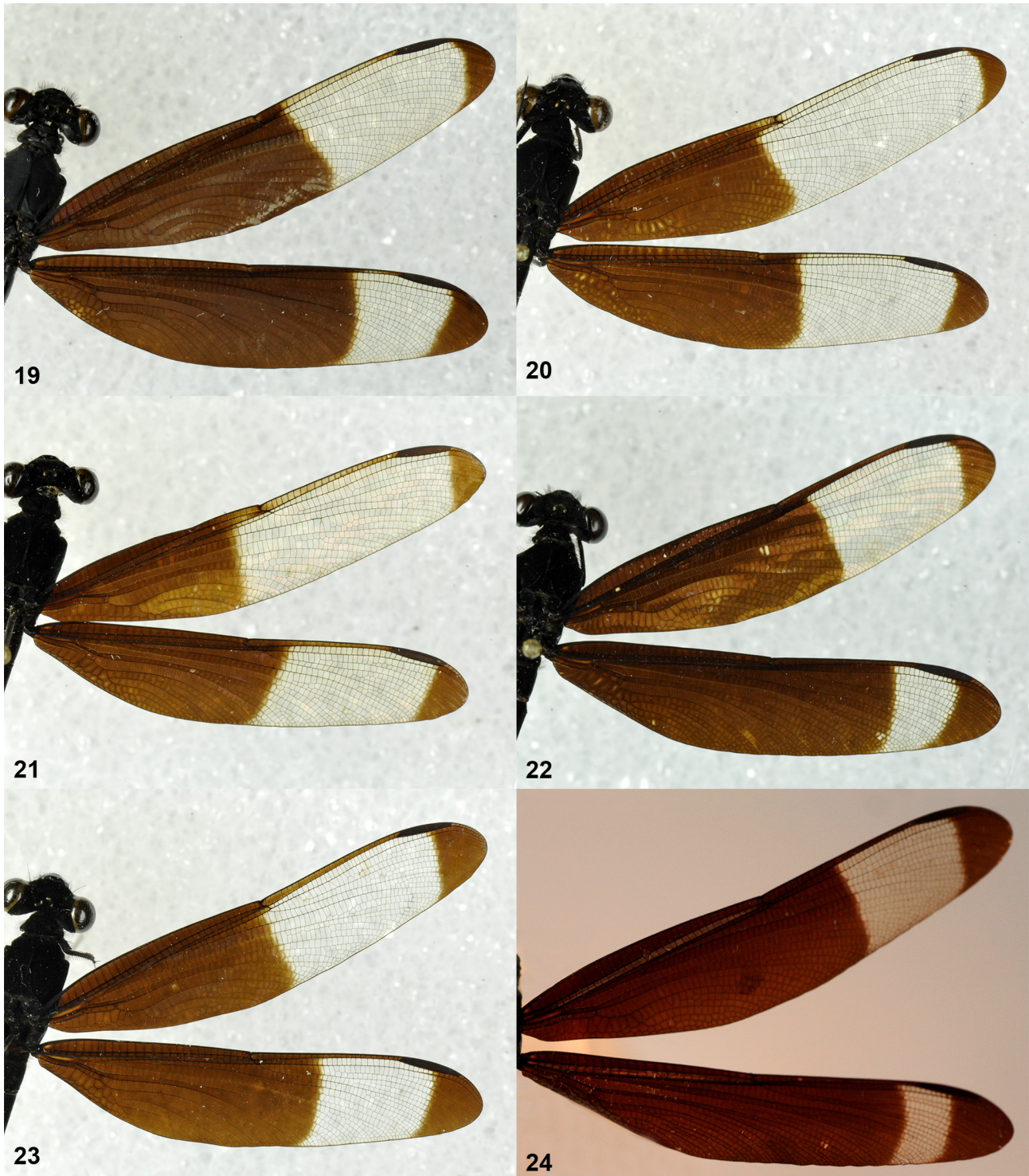
Measurements (mm): Hw 30–33.5; abdomen (apps. excl.) 30.5–33, cerci 1.

Variation in specimens from outside Java. Male. Thorax: Mature specimens from other areas of its range usually have fewer distinct pale markings on synthorax than those from Java, synthorax being either wholly black or having only obscure pale markings: stripe on metepisternum, extending from below stigma apicad above the second lateral suture, not reaching wing base; metepimeron obscurely pale ventrolaterally. Venter of synthorax either with or without tiny tubercles on metaposternum; tubercles present in all Bornean specimens studied (Fig. 17), with the exception of one male (RMNH) from Sungai Palum Tambun in the Danum Valley. Wings: In Fw basal opaque area extends at least to level of 3–4 cells before nodus, but usually extending a few cell rows or more beyond nodus (see Figs. 21–24). In Hw opaque area extends always beyond nodus, typically to level of 1/3–1/2 of distance between nodus and pterostigma. Extent of opaque colouration on wings is often subject to individual variation in same populations. Geographical variability is less clear, but in the northernmost populations in southern Thailand the opaque area is usually similar to that illustrated in Figs. 20–21. In a specimen (labelled ‘Labuan’) in Coll. Selys (IRSN), opaque area in Hw extends almost to proximal end of pterostigma and in Fw almost to halfway between nodus and pterostigma (Fig. 24). Costal field between nodus and pterostigma is usually opaque in both wings (therefore named ‘*limbata*’ by Selys), but there is rare individual variability, in some specimens the costal field in Fw hyaline. In some of these ‘*semilimbata*’ specimens the costal field in Hw is only

slightly darkened. Abdomen: usually entirely black, occasionally with very faint dorsal lateral marks at base of S4–7, slightly more distinct in living specimens (Figs. 78–79). Measurements (mm): Hw 27–33.5, abdomen (excl. cerci) 31–38, cerci 1.5–2. Abdomen/Hw ratio 1.10–1.19. **Female.** Thorax: Pale markings on synthorax are less extensive than in Javan specimens; especially on metepisternum and metepimeron the extent of black colour is distinctly greater (Figs. 64–65, 70–71). Wings: Quite similarly coloured to Javan specimens, but in many specimens whole surface of Hw is slightly brown tinted, with at most only a narrow irregular untinted area at proximal end of pterostigma; tint darker at wing tip. Abdomen: Yellow lateral stripes slightly narrower than in Javan specimens, dorsally projecting basal “tooth” on S3–7 is usually longer and more distinct. Measurements (mm): Hw 29.5–33.5, abdomen 29–33, cerci 1.



FIGURES 13–18. Synthorax male *Dysphaea*: **13)** *D. dimidiata* West Java; **14)** *D. lugens* Bakuan, Kalimantan Barat; **15)** *D. ulu* holotype; **16)** *D. vanida* holotype; **17)** metaposternum, *D. dimidiata* Brunei; **18)** metaposternum, *D. ulu* holotype.



FIGURES 19–24. Wings of *D. dimidiata* males: 19) West Java; 20) West Java; 21) Billiton; 22) Babi Djuton, Kalimantan Timur; 23) Perak; 24) Labuan.

Remarks. The lateral ends of the ‘flap’ of the hind lobe of the prothorax are often but not always curled upwards (cf. Figs. 57–59). The curvature of the ends of the flap might be the result of tandem formation with males; the female from Silago, Sumatra, is teneral in appearance and among the minority of specimens where the ends of the flap are uncurled. Fig. 59 shows a female from Billiton where the ends of the flap are not curled.

Dysphaea lugens Selys, 1873

Selected references:

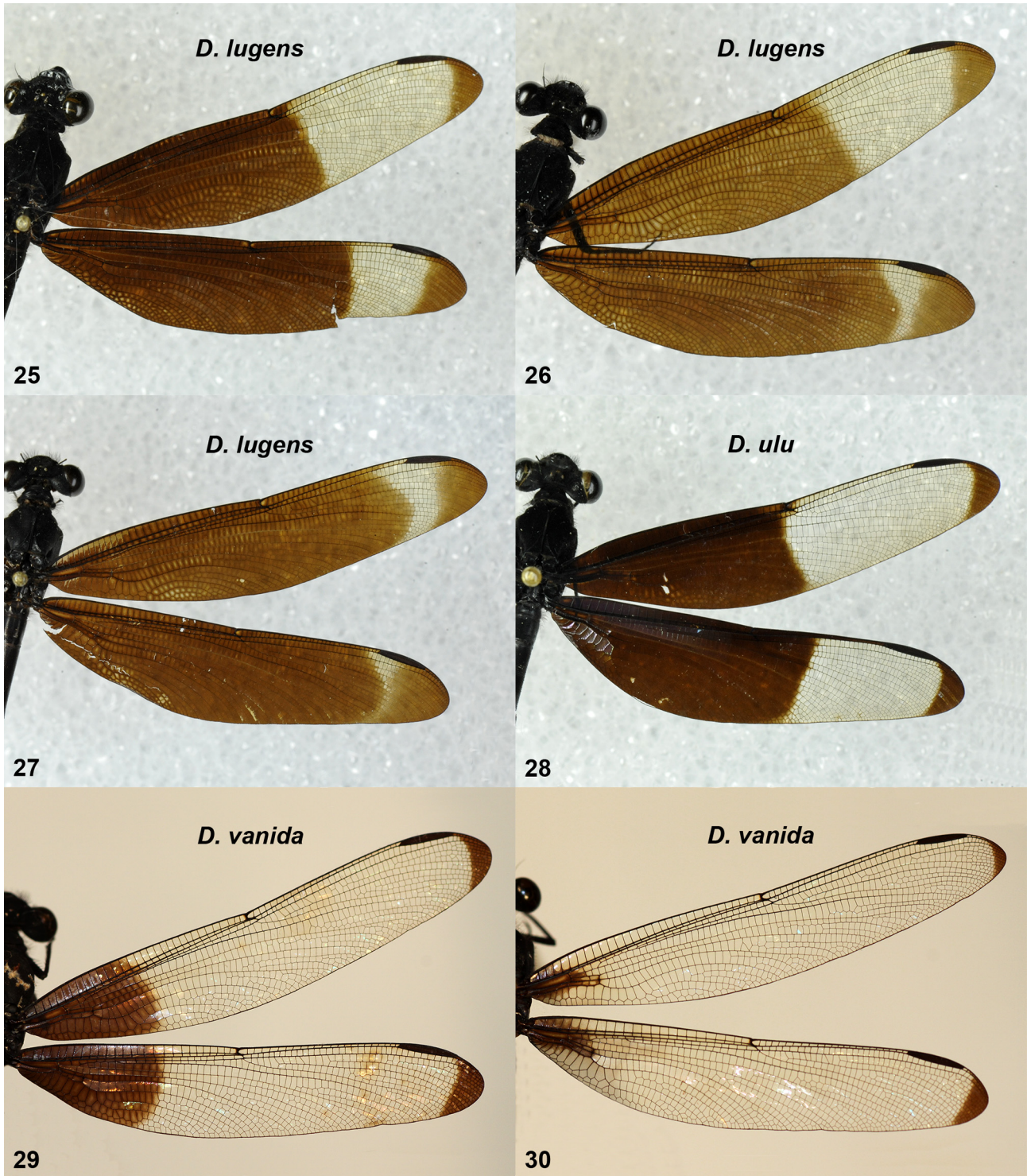
- Dysphaea lugens* Selys, 1873:—Selys Longchamps (1873: 485–486, reprint p. 21 (description of male, South Borneo, as ‘*Dysphaea lugens*, De Selys; Race de *dimidiata*?’);—Ris (1911: 232–233; Sintang, Borneo; description of ♀);—Kennedy (1920: pl. 1, Figs. 32–33, penis);—Laidlaw (1924: 300, characters discussed);—Laidlaw (1931: 241, West Central Borneo);—Coomans de Ruiter (1936: 74–76, Fig. 3, W. Borneo, notes);—Lieftinck (1953: 382, S. Borneo);—Lieftinck (1954: 20, distribution, habitat, references);—Asahina (1985: 31, 33, 34, 36, Figs. 48–50 penis, Fig. 68 (male wings, Sarawak);—Orr (2003: 58, part).
- Dysphaea dimidiata* [nec Selys, 1853]:—Orr (2002: 291, Central Kalimantan).
- Dysphaea limbata* ‘race *semilimbata*’ [nec Selys, 1873]:—Kimmins (1936: 78, specimens from River Kapah and junction of rivers Tinjar and Lejok; Mt Dulit area).

Study of the type material. Holotype. *D. lugens* was described from a single male specimen, which was sent to Selys by Robert McLachlan. Coll. Selys at IRSN (Brussels) includes nine pinned male specimens of *D. lugens* from Borneo (see below). Only one of them (Fig. 7) has the same measurements given in the original description, i.e. abdomen (incl. cerci) 40 mm, Hw 31. It is also the only specimen with the cerci in a crossed position, which matches the single illustration of *D. lugens* in the portfolio of coloured paintings of Odonata species in Coll. Selys, executed in the late 1800’s. In September 2014 only a single small yellow handwritten label ‘Lansbg.’ was attached to this specimen. ‘Lansbg.’ refers to Johan Wilhelm van Lansberge (1830–1903), who resided in the Netherlands East Indies from 1875 to 1881. He could not have been the collector of the holotype of species described in 1873. No doubt a mix-up in the labels had taken place at some phase after Selys’ time. This is evident also by the fact that the only identification label in Selys’ handwriting was attached to a specimen which does not match the measurements of the holotype. This label reads: “*Dysphaea* var. *lugens* Selys / ♂ / Sintang”. Later someone (not Selys) has crossed out the locality name ‘Sintang’ and replaced it with ‘W.K.’, which means West-Kust (an area presently known as West Kalimantan). We have removed the wrong collector label and restored the Selysian identification label to the holotype, which obviously was collected in Sintang in West Kalimantan, although in the original description reads only ‘Le sud de Bornéo’.

Other material studied. IRSN: 2 ♂, Borneo W.[est]-K[ust], Sintang, Coll. Clément; 2 ♂, Borneo W.K., Coll. Clément; 1 ♂, Borneo, N. Bartan, Coll. Clément; 2 ♂, [Borneo], leg. J. W. van Lansberge; 1 ♂, N. Borneo, D. limbata S. [nec Selys 1859].—**RMNH:** 2 ♂, S. Borneo, Sampit (0–50 m), Pemantang, 28 vii 1953, leg. M.A. Lieftinck; 3 ♂, S.E. Borneo, Ampah (0–20 m), iv–v 1948, leg. L.S. Liong; 1 ♀, E. Borneo, Gunung Sari, alt. 95 m, 2 viii 1956, leg. A.M.R. Wegner; 7 ♂, E. Borneo, Tabang, Bengen River, 20 viii–26 x 1956, leg. A.M.R. Wegner; 1 ♂, E. Borneo, Kutai, Damay Kendeng Pau, 17 ix 1938, leg. B.M. Hoeks; 1 ♂, W. Borneo, M., Singkawang, Bakuan, Selakau River, 16 ix 1932, leg. L. Coomans de Ruiter; 3 ♂, as above, but date 9 iv 1934; 1 ♂, 1 ♀, Borneo Exped. Dr Nieuwenhuis, Bloe-oe, Nov. 1898; 2 ♂, N. Borneo, Sei Bekan, 16 viii 1961, Exp. P. Jauffret & R. Pujol, (ex coll. A. Heymer); 1 ♂, Centre Borneo, Kapuas River, Sepauk, 20 viii 1961, Exp. Jauffret; 1 ♂, Centre Borneo, Kapuas River, Environs de Silat, 24 viii 1961, Exp. Jauffret; 2 ♂, N. Borneo, E. Sabah, Lahad Datu 60 km W, Danum Valley Field Centre, Sungai Segama, 160 m asl., 3 v 1987, leg. J. van Tol.—**BMNH:** 4 ♂, [Sarawak, foot of Mt Dulit], R. Tapah, tributary of Tinjar, 21–22 ix 1932, leg. B.M. Hobby and A.W. Moore, [published by Kimmins (1936) as ‘*D. limbata semilimbata*’]; 1 ♀, [Sarawak, foot of Mt Dulit], Junction of rivers Tinjar and Lejok, 2 x 1932, leg. B.M. Hobby and A.W. Moore; 2 ♂, N. Borneo [?Sabah], Coll. McLachlan.—**CUMZ:** 1 ♂, 1 ♀, C. Borneo, Kalimantan, vii–viii 1992, leg. C. Jiggins, [ex coll. D.A.L. Davies].—**Coll. Hämäläinen:** 1 ♂, E. Borneo, Tabang, Bengen River, 10 x 1956, leg. A.M.R. Wegner [ex coll. RMNH].

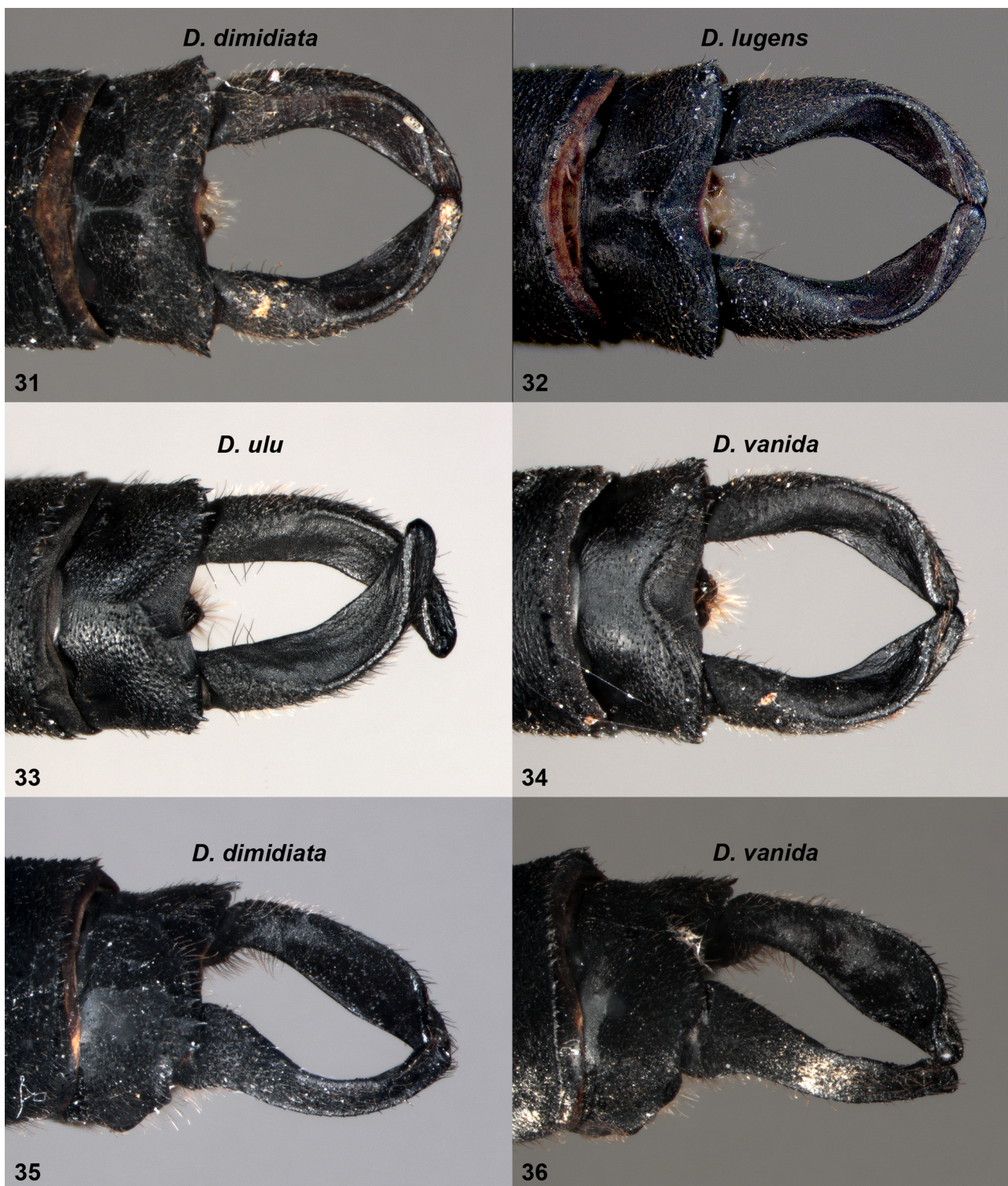
Descriptive notes on *D. lugens*. Diagnosis. Male: A species with a proportionally longer abdomen than other Sundaland *Dysphaea* species. Opaque area on wings wider than in most *D. dimidiata* specimens, colour of wings paler than in *D. dimidiata*, brownish opaque rather than blackish opaque. Apical arms of terminal segment of penis shorter than in the other species occurring in Borneo, each with a small squarish, apical expansion

Male (for habitus see Figs. 7, 10). Head: Labrum, base of mandibles and clypeus shining black, frons and vertex matt black, many individuals with two small faint brownish spots anterior to median ocellus; two specimens have an additional pair of small spots, placed outside the lateral ocelli. Thorax: Matt black, with obscure brownish stripes on synthorax as in Fig. 14; in many (more mature?) specimens there are stripes only on metepisternum and metepimeron. Narrow and usually very faint bronzy antehumeral stripes extending from ca 1/3 to 1/2 length are present on many specimens. Venter of thorax without tiny tubercles on metaposternum. Legs black, partly dark brownish.



FIGURES 25–30. Wings of *Dysphaea* males: **25)** *D. lugens* Pemantang, Kalimantan Tengah; **26)** *D. lugens* Ampah, Kalimantan Tengah; **27)** *D. lugens* Selekau River, Kalimantan Barat; **28)** *D. ulu* paratype, Temburong, Brunei; **29)** *D. vanida* spec. nov. paratype, Khlong Nakha, Ranong; **30)** *D. vanida* paratype, Khlong Nakha, Ranong.

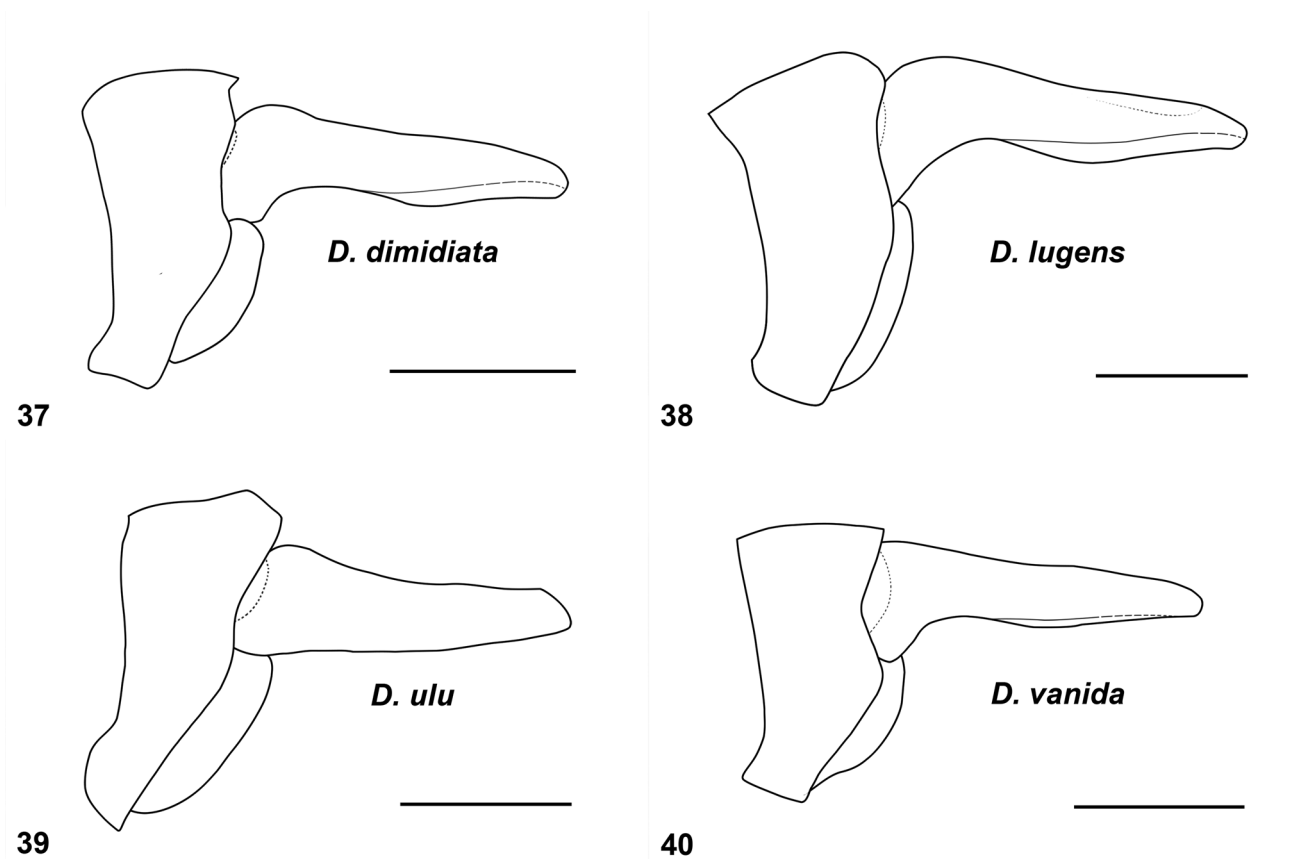
Wings: In Fw basal brownish opaque area usually extends 5–7 cells beyond nodus but sometimes as few as 2 or as many 11 cells beyond, in Hw much further apicad, usually to level of 3–7 cells proximal to pterostigma (Fig. 7, 25) but sometimes reaches the pterostigma. The opaque patch at wing tips extends anteriorly to level of distal end of pterostigma, or a little more apicad. In some specimens there remains only a narrow hyaline area between the opaque areas (Fig. 26–27).



FIGURES 31–36. Male anal appendages. Dorsal view: **31)** *D. dimidiata* West Java; **32)** *D. lugens* Bakuan, Kalimantan Barat; **33)** *D. ulu* holotype; **34)** *D. vanida* holotype. Dorso-lateral views: **35)** *D. dimidiata* Terengganu; **36)** *D. vanida* paratype Lam Khlong Gnu, Kanchanaburi.

Abdomen: Matt black; S1 with obscure brownish patch; S2–5 with narrow, brown lateral stripes, stripe on S2 placed midlaterally, those on S3–5 ventrolaterally. Appendages (Fig. 32) black, similar to *D. dimidiata*; in lateral view ventral margin of cercus distinctly arched at base (Fig. 38). Penis: Terminal segment with two short apical arms, directed outwards, upwards, then downwards; transversely expanded at apex (Fig. 42, 46).

Measurements (mm): Hindwing 30–35 (usually 32–34), abdomen (apps. excl.) 37–43 (usually 39–42), cerci 2 mm. Abdomen/Hw ratio 1.20–1.25.



FIGURES 37–40. Male anal appendages, lateral view (scale bars 1 mm): **37)** *D. dimidiata* west Java; **38)** *D. lugens* Bakuan, Kalimantan Barat; **39)** *D. ulu* holotype; **40)** *D. vanida* holotype.

Female (for habitus see Fig. 50). Head: Labium shining black with lateral lobes largely yellow, with black hooks. Labrum shining black, with broadly yellow centre, indented by black basally. Base of mandibles largely yellow, with incomplete black stripe medially. Anteclypeus shining black with narrow yellow stripe on postclypeus along ridge. Frons matt black, yellow below antennae except for a transverse central stripe, yellow colour continuing over much of genae, and narrowly along eye margin almost to narrowest point of vertex. Antennae black and dark brown, yellow anterior mark on scape. Vertex and occiput matt black, with a transverse yellow stripe on either side of the median ocellus, and a yellow spot adjacent to each lateral ocellus (Fig. 54), in the females from Bloe-oe and Mount Dulit these marks joined on one (Dulit) or both sides; two tiny yellow spots on occiput.

Thorax: Prothorax black with rounded large yellow spots on either side of dorsum of middle lobe, small yellow mark just anterior to central pit, pair of smaller dorsal spots on anterior lobe. Posterior part of hind lobe raised upwards to form an elongate rectangular flap; lateral parts almost perpendicular to base and central part at an oblique angle, appearing as a square tongue in dorsal view (Fig. 60); flap narrowly bordered by yellow, more broadly so at sides, with a separate paler area centrally in the female from Bloe-oe (not illustrated). Ends of flap prominent laterally. Synthorax matt black, with yellow stripes as in Figs. 66, 72. Yellow stripes on mesepisternum and mesepimeron forming loops. Metepisternum and metepimeron mostly yellow. Legs black, yellow markings on both apical and posterior sides of coxae, small yellow mark upper anterior femur, large yellow mark upper ca 1/3 middle femur and ca 2/3 posterior femur.

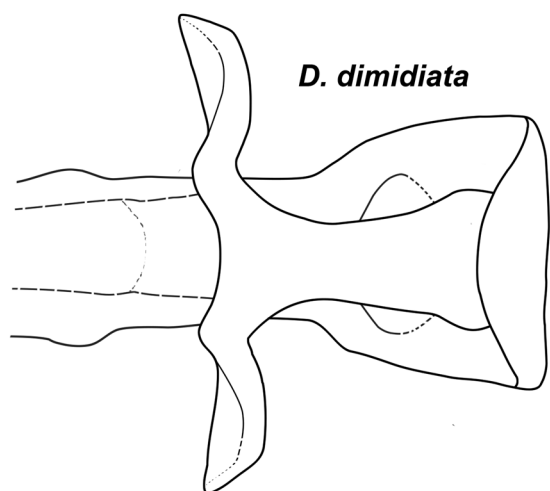
Wings: Hyaline with slight brownish tint around costal and subcostal space from base to nodus in both wings and faintly darkened area at extreme wing tips (Fig. 50). Fw with 32–36 antenodals in first row; Hw with 28–31. Quadrangle with 3–5 crossveins. Pterostigma long, covering 10–12 underlying cells in Fw, 9–10 in Hw.

Abdomen: Matt black, with pale markings as follows: S1 mostly yellow laterally, extending upwards and downwards at apex of segment. S2–7 with yellow lateral stripe, becoming orange on S6–7, broadest on S2–3 and gradually narrowing towards apical segments, narrowly interrupted at near base from S4 or S6. Separate small

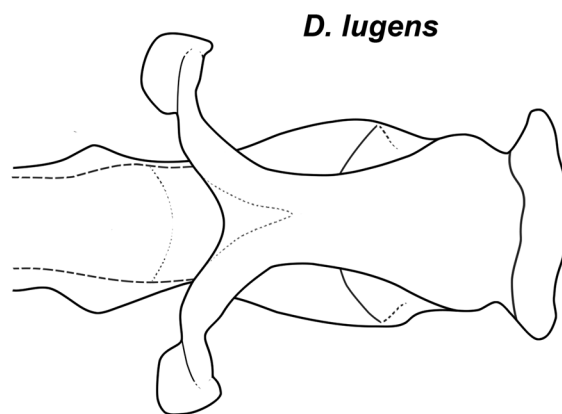
lateral spots at apex of S6–7. Faint, interrupted, narrow orange lateral stripe on S8, absent on one female, only apical part present on another, irregular orange lateral mark on S9. Appendages black.

Measurements (mm): Hw 30.5–34, abdomen (apps. excl.) 33.5–35, cerci ca 1.

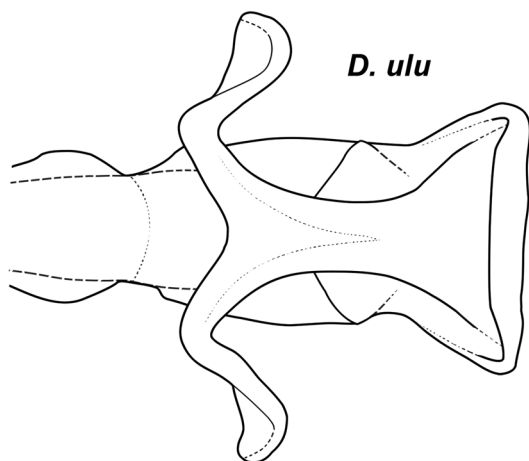
Remarks. Unfortunately no fresh specimens of *D. lugens* were available for the molecular study. However, due to the considerable structural differences, the specific status of *D. lugens* is not in doubt. The association of female specimens with *D. lugens* is a supposition based on occurrence at the same sites and differences from *D. dimidiata* females. The fact that some males bear faint markings on the vertex in equivalent positions to the females (never seen in the other species occurring in Borneo) lends support to the association of the sexes. The description by Ris (1911: 232) of female *D. lugens* mentions “between antenna and ocelli weakly reddish-brown spots”. It seems likely that the markings on the vertex of males are age dependent, fading with maturity.



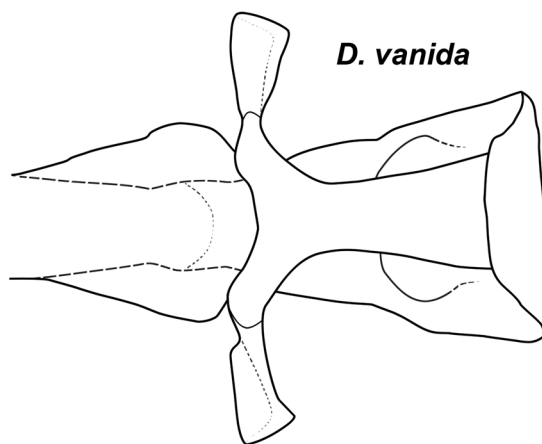
41



42



43



44

FIGURES 41–44. Penis, ventral view: **41)** *D. dimidiata* west Java; **42)** *D. lugens* Selekau River, Kalimantan Barat; **43)** *D. ulu* holotype; **44)** *D. vanida* paratype, Khlong Nakha, Ranong.

***Dysphaea ulu* spec. nov.**

(Figs. 11, 15, 28, 33, 39, 43, 47, 51, 55, 61, 67, 73, 80, 85)

Dysphaea dimidiata [nec Selys, 1853];—Schmidt (1934: 330–331, part: Baram, plate 16, fig. 8);—Lieftinck (1954: 19–20,

part: Borneo);—Orr (2001: 178, specimens from Kuala Belalong Field Studies Centre, Sites 1,2; except one male which was *D. dimidiata* Selys, 1853);—Orr (2003: 37, part; 58 part; p. 59, fig. 72; plate 3h);—Orr (2005: 26, illustration);—Dow (2005: 11, Gunung Mulu National Park, part);—Dow & Reels (2008: 3, Gunung Mulu National Park, part);—Dow & Reels (2009: 13, Mount Dulit);—Dow & Reels (2010: 15, Kubah National Park, part);—Dow, Reels & Butler (2013a: 9, Dulit range);—Dow, Reels & Butler (2013b: 11, Kubah National Park, part).

Dysphaea limbata semilimbata [nec Selys, 1873];—Laidlaw 1920: 328 (specimen from Baram).

Dysphaea species;—Dow, Reels & Ngiam (2015: 11, Usun Apau).

Material studied: **Holotype** ♂ (SAR13_14_EUP15): Borneo, Sarawak, Miri division, Upper Baram, Sungai Pejelai, Ulu Moh, 24 viii 2014, leg. M. Tegong. Deposited at RMNH, Leiden. **Paratypes** (47 ♂, 2 ♀; all from Borneo; deposited in Coll. Dow unless otherwise stated).—From **Sarawak**: 1 ♀ (SAR13_14_EUP15, in tandem with holotype), Sarawak, Miri division, Upper Baram, Sungai Pejelai, Ulu Moh, 24 viii 2014, leg. M. Tegong; 3 ♂ (SAR13_14_EUP24–26), same location and date as above, leg. N. Sigau; 1 ♂ (SAR13_14_EUP23), same location as above, 26 viii 2014, leg. M. Tegong, E. Aran & N. Sigau; 1 ♂ (SAR13_14_EUP29), same location as above, 27 viii 2014, leg. E. Aran & O. Uda; 1 ♂ (SAR13_14_EUP19), Sarawak, Miri division, Upper Baram, tributary of Sungai Pejelai, Ulu Moh, 23 viii 2014, leg. Y. Tegong; 1 ♂ (SAR13_14_EUP35), same area as above, Sungai Moh, 24 viii 2014, leg. R.A. Dow; 1 ♂ (SAR13_14_EUP27), same area as above, Sungai Sii, 10 vii 2014, leg. R.A. Dow; 1 ♂ (SAR13_14_EUP34), same location as above, 12 vii 2014, leg. R.W.J. Ngiam; 1 ♂ (SAR13_14_EUP36), same location as above, 13 vii 2014, leg. N. Pawi; 1 ♂ (SAR13_14_EUP31), same location as above, 15 vii 2014, leg. O. Uda; 1 ♂ (SAR13_14_EUP17), same location as above, 17 vii 2014, leg. O. Uda; 1 ♂ (SAR09_10_EUP142, in RMNH: RMNH.INS.503424), Sarawak, Miri division, Upper Baram, Sungai Pawan, 19 vii 2010, leg. L. Southwell; 2 ♂ (SAR06_EUP18–19), Sarawak, Miri division, foot of Mount Dulit, Sungai Nuam, 30 iii 2006, leg. R.A. Dow; 1 ♂ (SAR06_EUP17, in RMNH: RMNH.INS.509905), same area as above, Sungai Long Aton, 31 iii 2006, leg. G.T. Reels; 1 ♂ (SAR09_10_EUP100; Coll. Hämäläinen), Sarawak, Miri division, Upper Tinjar River, Sungai Lobang, 4–5 v 2010, leg. L. Southwell; 1 ♂ (SAR11_12_EUP159), Sarawak, Miri division, Usun Apau National Park, Sungai Julan, 1 v 2012, leg. C. Wilfred; 1 ♂ (SAR07_8_EUP48, in RMNH: RMNH.INS.509906), Miri division, Gunung Mulu National Park, foot of Gunung Mulu, stream on old trail to Sarawak Chamber, 10 ix 2008, leg. R.A. Dow; 1 ♂ (SAR05-EUP57; Coll. Hämäläinen), Sarawak, Miri division, Gunung Mulu National Park, Long Lansat, 19 iv 2005, leg. R.A. Dow; 1 ♂ (SAR05-EUP31), Sarawak, Miri division, Kelabit Highlands, Bario area, Pa'Dapur river, 5 iv 2005, leg. G.T. Reels; 1 ♂ (SAR06_EUP33), Sarawak, Kuching division, Matang Range, Kubah National Park, Sungai Rayu at Matang Wildlife Centre, 25 i 2006, leg. G.T. Reels; 2 ♂ (SAR07_8_EUP37; SAR07_8_EUP49 in RMNH: RMNH.INS.509907), Sarawak, Sri Aman division, Batang Ai National Park, Sungai Bebiong Besar, 4 xii 2007, leg. R.A. Dow; 1 ♂ (SAR07_8_EUP12), same location and date as above, leg. G.T. Reels; 3 ♂ (SAR13_14_EUP7–8, SAR13_14_EUP2 in RMNH: RMNH.INS.557687), Sarawak, Kapit division, Lanjak Entimau Wildlife Sanctuary, Ulu Katibas, Sungai Datai, 22 viii 2013, leg. R.A. Dow; 1 ♂ (SAR13_14_EUP12), same location and date as above, leg. J. ak Awan & M. ak Adau.—From **Brunei**: 2 ♂ (RMNH, ex. collection P. Mill), (Temburong district), Ulu Temburong, 1978, leg. S.L. Sutton; 1 ♂ (RMNH), 1 ♀ (Coll. A.G. Orr) Brunei (Temburong district), Kuala Belalong Field Studies Centre, iii 1991, leg. A.G. Orr; 1 ♂ (RMNH), same data, x 1991; 1 ♂ (RMNH), same data, vii 1992; 1 ♂ (RMNH), same data, 29 ix 1992; 1 ♂ (RMNH), same data, 23 i 1993; 1 ♂ (RMNH), same data, vii 1993; 1 ♂ (CUMZ), Brunei, Temburong, 10 x 1978, leg. T. Harman (ex coll. D.A.L. Davies); 3 ♂ (CUMZ), Brunei, Snake Creek, 16 ii 1982, leg. T. Harman (ex coll. D.A.L. Davies).—From **Sabah**: 3 ♂ (RMNH), Sabah, 105 km S of Beaufort, Long Pasia area, Sungai Padas, S. of Kampong Long Pasia, 1030 m asl., 4 24'N, 115 44'E, 12–13 iv 1987, leg. J. van Tol; 1 ♂ (RMNH), Sabah, surr. Long Pasia, Sg. Matang, leg. J. van Tol.; 2 ♂ (CUMZ), Borneo, Sabah, Maliau Basin, tributary to Sungai Maliau near Maliau Basin Field Centre, 14 v 2013, leg. S. Luke.

Etymology. The species epithet is based on the word 'ulu', the form generally in use in Borneo of the Bahasa Melayu/Indonesia word 'hulu', which means upstream. The species epithet is used as a noun in apposition. The species typically inhabits 'upstream' habitats.

Diagnosis. A narrow-winged *Dysphaea* species with male wings broadly opaque at basal half and at wing tips. Cerci with lower border nearly straight in lateral view.

Description of holotype male (Fig. 11). Head: Labium, labrum, base of mandibles and clypeus shining black, frons and vertex matt black.

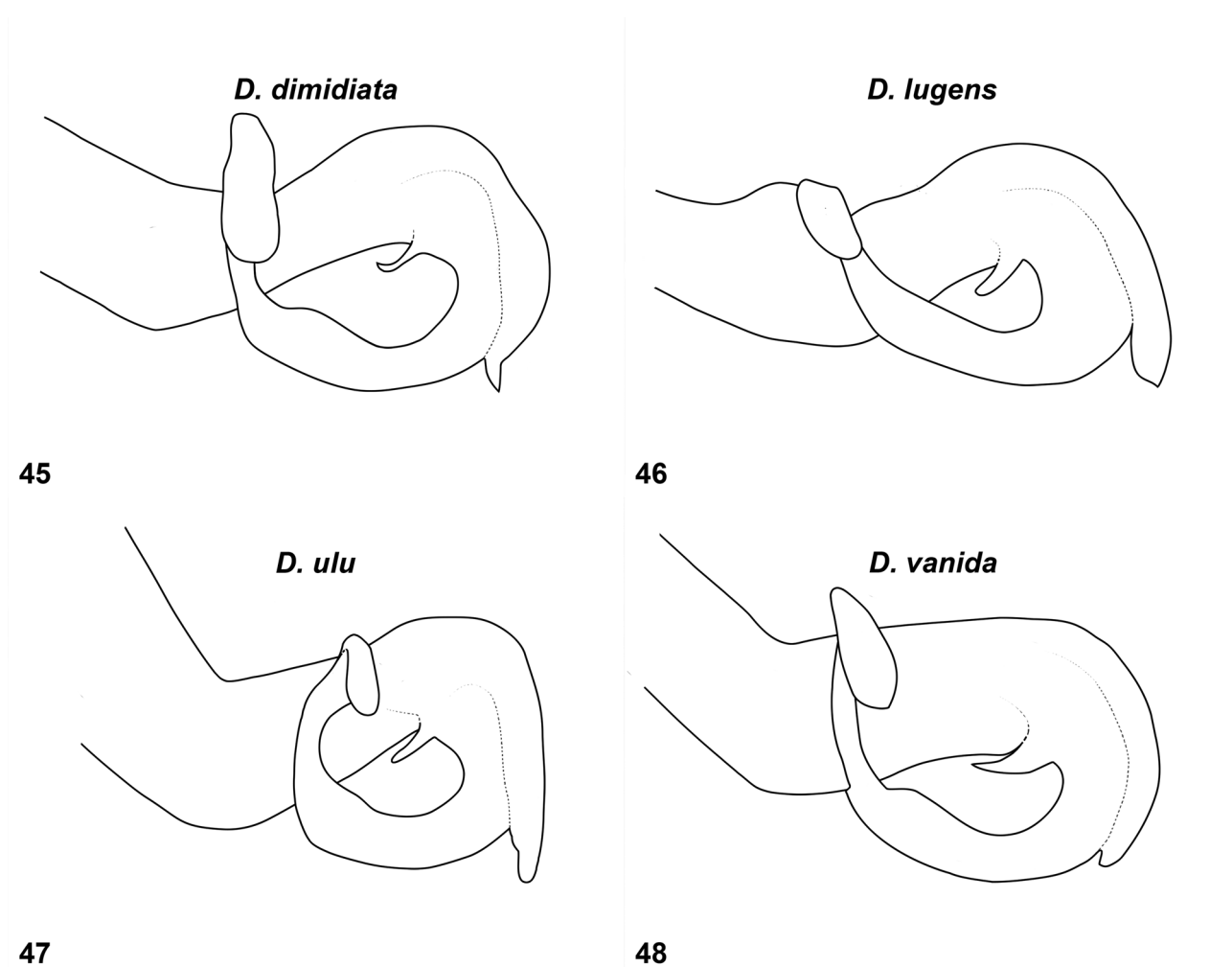
Thorax: Matt black, with very faint obscure brown marking on metepisternum above second lateral suture and

similar marking on metepimeron (Fig. 15). Venter of thorax without tiny tubercles on metaposternum (Fig. 18). Legs wholly black.

Wings: Basal half of wings opaque black with strong metallic blue reflections. In Fw opaque area extends to level of 3–4 cells before nodus, except in costal field where the opaque stripe extends 1 or 2 cells beyond the nodus. Otherwise costal field between nodus and pterostigma hyaline. In Hw basal opaque area extends more apicad, not quite reaching half way between nodus and proximal border of pterostigma; costal field between nodus and pterostigma opaque throughout. Tips of wings narrowly opaque, in Hw slightly more extensively than in Fw (Fig. 11). Venation typical of genus. Fw with 37 antenodals in first row; Hw correspondingly with 27 antenodals. Quadrangle with 2 crossveins in Fw, 2–3 in Hw. Pterostigma long and narrow, broadest in middle; covering 14 underlying cells.

Abdomen: Matt black throughout. Appendages black; cerci in dorsal (Fig. 33) and ventral view of typical shape for genus; in lateral view ventral margin of cercus almost straight (Fig. 39). Paraprocts very short, rounded and featureless.

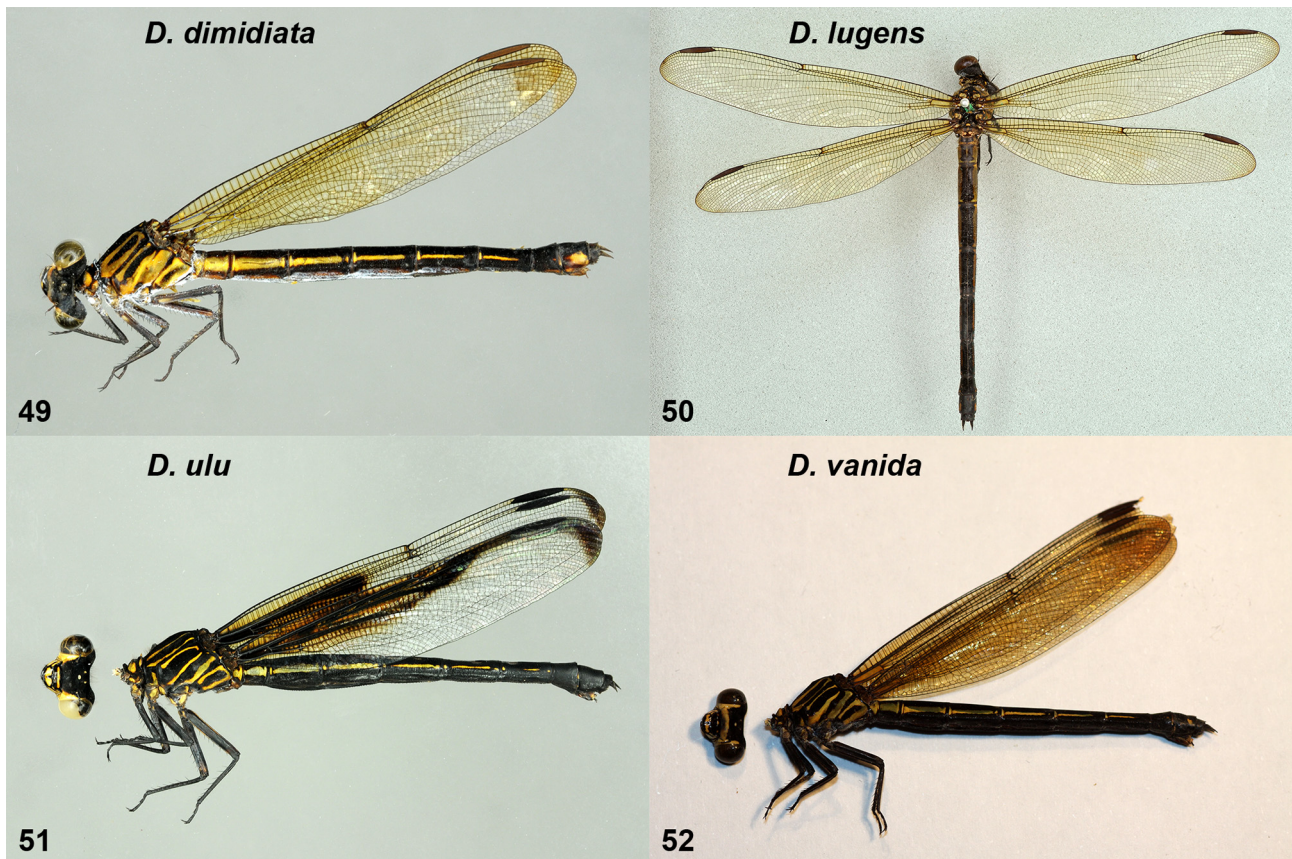
Penis: Terminal segment with two apical arms directed upwards on either side of shaft, turning out and down for short distance at ends, slightly expanded in this part (Figs. 43, 47).



FIGURES 45–48. Penis, lateral view: **45)** *D. dimidiata* west Java; **46)** *D. lugens* Selekau River, Kalimantan Barat; **47)** *D. ulu* holotype; **48)** *D. vanida* paratype, Khlong Nakha, Ranong.

Measurements (mm). Fw 33, Hw 31, abdomen (apps. excl.) 35.5, cerci 2.

Description of female (Fig. 51). Head: Labium shining black with lateral lobes largely yellow, with black hooks. Labrum shining black, with broadly yellow centre, indented by black basally. Base of mandibles largely yellow, with black incomplete stripe medially. Clypeus shining black with narrow yellow stripe along ridge. Frons matt black with sides below antennae yellow, yellow colour continuing over genae (Fig. 55). Antennae black. Vertex and occiput matt black, with two tiny yellow spots on occiput.



FIGURES 49–52. Habitus of female *Dysphaea*: **49)** *D. dimidiata* west Java; **50)** *D. lugens* Mount Dulit, Sarawak, photograph by Benjamin Price; **51)** *D. ulu* paratype; **52)** *D. vanida* paratype Kanchanaburi.

Thorax: Prothorax black with rounded large yellow spots on either side of dorsum of middle lobe. Posterior part of hind lobe raised obliquely upwards to form an elongate rectangular flap, which is narrowly bordered by yellow, more broadly so at sides (Fig. 61). Lateral parts of flap not prominent, lying in ca same plane as median part. Synthorax matt black, with moderately narrow yellow stripes as in Figs. 67, 73. Yellow stripes on mesepisternum not connected at wing base, but those on metepimeron forming a loop at wing base. Legs black, with yellow markings on both apical and posterior sides of coxae and obscure streaks on hind femora.

Wings: Hyaline with broad blackish opaque streaks in middle section of wings, at base from subcostal field to MA, costal field and much of lower part of wing hyaline (Fig. 51). In Fw opaque streak extends to level of 12 cells before nodus, in Hw it extends gradually narrowing to proximal end of pterostigma. Apex of Fw narrowly darkened, slightly more extensively on Hw. Fw with 37 antenodals in first row; hindwings with 26–28. Quadrangle with 3 crossveins in Fw, 5 in Hw. Pterostigma long, covering 11–13 underlying cells.

Abdomen: Matt black, with yellow markings as follows: S1 with lateral spot, extending upwards and downwards at apex of segment. S2–7 with lateral stripe, broadest on S2–3 and gradually narrowing towards apical segments. Separate small lateral spots at base of S3–7. On S2–5 stripe occupies almost whole segment length, on S6–7 stripe is interrupted.

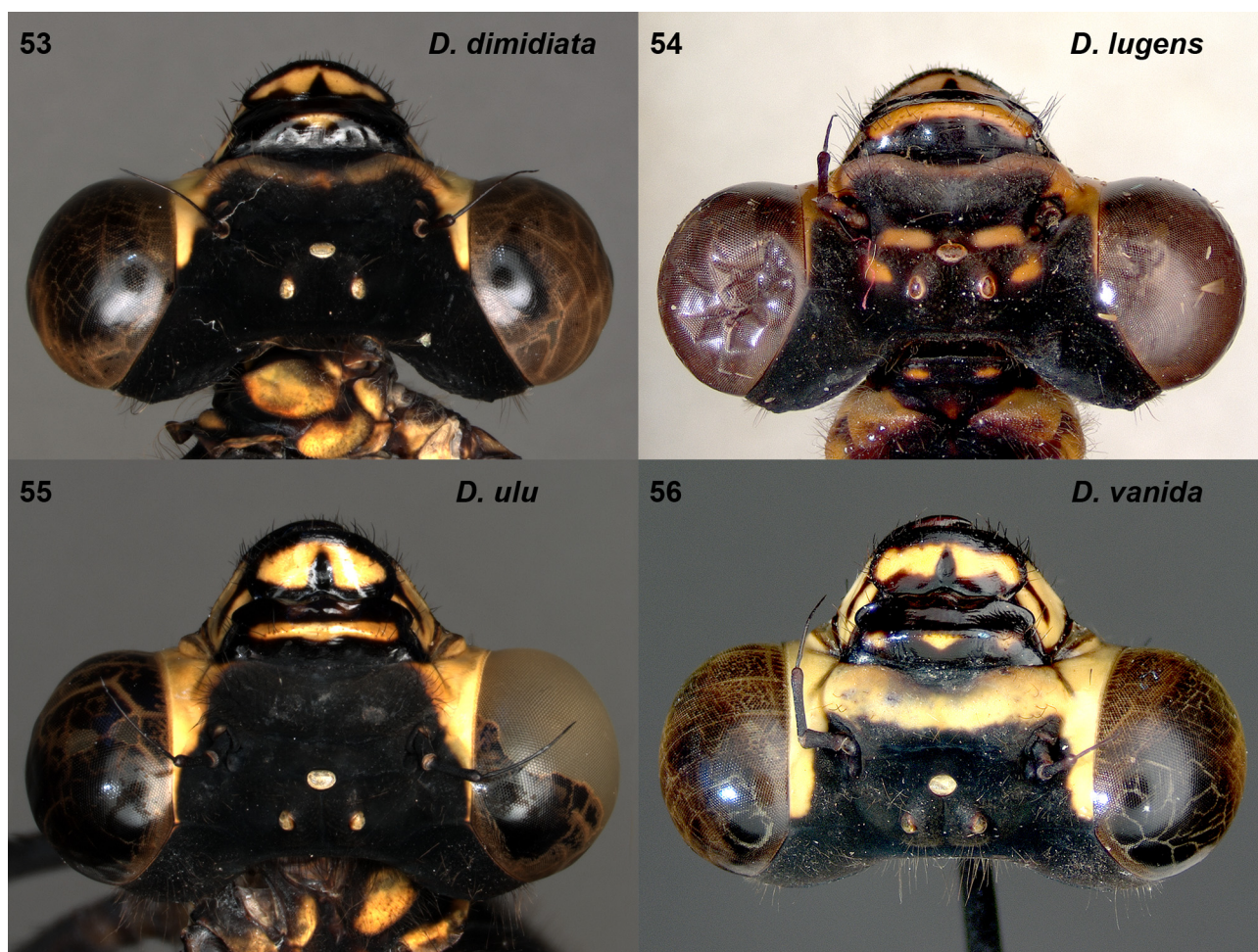
Measurements (mm). Hw 31.5–33, abdomen (apps. excl.) 30.5–32, cerci 1.

Variation in male paratypes. In some specimens the pale markings on the synthorax are slightly more distinct, in others they are entirely absent; clearly this is an age dependent character. The extent of the opaque area in wings is somewhat variable. In some specimens the opaque basal area in the Fw extends to the level of the nodus or even 1–4 cells beyond the nodus (up to 8 in costal field) and in Hw beyond half way between the nodus and proximal border of pterostigma. There is also some slight variability in venational details.

Measurements (mm): Hw 27.5–32.5, abdomen (apps. excl.) 32.5–37.

Distinguishing characters. Male: Superficially *D. ulu* male closely resembles *D. dimidiata*, a species with which it co-occurs in many locations in northern Borneo. However, these species are easy to separate by the shape

of cercus as seen in lateral view; in *D. ulu* (Fig. 39) the ventral margin of the cercus is almost straight, but distinctly arched in *D. dimidiata* (Fig. 37). Other characters, although less consistent, include the colour of the costal field between nodus and pterostigma in the Fw; in *D. ulu* (Fig. 28) the field is hyaline, but in most specimens of Bornean *D. dimidiata* the costal field in the Fw is opaque (Fig. 22). In *D. ulu* the venter of the thorax is always without tiny tubercles on metaposternum (Fig. 18), whereas in Bornean *D. dimidiata* they are almost always present (Fig. 17). There are also differences in the shape of the apical arms of the penis: the terminal, upward directed part is distinctly shorter in *D. ulu* than in *D. dimidiata*, best seen in lateral view (cf. Figs. 45 and 47), and is more rounded in ventral view (cf. Figs. 41 and 43). **Female:** *D. ulu* is easy to separate by the distinct opaque streak in both wings (Fig. 51). In *D. dimidiata* the wings are largely hyaline or semihyaline with brownish tinge, the tips being slightly darkened (Fig. 49). In *D. ulu* the yellowish stripes on thorax are narrower (Fig. 67) than in *D. dimidiata* (Figs. 63–65). *D. ulu* lacks the conspicuous yellow stripe on antefrons (Fig. 55), which is often present in *D. dimidiata* (Fig. 53).



FIGURES 53–56. Female head: **53**) *D. dimidiata* Sarawak, dorsal view; **54**) *D. lugens* Gunung Sari, Kalimantan Timur, dorsal view; **55**) *D. ulu* paratype, dorsal, slightly frontal view; **56**) *D. vanida* paratype, Kanchanaburi, dorsal, slightly frontal view.

Remarks. Some published records on Bornean *Dysphaea* species still remain uncertain as regards the real identity of the species. The *D. dimidiata* record from Lanjak Entimau Wildlife Sanctuary in Sarawak by Norma-Rashid & al. (2010, p. 326) could refer to either to *D. dimidiata* or *D. ulu*; both species are known to occur there. The *D. dimidiata* record from ‘Sarawak, Kampong Seku’ by Asahina (1966) might just as well refer to *D. ulu*.

***Dysphaea vanida* spec. nov.**

(Figs. 12, 16, 29–30, 34, 36, 40, 44, 48, 52, 56, 62, 68, 74, 81–82, 86)

Dysphaea dimidiata Selys forma (?);—Asahina (1985: 34, 36, Figs. 45–47, 67, ‘South Thailand’).

Dysphaea dimidiata [nec Selys, 1853]; Asahina (1981: 6; same specimens as above);—Asahina (1990: 10–11, 17, Figs. 40–41; Ranong and Chumphon);—Hämäläinen & Pinratana (1999: 29, 123, part; records from Tak, Kanchanaburi and Ranong);—Michalski (1992: 61, Kanchanaburi);—Donnelly (1998: 140, Tak);—Donnelly (2000: 162, Kanchanaburi);—Khunwiset & Chanpaisaeng (2002: 193, Kanchanaburi);—Kitagawa & Katatani (2005: 26, 27, Figs. 9–10, Kanchanaburi).
Dysphaea walli [nec Fraser, 1927];—Hämäläinen (1988: 24, Kanchanaburi); Hämäläinen (1989: 34, Ranong).

Material studied: Holotype ♂: Thailand, Ranong province, Khlong Nakha, Khlong Bang Man, alt. 20–40 m, 12–13 v 1999, leg. M. Hämäläinen. Deposited at RMHN, Leiden. **Paratypes** (30 ♂, 2 ♀, all from Thailand), deposited in Coll. Hämäläinen, if not otherwise stated; 4 ♂, Ranong, same data as for holotype; 3 ♂, as above, but date 8–10 ii 1988; 2 ♂, as above, but date 10–11 iv 1998; 1 ♂, as above, but date 9–11 iv 2000; 2 ♂ (in RMNH: RMNH.INS.505755, 505749), as above, but date 25–26 iii 2001; 2 ♂ (1 ♂ in RMNH, RMNH.INS.505799, as above, but date 8–12 v 2002; 1 ♂ (in RMNH: RMNH.INS.505742), as above, but date 5 iv 2003; 2 ♂, Kanchanaburi province, Thong Pha Phum District, Lam Khlong Ngu, alt. 490 m, 3 x 1986, leg. M. Hämäläinen; 3 ♂, as above but date 8–9 v 1999, leg. M. Hämäläinen; 2 ♂ (in Coll. Dow), as above, but date 4–6 v 2002; 2 ♂ (in RMNH, RMNH.INS.509984, 509985), as above but date 25 v 2003; 1 ♂, 1 ♀ (in tandem), Kanchanaburi, Thong Pha Phum District, Nang Kroan, alt. 600 m, 20 x 1999, leg. M. Hämäläinen; 1 ♂, Thong Pha Phum District (obviously Lam Khlong Ngu), 1990s, ex. coll. A. Pinratana; 1 ♂, 1 ♀, Tak province, Mae La Mao, 6 v 1998, ex coll. A. Pinratana; 1 ♂ (in Coll. André Günther), Surat Thani province, Khao Sok, Sok river, 22 ii 2001, leg. A. Günther; 1 ♂ (in Coll. André Günther), Surat Thani, Khao Sok, Bang Laen river, 21 ii 2001, leg. A. Günther; 1 ♂ (in Coll. André Günther), Phangnga province, Khao Lak, Bang Niang river, 9 iv 2009, leg. A. Günther. **Other material.** Earlier the first author has studied ca. 30 male specimens, collected in 1987–2003 by Bro. Amnuay Pinratana and his co-workers in the same sites as the paratypes from Ranong, Kanchanaburi and Tak provinces. These specimens are preserved at Insect Museum at St Gabriel's College (Bangkok), which houses Pinratana's collection.

Etymology. The species epithet is based on the common Thai girl name Vanida. In Thai the name means 'girl'. The name is a noun in apposition and is not named after any particular person.

Diagnosis. A narrow winged *Dysphaea* species, males of which have only a small opaque patch at the wing base. Wing tips narrowly darkened.

Description of holotype male (Fig. 12). Head: Labium, labrum, base of mandibles and clypeus shining black, frons and vertex matt black.

Thorax: Synthorax matt black with rather obscure, narrow, brownish stripes on sides as in Fig. 16. The upper stripe on mesepimeron, below the humeral suture, very narrow. Venter of thorax without tiny tubercles on poststernum. Legs wholly black, except posterior corner of hind coxa brownish.

Wings: Basal area of wings opaque black, with slight violet lustre. In Fw opaque area extends to half way between base and nodus. In Hw basal opaque area extends slightly more apicad, over half way between base and nodus. Tips of wings narrowly opaque, in Hw slightly more extensively than Fw (cf. Fig. 29). Venation typical for the genus. Fw with 33–34 antenodals in first row; Hw correspondingly with 26–27 antenodals. Quadrangle with 0–1 crossveins in Fw, 1–2 in Hw. Cubital field with 3 crossveins in Fw and Hw, all crossveins in the apical half of the field. Pterostigma long and narrow, broadest in middle; covering 9–11 underlying cells.

Abdomen: Matt black, with obscure remnants of brownish lateral stripes on S2–S4. Small pale dorsolateral markings at base of S3–S6. Appendages black; cerci in dorsal and ventral view of typical shape for genus; in lateral view ventral margin of cercus distinctly arched (Figs. 34, 40). In oblique dorsal view, cerci clearly broader in the middle part (Fig. 36). Paraprocts rudimentary.

Penis: Terminal segment with two long, flat, rectangular, apical arms directed straight upwards on either side of shaft, then outwards and downwards (Figs. 44, 48).

Measurements (mm): Fw 35, Hw 33, abdomen (apps. excl.) 36, cerci 2.

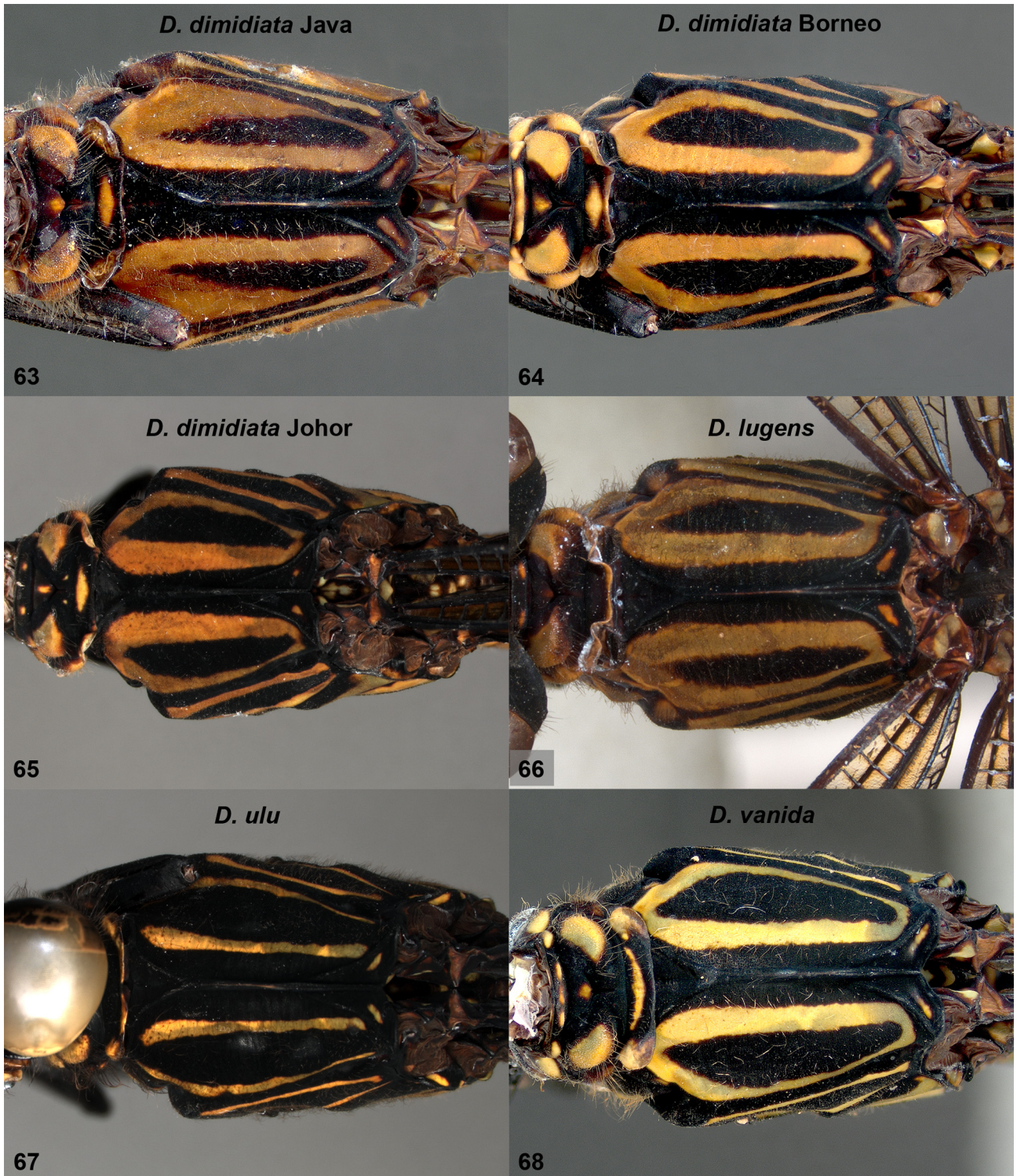
Description of female. Based on a specimen collected in tandem with a male paratype at Nang Kroan in Kanchanaburi (Fig. 52).

Head: Labium shining black with lateral lobes and sides of middle lobe yellow in basal half. Labrum shining black, with yellow marking in centre, indented with black basally. Base of mandibles largely yellow with black incomplete stripe medially. Clypeus shining black with three tiny yellow spots along ridge. Frons matt black with broad yellow band throughout antefrons, colour contiguous with yellow genae (Fig. 56). Antennae black. Yellow of genae extends almost to the level of lateral ocelli. Vertex and occiput matt black, with two tiny yellow spots on occiput. Eyes in life chestnut brown above, pale greenish below.

Thorax: Prothorax black with a row of tiny yellow spots on anterior lobe, rounded large yellow spots on either side of dorsum of middle lobe and a tiny spot medially. Posterior part of hind lobe raised obliquely upwards to form an elongate rectangular flap with prominent lateral ends (Fig. 62). Flap long, the median part slightly more than half length of entire hind lobe, with narrow yellow median stripe and with ends broadly yellow laterally. Synthorax matt black, with pale (pale greenish in life) stripes as in Figs. 68, 74. Stripes on mesepisternum and metepimeron forming a complete loop. Legs black, with yellow markings on posterior side of coxae.



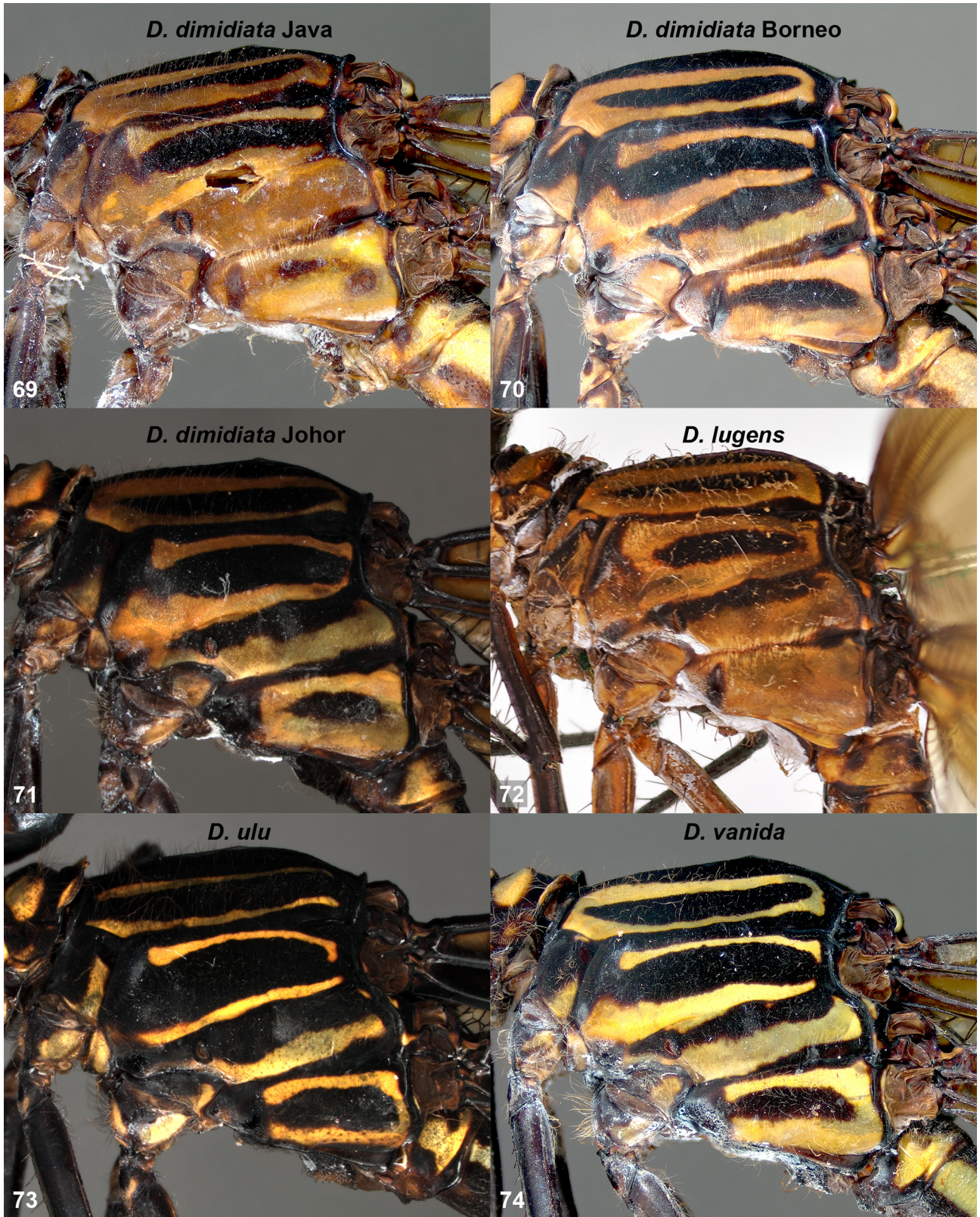
FIGURES 57–62. Female prothorax, dorsal view: **57)** *D. dimidiata* west Java; **58)** *D. dimidiata* Sarawak; **59)** *D. dimidiata* Tandjong Pandan, Billiton; **60)** *D. lugens* Gunung Sari, Kaliamatan Timur; **61)** *D. ulu* paratype; **62)** *D. vanida* paratype, Kanchanaburi.



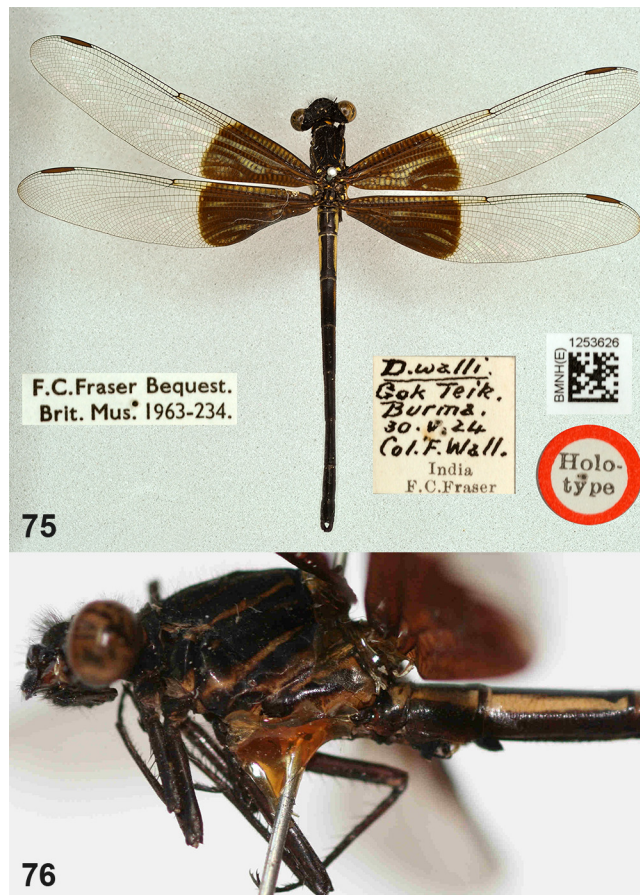
FIGURES 63–68. Female synthorax, dorsal view: **63)** *D. dimidiata* west Java; **64)** *D. dimidiata* Sarawak; **65)** *D. dimidiata* Johor; **66)** *D. lugens* Gunung Sari, Kaliamantan Timur; **67)** *D. ulu* paratype; **68)** *D. vanida* paratype Kanchanaburi.

Wings: Hyaline with slightly brownish tinge, especially at tips of wings. Fw with 31 antenodals in the first row; Hw with 26–27. Quadrangle with 1–2 cross veins in Fw, 2–3 in Hw. Pterostigma long, covering 8–9 underlying cells.

Abdomen: Matt black, with pale (pale greenish in life) markings as follows: S1 with large lateral spot, covering most of the side of segment. S2–7 with lateral stripes, broadest on S2–3 and gradually narrowing towards the apical segments. Obscure tiny lateral spot on S8 and a little larger, distinct lateral spot at S 9. Appendages black.



FIGURES 69–74. Female synthorax, lateral view: **69)** *D. dimidiata* west Java; **70)** *D. dimidiata* Sarawak; **71)** *D. dimidiata* Johor; **72)** *D. lugens* Mount Dulit, Sarawak, photograph by Benjamin Price; **73)** *D. ulu* paratype; **74)** *D. vanida* paratype Kanchanaburi.



FIGURES 75–76. *Dysphaea walli* holotype: **75**) habitus and labels, image constructed from photographs by Benjamin Price; **76**) synthorax lateral view (photo by Matti Hämäläinen).

Measurements (mm): Hw 33, abdomen 31 (apps. excl.), cerci 1.

Variation in male paratypes. In some specimens the pale markings on synthorax and on sides of the basal abdominal segments are more distinct, clearly an age-dependent character. In younger specimens the small yellowish dorsolateral markings at the base of S3–6 are more distinct (cf. Figs. 81–82). The extent of the opaque area in the wings is somewhat variable. In some specimens from the type locality the opaque basal area in the Fw extends only one third of the length of area between base and nodus and in the Hw less than half of this distance. In one specimen from the type locality the opaque patch on wings is very small, reaching only to the apical end of quadrangle (Fig. 30). A specimen from the same site with quite similarly reduced wing patches was illustrated by Asahina (1990, Fig. 40 on p. 17). In a few specimens from Kanchanaburi the opaque area is slightly more extensive than in the holotype, in the Fw reaching over the half way of the distance between base and nodus, in the Hw reaching to the level of 7 cells before the nodus. There is also slight variability in venational details.

Measurements (mm): Hw 33–35, abdomen (excl. cerci) 38–39.5.

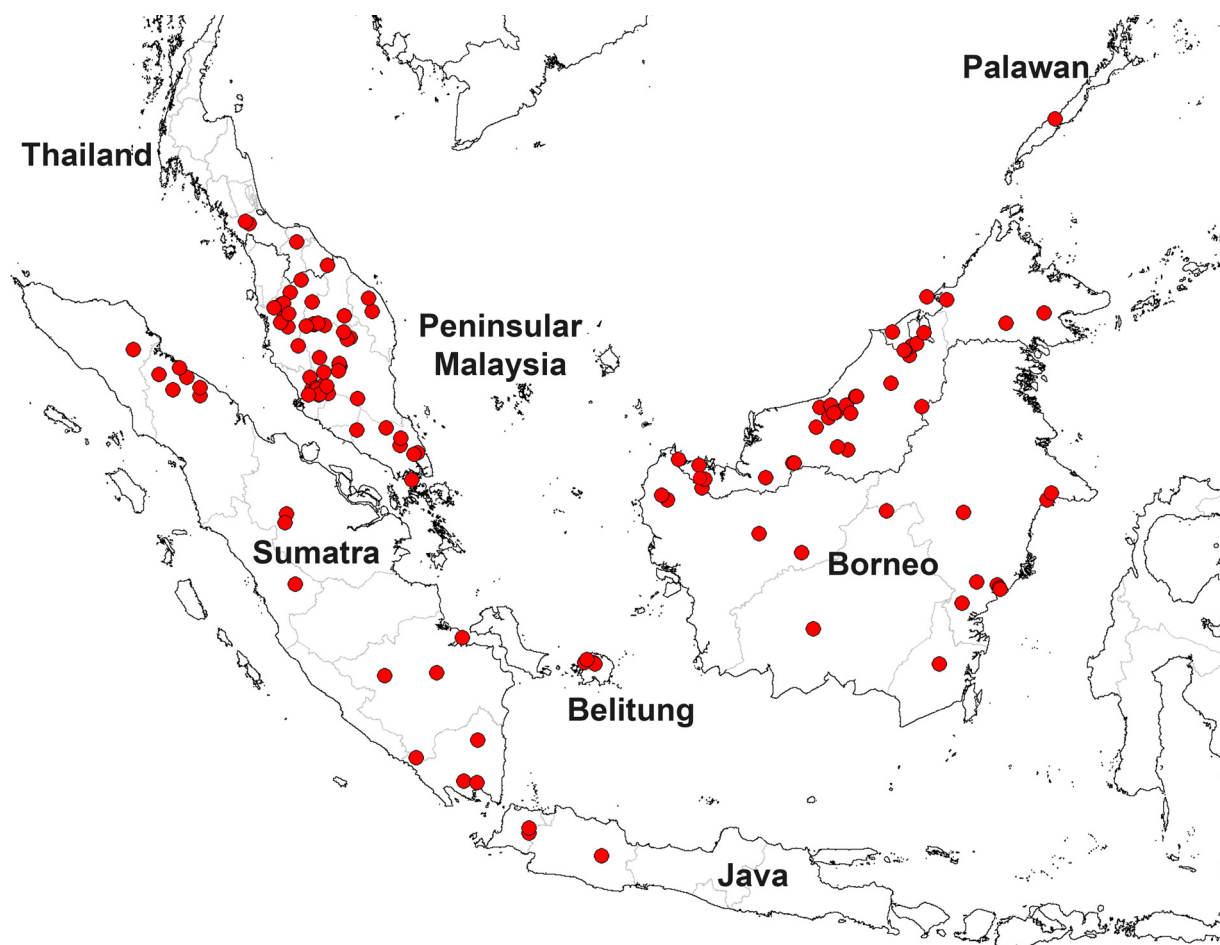
Variation in female paratypes. Specimen from Tak is slightly larger in size; Hw 34 mm, abdomen 32 (apps. excl.) mm, cerci 1 mm. Colour pattern of body and wings is quite similar. Fw with 33–35 antenodals in the first row; Hw with 25–27. Quadrangle with 1–2 crossveins in Fw, 2–3 in Hw. Pterostigma long, covering 8–11 underlying cells.



FIGURES 77–82. *Dysphaea* males in life: **77)** *D. basitincta* Hainan (photo by Mo Shanlian) **78)** *D. dimidiata* Sarawak (photo by Graham T. Reels); **79)** *D. dimidiata* Negeri Sembilan (photo by C.Y. Choong); **80)** *D. ulu* Sarawak (photo by Graham T. Reels); **81)** *D. vanida* Ranong (photo by Matti Hämäläinen); **82)** *D. vanida* Surat Thani (photo by André Günther).

Distinguishing characters. Male: *D. vanida* is easy to separate from *D. dimidiata* by the less extensive basal opaque area in both wings. The shape of the cerci of these two species differs, clearly broader in the middle in *D. vanida* (Fig. 36) than in *D. dimidiata* (Fig. 35) in oblique dorsal view. The extent of the basal opaque patch on wings of *D. vanida* resembles that of the north Burmese species *D. walli* Fraser, 1927, and the Indochinese and southern Chinese *D. basitincta* Martin, 1904. However, in *D. walli* the wing tips are hyaline and the wings (Fig. 75) are proportionally considerably broader than in *D. vanida* (Figs. 29–30). *D. walli* has more distinct pale markings on the thorax and abdomen (Fig. 75–76); according to the description by Fraser (1927, 1934) the markings on the abdomen are pale blue. Fraser’s (1927) description of *D. walli* was based on four male specimens from ‘Maymyo, North Shan States, Upper Burma’. Only the holotype is available at BMNH (Kimmins 1966); the three paratypes

appear to be lost. *D. basitincta* is larger in size (Hw 37–41 mm), and the opaque area in wing tips is larger (Fig. 77). The penis structure of *D. basitincta* is entirely different, the apical arms not being extended laterally but curled downwards close to the stem (cf. Wilson & Reels 2001: 158, Figs. 8–9). **Female:** The female resembles that of *D. dimidiata* quite closely, but the wing tip is not as distinctly darkened as in *D. dimidiata*.

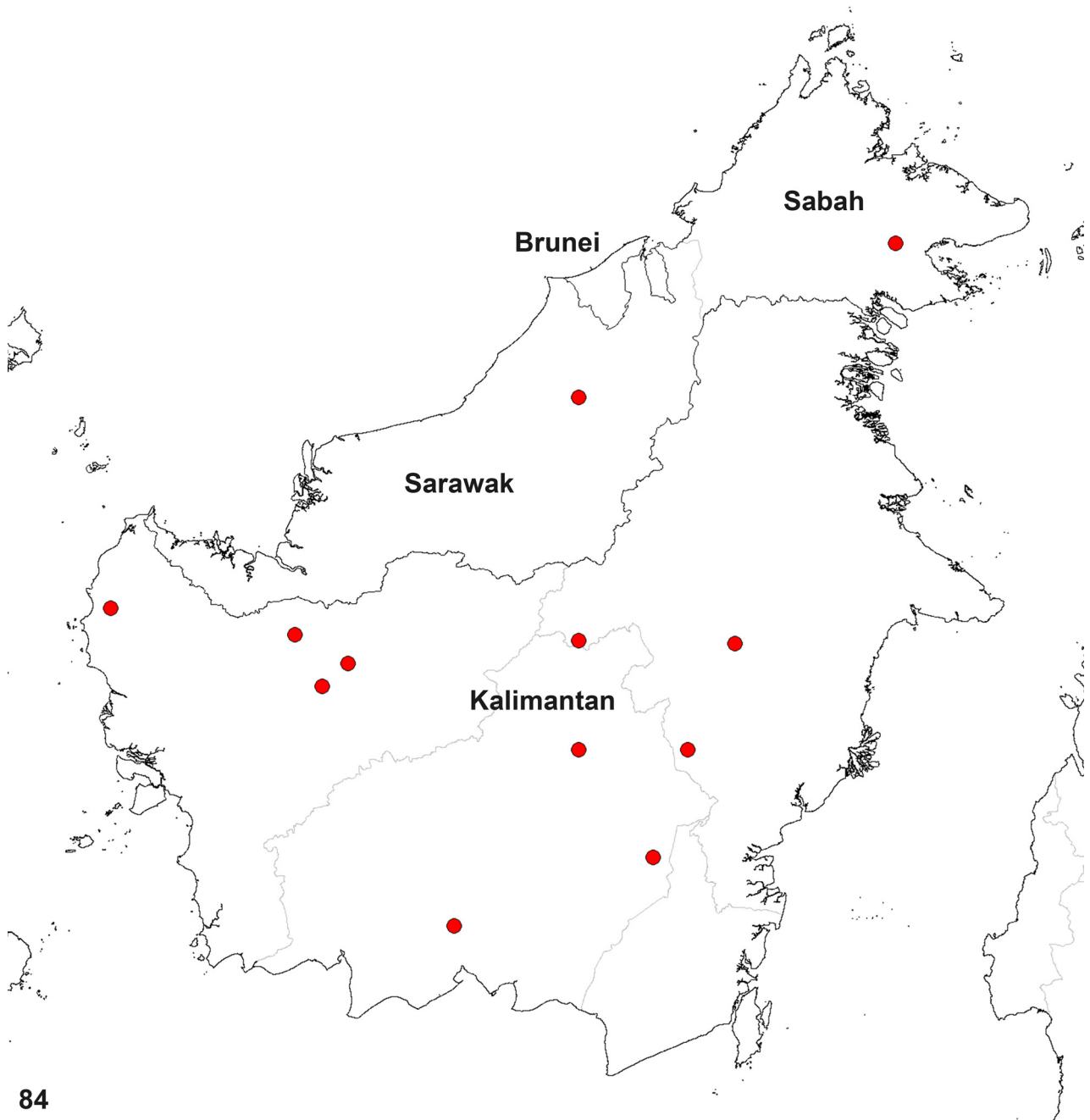


83

FIGURE 83. Distribution map of *Dysphaea dimidiata*.

Key to males of Sundaland species

1. Basal opaque area in both wings terminating well before nodus (Figs. 29–30) *D. vanida*
- Basal opaque area in Hw always extending beyond nodus, in Fw around nodus or after nodus (Figs. 19–28) 2
2. Cerci with ventral side nearly flat in lateral view (Fig. 39) *D. ulu*
- Cerci with ventral side with distinct curve near base in lateral view (Figs. 37–38) 3
3. Apical arms of terminal segment of penis short (Fig. 42); apex strongly expanded (Fig. 46); in mature specimens opaque area of wings brownish; ratio of abdomen (excl. cerci) to Hw more than 1.20 *D. lugens*
- Apical arms of terminal segment of penis long (Fig. 41), apex quadrangle shaped, moderately expanded (Fig. 45); in mature specimens opaque area of wings black; ratio of abdomen (excl. cerci) to Hw usually less than 1.20 *D. dimidiata*



84

FIGURE 84. Distribution map of *Dysphaea lugens*.

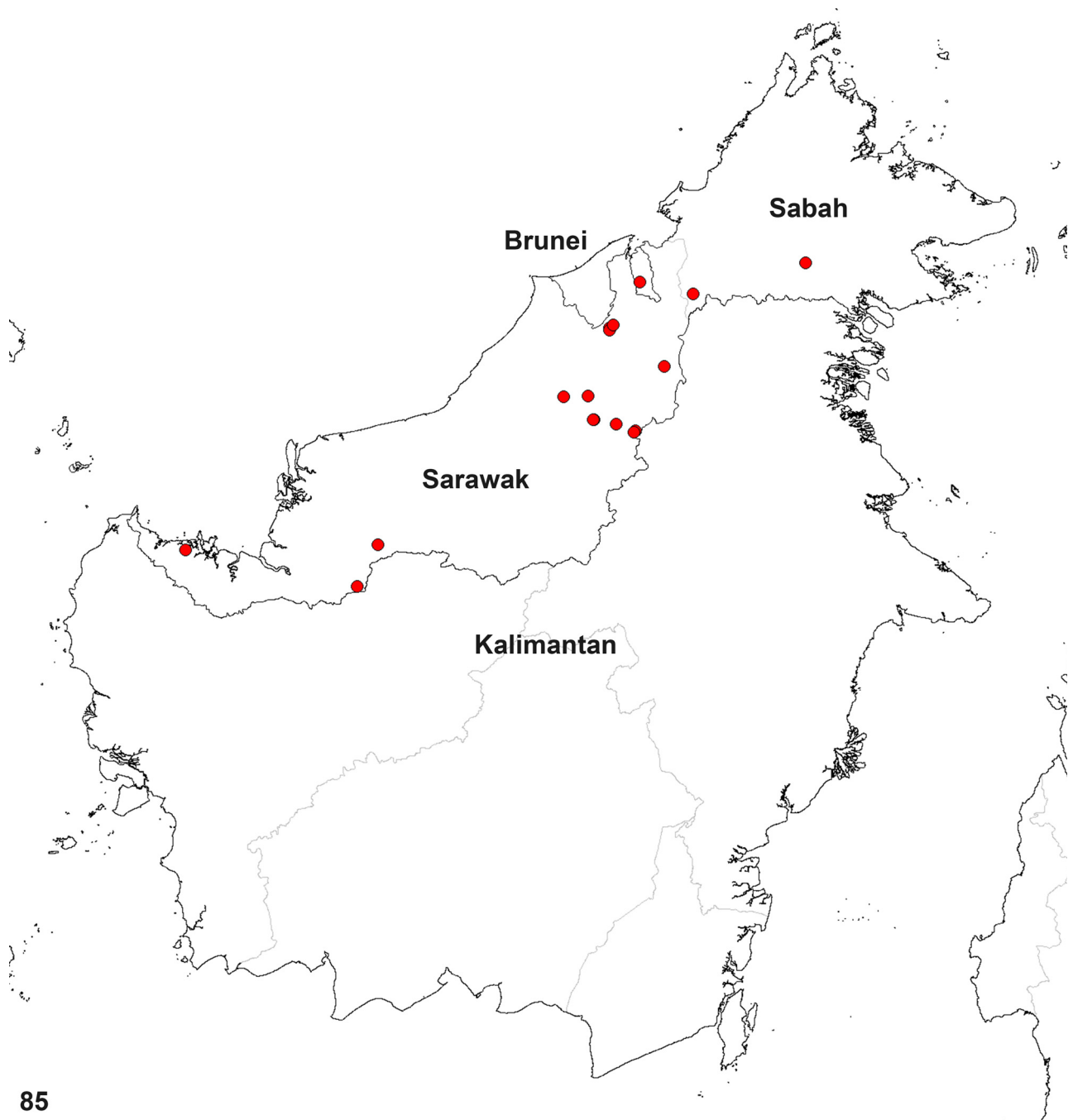
Key to females of Bornean species

- 1. Vertex with yellow markings outside of ocelli (Fig. 55)..... *D. lugens*
- Vertex without any pale markings (Figs. 53, 55) 2
- 2. Distinct opaque streaks in middle section of wings, longer streak in Hw (Fig. 51)..... *D. ulu*
- Wings with only slight brownish tint, more distinctly so at tips (Fig. 49) *D. dimidiata*

Discussion

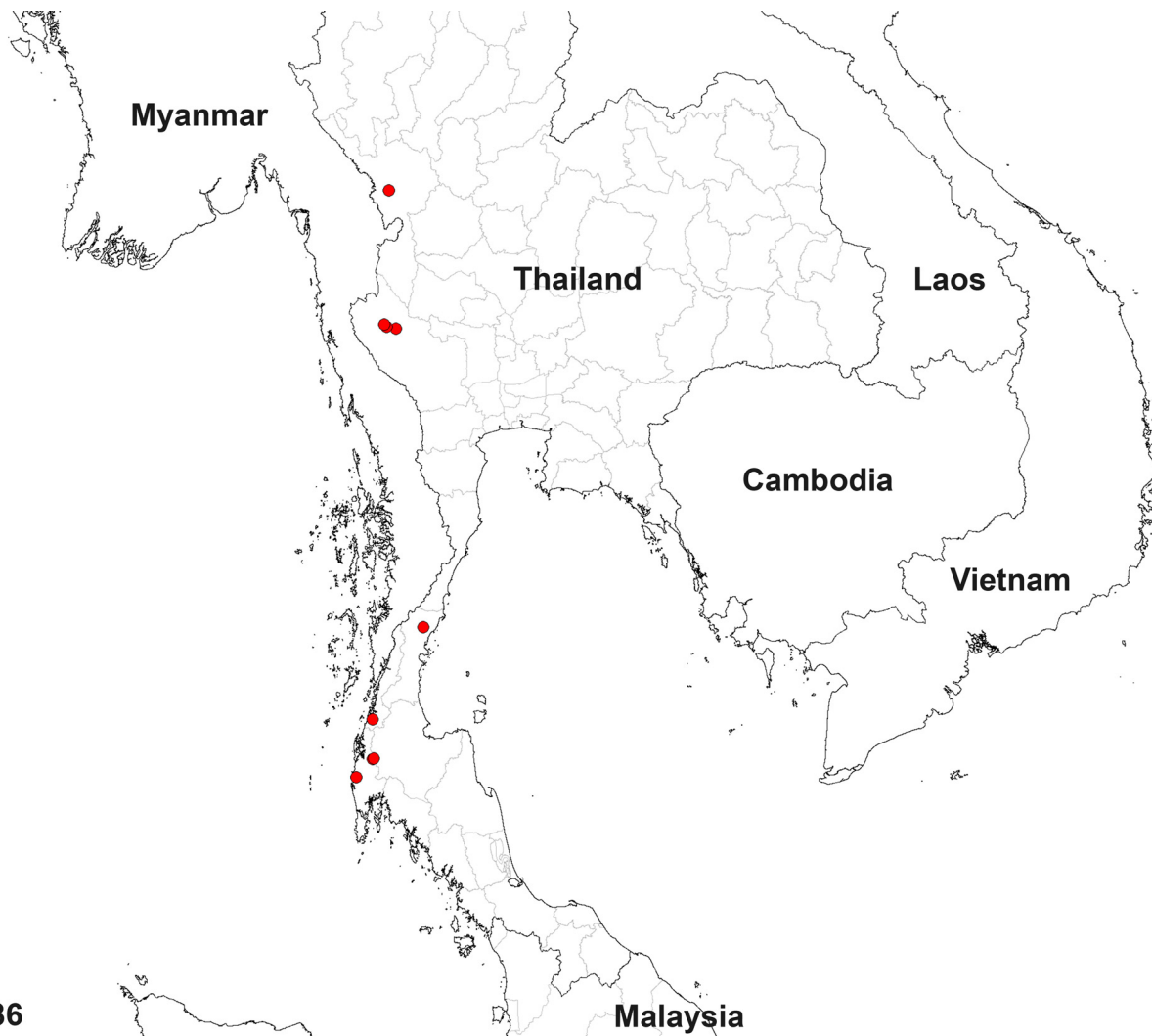
The relationships between Javan *D. dimidiata*, *D. dimidiata* from Borneo and *D. dimidiata* from elsewhere are not entirely clear. There are only very slight consistent morphological or pattern differences between these populations,

but most of our molecular analyses recover the Bornean population as a separate clade from the Sumatran, peninsular Malaysian, and Thai populations; the exception is the ML analysis of the combined COI+16S+28S dataset, where their relationship is not resolved. However, since no fresh specimens of the topotypical Javan *D. dimidiata* were available for molecular analysis, it would be premature to consider infraspecific splitting of this species based on observed variation. The species-group names *limbata* and *semilimbata* are available for this purpose. Obtaining fresh material of *D. dimidiata* from Java may be difficult, since the species has not been recorded there during the last 60 years, and it may even be extinct in this island. On the other hand ancient DNA methods might allow the use of the old available specimens from Java in the future. In any event an analysis involving additional markers is desirable to resolve these issues, especially as our analysis relies mainly on mitochondrial markers, but species level paraphyly and polyphyly are relatively common in these markers (e.g. Funk & Omland 2003). We find the use of genetic distances calculated for some individual marker or some set of markers as a means of distinguishing species to be arbitrary and of little value; for this reason we have not calculated such distances.



85

FIGURE 85. Distribution map of *Dysphaea ulu*.



86

FIGURE 86. Distribution map of *Dysphaea vanida*.

The relationship of *Dysphaea vanida* to *D. dimidiata* is also not completely clear from our molecular results, with *D. vanida* either appearing as the sister of *D. dimidiata* or as a distinct clade nested within a combined *D. dimidiata* + *D. vanida* clade. The two species are very obviously closely related and probably (given the rather small differences seen in the markers studied here) separated relatively recently, but they are clearly separated morphologically.

Dysphaea ulu differs in its anal appendages from all of the other species studied, so the fact that it appears as the sister of all the other species in all molecular analyses is not surprising. Although *D. lugens* has very similar anal appendages to *D. dimidiata* and *D. vanida*, it differs from those species, and from *D. ulu*, quite considerably in penis structure; it will be interesting to see what molecular analysis will reveal about the relationships of *D. lugens* to the other species, should fresh material become available.

Acknowledgements

The molecular studies presented here are a part of the Naturalis Biodiversity Center project ‘Phylogeny and biogeography of Zygoptera (Odonata)’, headed by Jan van Tol. We are grateful to him and the other members of the team: Klaas-Douwe B. Dijkstra and Vincent Kalkman. Kevin Beentjes and Camiel Doorenweerd advised on molecular analysis. The following collection managers or museum curators let us to study specimens under their care and provided other help: Yvonne van Nierop (RMNH), Russell Stebbings (CUMZ), Jérôme Constant (IRSN)

and Benjamin Price (BMNH). The latter two curators also provided photographs of some type specimens. C.Y. Choong, André Günther, Sarah Luke, Shanlian Mo, Robin Ngiam, Albert G. Orr, Graham T. Reels, Philip Steinhoff and Hao-miao Zhang provided specimens and/or field photos to be used in this paper. Albert G. Orr and Jan van Tol kindly reviewed the manuscript before submitting and made useful suggestions. The first author received support from the SYNTHESYS Project [<http://www.synthesys.info/>] which is financed by European Community Research Infrastructure Action. The second author is grateful to the Sarawak Forest Department and Sarawak Forestry Corporation for granting permission the collect specimens in Sarawak and much assistance, as well as to the International Dragonfly Society, The Worldwide Dragonfly Association, the Mohamed bin Zayed Species Conservation Fund and Singapore National Parks for providing funding for field trips during which some of the material used in this paper was collected.

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