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A new Bornean species of *Drepanosticta* allied to *D. actaeon* Laidlaw, with notes on related species (Odonata: Zygoptera: Platystictidae)

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Abstract

Drepanosticta kosterini sp. nov. (holotype ♂, from Gunung Penrissen, Kuching Division, Sarawak, Malaysian Borneo, deposited in RMNH) is described from both sexes. It is the sister species of *D. actaeon* Laidlaw, 1934; a fresh description of the male of *D. actaeon* and the first description of the female are given, along with discussion of variation in this species. Both *D. actaeon* and *D. kosterini* are considered to belong to a species group also including *D. rufostigma* (Selys, 1886) and a preliminary discussion of variation in this species is given, along with illustrations of both sexes. A neighbour joining COI gene tree for *D. actaeon* and *D. kosterini* is presented. The relationships of *D. actaeon*, *D. kosterini* and *D. rufostigma* to other members of the Platystictidae are briefly discussed.

Key words: Odonata, Zygoptera, Platystictidae, *Drepanosticta*, *actaeon*, *kosterini*, *rufostigma*, COI, DNA barcoding, Borneo, Sarawak, new species

Introduction

The number of Platystictidae known from Borneo has increased markedly in recent years, with 17 new species described since 2010. However the majority (14) of newly described species are in *Telosticta* Dow & Orr, 2012, with only *Drepanosticta burbachii* Dow, 2013, *D. sbong* Dow, 2010 and *D. simuni* Dow & Orr, 2012 currently placed in *Drepanosticta* Laidlaw, 1917. Many species are yet to be described, and here I deal with a new species, allied to *D. actaeon* Laidlaw, 1934, discovered on Gunung Penrissen in south west Sarawak. The new species is described as *D. kosterini* sp. nov.

The new species and *D. actaeon* are most closely related to *D. rufostigma* (Selys, 1886); this is clear both from morphology (e.g. similarity of anal appendages and colouration, see the illustrations below) and molecular results (e.g. see Fig. 48 in van Tol et al. (2009), Fig. 2 in Dijkstra et al. 2014, Fig. 1 here). I consider these three species to form a natural grouping, referred to below as the *D. rufostigma*-group. A neighbour joining gene tree using the standard DNA Barcoding marker COI for *D. actaeon* and *D. kosterini*, and also including *D. rufostigma* is shown in Fig. 1. The relationship of these three species to the rest of the Platystictidae is discussed briefly below and will be discussed in more detail elsewhere.

The holotype of *D. actaeon* is damaged, which led to an inaccurate illustration of the anal appendages in the original description in Laidlaw (1934). That original description is very brief and only the male had been described until now. Additionally *D. actaeon* exhibits colour variation in different parts of its range (e.g. Dow & Ngiam 2012), which has previously caused me to wonder whether or not only one species was involved. To clarify matters, a fresh description of an intact and close to topotypical *D. actaeon* male, agreeing very well with the holotype, is given, together with the first description of a female and discussion of variation in this species. Fresh illustrations of *D. rufostigma* are also provided and this species is discussed.

Table 1. Primer combinations used for amplification of COI.

Primer name	Target	Direction	Sequence (5' to 3')	Reference
ODO_LCO1490d	COI	F	TTCTACWAACCAAYAAAGATATTGG	Dijkstra <i>et al.</i> 2014
ODO_HCO2198d	COI	R	TAAACTTCWGGRTGCCAAARAATCA	Dijkstra <i>et al.</i> 2014
LepF1	COI	F	ATCAACCAATCATAAAGATATTGG	Hebert <i>et al.</i> 2004
LepR1	COI	R	TAAACTTCTGGATGTCAAAAAATCA	Hebert <i>et al.</i> 2004
LCO1490	COI	F	GGTCAACAAATCATAAAGATATTGG	Folmer <i>et al.</i> 1994
HCO2198	COI	R	TAAACTTCAGGGTGACCAAAAAATCA	Folmer <i>et al.</i> 1994

Table 2: Collection codes and BOLD Process IDs for specimens used for molecular analysis: all specimens are from the states of Sabah and Sarawak in Malaysian Borneo, the state, division and approximate location are listed for each specimen. The collection codes can be used to locate the COI sequences on the BOLD website, and also appear as BOLD Sample IDs there. COI sequences for RMNH.INS.503455, RMNH.INS.503447 and RMNH.INS.500011 were already used in, for instance, Dijkstra *et al.* 2014.

Species	RMNH number	State	Division	Location	BOLD process ID
<i>D. actaeon</i>	RMNH.5008405	Sarawak	Miri	Sungai Alah	ODOBP457-16
	RMNH.INS.228955	Sarawak	Miri	Gunung Kalulong	ODOBP7450-16
	RMNH.INS.503453	Sarawak	Miri	Gunung Kalulong	ODOBP2132-16
	RMNH.INS.503454	Sarawak	Kapit	Sungai Sebabei	ODOBP2133-16
	RMNH.INS.503455	Sarawak	Miri	Gunung Kalulong	ODOPH307-13
	RMNH.INS.503456	Sarawak	Miri	Gunung Mulu	ODOBP2134-16
	RMNH.INS.503664	Sarawak	Miri	Gunung Kalulong	ODOBP2302-16
	RMNH.INS.503904	Sarawak	Kapit	Sungai Sebabei	ODOBP2372-16
	RMNH.INS.506253	Sarawak	Bintulu	Bukit Kana	ODOBP3681-16
	RMNH.INS.506863	Sarawak	Bintulu	Bukit Kana	ODOBP5205-16
	RMNH.INS.507659	Sabah	West Coast	Mount Kinabalu: Poring	ODOBP5559-16
	RMNH.INS.507660	Sabah	West Coast	Mount Kinabalu: Poring	ODOBP5560-16
	RMNH.INS.507676	Sabah	West Coast	Mount Kinabalu: Poring	ODOBP5573-16
	RMNH.INS.507719	Sabah	West Coast	Mount Kinabalu: Sayap	ODOBP5611-16
	RMNH.INS.507723	Sabah	West Coast	Mount Kinabalu: Sayap	ODOBP5613-16
RMNH.INS.509641	Sarawak	Kapit	Gunung Kumbong	ODOBP7096-16	
RMNH.INS.509642	Sarawak	Kapit	Gunung Kumbong	ODOBP7097-16	
<i>D. attala</i>	RMNH.INS.503447	Sarawak	Kapit	Gunung Mulu	ODOPH308-13
<i>D. dulitensis</i>	RMNH.INS.500011	Sarawak	Miri	Mount Dulit	ODOPH311-13
<i>D. kosterini</i>	RMNH.5008433	Sarawak	Kuching	Gunung Penrissen	ODOBP485-16
	RMNH.INS.506814	Sarawak	Kuching	Gunung Penrissen	ODOBP5160-16
	RMNH.INS.506815	Sarawak	Kuching	Gunung Penrissen	ODOBP5161-16
	RMNH.INS.506817	Sarawak	Kuching	Gunung Penrissen	ODOBP5163-16
<i>D. rufostigma</i>	RMNH.INS.504003	Sarawak	Kuching	Matang Wildlife Centre	ODOBP2460-16
	RMNH.INS.507818	Sarawak	Kuching	Gunung Pueh	ODOBP5689-16

Material & Methods

Material examined. All available material of *D. kosterini* was collected by the author and G.T. Reels, and is currently either in collection Dow or in the collections of the Naturalis Biodiversity Center (RMNH). Material of *D. actaeon* and *D. rufostigma* from RMNH, collection Dow and the Natural History Museum London (BMNH) was examined. Because rather long series of *D. actaeon* and, especially, *D. rufostigma* were examined, non-type material that has not been published previously and is not used for an illustration or as the basis of a description, is listed in an appendix for these species; the reader is referred to other publications where non-type material has previously been published. Material collected by the author and associates and, at least initially, in his collection, has a reference code; this code is stated for type material and for others specimens that are used in descriptions and illustrations.

Molecular analysis. 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 mitochondrial COI gene (658 bp) were amplified using primer combinations provided in Table 1. Twenty-five microlitres of PCR reaction mix for 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. 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 MacroGen Europe and at BaseClear, Leiden, The Netherlands.

COI sequences were edited with Sequencher 4.10.1 (Gene Codes Corporation) and checked for stop-codons using the invertebrate mitochondrial genetic code in Geneious pro 6.1.8 (Kearse et al. 2012). Analysis for this publication was made using Geneious pro 6.1.8. Details of specimens used for the DNA analysis are given in Table 2. 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).

Results of the molecular analysis

A simple neighbour joining (uncorrected p-distance) COI gene tree for *D. actaeon* and *D. kosterini* is shown in Fig. 1, with samples of *D. rufostigma* also included. The holotype and three paratypes of *D. kosterini* are included in the analysis. Two more distantly related *Drepanosticta* species are included as outgroups. This analysis uses a non-phylogenetic method, so it is debateable how informative it is about relationships between species; but, accepting the limitations of the method, it nevertheless shows a sister species relationship between *D. actaeon* and *D. kosterini*, and *D. rufostigma* as a sister to *D. actaeon* plus *D. kosterini*.

The four *D. kosterini* sequences analysed are 100% identical to one another, and differ from the *D. actaeon* sequences in from 67 to 73 base pairs. The *D. actaeon* sequences are identical in 641 sites. The red-eyed populations (represented by samples from

Gunung Kalulong, Sungai Alah and Gunung Mulu, see the discussion under *D. actaeon* below; indicated by red text in Fig. 1) differ from non-red-eyed samples in only 1-7 base pairs and differ amongst themselves in 0-6 base pairs. All 17 *D. actaeon* sequences analysed share the same Barcode Index Number (BIN) on the Barcode of Life Database website.

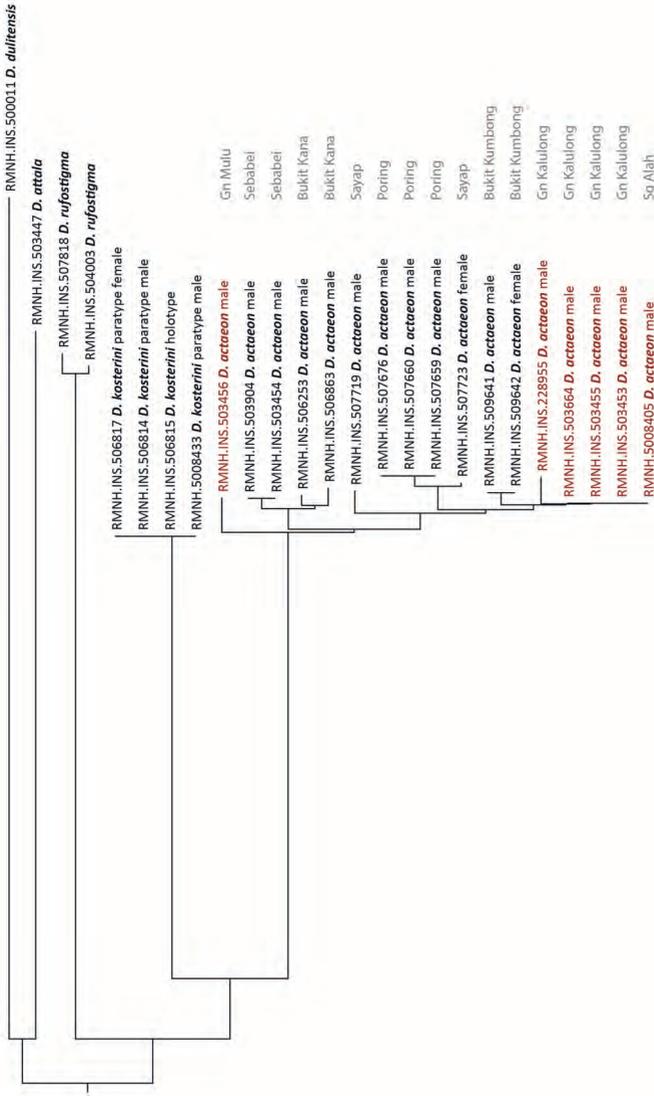


Figure 1. COI neighbour joining gene tree for *D. actaeon* and *D. kosterini* and with samples of *D. rufostigma* also included. *Drepanosticta affata* and *D. dullifensis* are included as out groups. Red-eyed populations of *D. actaeon* are indicated by the species name in red text.

***Drepanosticta actaeon* Laidlaw, 1934**

(Figs. 1, 2, 4, 8, 12, 16, 17, 22, 23, 28, 31, 36, 39, 40, 45, 48, 49, 50, 51, 56)

Drepanosticta actaeon Laidlaw 1934: 558–559, Fig. 3 (original description holotype male from Kabayau, Kinabalu, illustration of anal appendages); — Liefinck 1954: 32, 176; — Kimmins 1970: 174 (notes on holotype); — van Tol 1992: 26; — Hämäläinen 1994: 80 (Poring and Danum Valley); — Orr 2003 38, 71; — van Tol et al. 2009: 60–61, 66, 67, 70, Figs. 48, 45; — Choong 2011: 155 (Imbak Canyon); — Dow, Reels & Butler 2013b: 10 (Mount Dulit); — Dijkstra et al. 2014: Figs. 2, 3, Table S2; — Dow & Ngiam 2014: 25, 42, 43, 44 (Ulu Baleh and Ulu Balui); — Dow & Ngiam 2015: 15 (upper Baram); — Dow et al. 2015a: 18, 19 (Sebabei Recreational Park); — Luke et al. 2017: Table S2 (south-east Sabah).

Drepanosticta ?actaeon; — Dow & Reels 2009: 13 (Mount Dulit).

Drepanosticta sp cf *actaeon*; — Dow & Ngiam 2012: 9 (Hose Mountains).

Drepanosticta species near *rufostigma*; — Dow & Reels 2008: 3 (Gunung Mulu National Park).

Material examined. Type material. Holotype ♂, Kabayau, Mount Kinabalu [?], Sabah, 600 ft, 8 v 1929. Leg. H.M. Pendlebury, in BMNH. Other material. 1 ♂ (SAR07_8_PST130), Sungai Sebabei and tributaries, near Kapit Town, Kapit Division, Sarawak, Malaysia, 7 ii 2008, leg. R.A. Dow, in collection Dow; 1 ♂ (SAR09_10_PST158), stream south of main peak of Gunung Kalulong, upper Baram, Miri Division, ca 750–930m, 7 x 2009, leg. R.A. Dow, in collection Dow; 1 ♂ (SAR07_8_PST196, RMNH.INS.503456), Camp 2 stream system, Gunung Mulu, Gunung Mulu National Park, Miri Division, Sarawak, Malaysia, 5 i 2008, leg. RAD, in RMNH; 1 ♂, same location, 11 ix 2008, leg. R.A. Dow, in collection Dow; 3 ♂ (SAB12_PST12; SAB12_PST80, RMNH.INS.507676; SAB12_PST81, RMNH.INS.507660), stream running into Bamboo Garden, Poring Hots Springs, Mount Kinabalu National Park, Sabah, Malaysia, 10 ix 2012, leg. R.A. Dow, those with RMNH.INS numbers in RMNH; 1 ♀ (SAB12_PST17), Sungai Kemanfis and tributaries, Sayap Station, Mount Kinabalu, same national park, 14 ix 2012, leg. RAD, in collection Dow; 1 ♀ (SAB12_PST68, RMNH.INS.507723), same data but in RMNH. Specimens listed in Dow, Reels & Butler 2013b, Dow & Ngiam 2014, Dow & Ngiam 2012, Dow & Ngiam 2015 and Dow et al. 2015a were examined. Additional material, not previously published, is listed in the appendix.

Description of male. Based on SAB12_PST12 (Fig, 48), Poring, Sabah (illustrations, except for the dorsal and lateral views of the anal appendages, made from different specimens collected at the same location on the same day).

Head: Labium almost entirely pale. Basal ca one-third labrum yellowish, rest black. Anteclypeus, mandible bases and adjacent parts of genae yellow. Post clypeus black and dark brown with indistinct yellowish marks laterally (absent in male shown in Fig. 2). Vertex frons, occiput and underside of head black. Ratio of width of compound eye to width of vertex measured at level of lateral ocelli ca 0.8. Transverse occipital

carina with lateral extremities angulated, prominent. Ocelli whitish. Antenna with scape brown, remainder missing.

Thorax (as in Figs. 8, 12, 22): Propleuron yellow, indistinct darker areas to rear. Anterior pronotal lobe black on raised frontal part, yellow to rear and lateral extremities. Middle pronotal lobe almost entirely yellow except small darker area centrally at rear. Posterior lobe black, free margin rather abruptly raised to rear and laterally (as in Fig. 12). Synthorax: Mesepisternum entirely bronzy black. Antealar triangles black. Mesepimeron almost entirely black. Metepisternum black with a yellow band evenly narrowing from legs to antealar carina (as in Fig. 22), a small indistinct pale area in lower corner by antealar carina. Metepimeron yellow with poorly defined brown area centrally below metepleurale suture. Venter of synthorax yellow. Legs: each with coxa and trochanter yellow, femur mottled yellow and grey, black around joint with tibia, tibia and tarsi brown and black. Wings: 12 Px in Fw, 11 in Hw. Basal Ax strongly slanted in all wings. Vein ab present in right Fw where narrowly separated from ac, incomplete in left Fw and right Hw, absent in left Hw. Arculus slightly distal to Ax2. R4 arising distal to subnodus (at subnodus in right Hw), IR3 joined to it by a short stalk. Pterostigma trapezoidal with costal side shorter than anal side, strongly reddish brown with narrow pale border, covering just more than one underlying cell.

Abdomen: S1 mostly yellow laterally, brownish above. S2 brown above, yellowish below. S3–6 dark brown to black above, paler lower laterally on S3–4S, all with narrow pale basal annulus, poorly defined dorsally. S7–9 largely dark brown with indistinct reddish brown areas (Fig. 31 shows S8–10 of an identical male), S7 also with poorly defined pale basal annulus. S10 black. Anal appendages (Figs. 39, 40; 45 shows an identical male) largely dark brown and black, paler areas anteriorly on cerci apically and apices of paraprocts. Cerci ca 2.5 times length of S10, in lateral view (Fig. 39) broad at base then abruptly narrowing and forming small arch along lower margin before running approximately straight to near apex, bearing well developed dorsal spine at ca one-third length from base, directed upwards and rearwards. Apices of cerci shallowly bifurcated. Small apical dorsal interior projection visible in lateral view, continued anteriorly as ridge running onto lower arm of bifurcated apex (Fig. 40). Paraprocts slightly longer than cerci, broad at base, narrowing over their length, articulated at ca one-third of their length from base, apical part strap-like (as in Fig. 45), robust spine arising at base of strap-like section, directed inwards, upwards and slightly rearwards. Genital ligula (Fig. 28 shows that from a specimen from Miri Division, Sarawak but no differences are apparent) unremarkable, internal fold well developed, terminal segment with pair of apical arms, slightly convex between these, apices of arms expanded.

Measurements (mm): abdomen without anal appendages 31.5, cercus ca 0.9, Hw 20.

Female. Based on SAB12_PST17 (Fig. 49). As male except as noted below.

Head: Pale marking on labrum narrowly extended laterally (Fig. 4). Postclypeus entirely black.

Wings: 14 Px in Fw, 13 Px in Hw. Vein ab present in all wings, joined to ac by a short stalk.

Abdomen: Dorsum of S1–9 brown. S3–67 with indistinct yellowish lateral areas, these only apparent dorsally on S6–7, where diffuse and poorly defined. S10 dark brown. Cerci conical, a little shorter than S10, ovipositor extending distinctly further than tips of cerci, yellow and brown, styles missing (Fig. 36).

Measurements (mm): abdomen without anal appendages or ovipositor 30.5, Hw 23.

Remarks on variation. The greatest variation in colouration from the specimens described here, and the holotype, is in populations in Sarawak's Miri Division. These have bright red eyes in life, a reddish cast to the lower, pale parts of the thorax and the terminal abdominal segments in life, and pale markings on the labrum and clypeus strongly orange in males. Apart from the colour of the eyes, labrum and clypeus, these colour differences are barely apparent in preserved specimens (e.g. Figs. 50, 51 show specimens from red-eyed populations in Miri Division, but little difference is apparent compared with more typical specimens from Kapit Division shown in Figs. 48, 49). There is variation in the extent of pale colour on the labrum across all populations, often the pale marking is narrower and even broken into two parts; the postclypeus is normally completely black in both sexes. In a few females the pale mark on the labrum is reduced to a pair of small faint lateral marks immediately adjacent to the upper parts of the mandible bases. In females from south-east Sabah the pale marks on the labrum and anteclypeus are bluish. The anterior pronotal lobe is often more extensively black, and the dark areas centrally on the rear of the middle pronotal lobe are often larger. The brown area centrally below the metapleural suture is sometimes better defined and in some populations from central Sarawak it is always well defined and black; the abdomen is darker in the same populations, black dorsally from S1 in males and with the pale basal annuli on S3–6 not extending onto the dorsum. There is considerable variation in the colour of the legs, from femur largely pale with dark stripes on the extensor surfaces to femur much darker, and both paler and darker tibiae occur as well. Vein ab is typically present in all wings. The strap-like apical part of the paraprocts is curled to various degrees within all populations examined. There is considerable variation in size, particularly in males (see measurements below). This is largely correlated with altitude, with larger specimens occurring at higher altitudes.

Measurements (mm): males: abdomen without anal appendages 26–36, Hw 16–22, Px 12–14 in Fw, 11–13 in Hw; females: abdomen without anal appendages or ovipositor 28–32, Hw 20–23, Px 13–14 in Fw, 10–13 in Hw.

Other remarks. As in *D. kosterini* and *D. rufostigma*, the apical parts of the paraprocts of *D. actaeon* are strap-like (Figs. 39, 40, 41). However the apical part of the right paraproct is broken off in the holotype, and is glued to a card on the pin, the left paraproct has most of the strap broken off (and missing). Plainly this was the condition when Laidlaw (1934: Fig 3) illustrated the holotype, since in Laidlaw's illustration the paraproct appears shorter than it does in intact specimens. The genital ligula of the holotype is exposed and agrees with that illustrated in Fig. 28 here.

As noted above, populations in Sarawak's Miri Division have bright red eyes in life, which is not the case in the other known populations, and this had led me to wonder if they were a separate species. The locations of the red-eyed populations are shown

in red in Fig. 56; other populations in black. However there is no difference in the male anal appendages, nor in the structure of the genital ligula (checked in 13 individuals from populations across the known range of the species) between different populations. Additionally the Miri population is not distinguished from others using the standard DNA bar coding marker COI. Note that, given the high similarity between the sequences, it is highly unlikely that even if the same COI sequences were analysed using a phylogenetic method, the red-eyed populations would form a clade even slightly distinct from the rest. Although further investigation is desirable, the evidence available at this time supports treatment of the red-eyed populations as *D. actaeon* rather than as a separate species or subspecies.

The apparent variation in the apical parts of the male paraprocts is also a potential cause of confusion in *D. actaeon*, but examination of long series of specimens has shown that this is due to differences in the extent of curling of these strap-like structures and a wide range can be found within individual populations. It is worth noting that the pterostigma of *D. actaeon* is typically more red than that of *D. rufostigma*.

Although the type locality, Kabayau, is linked to Mount Kinabalu on the labels of the holotype, I have not been able to find any location with this name on the Kinabalu massif. There is a village called Kabayau approximately 37 km from the peak of Mount Kinabalu, near to Kota Kinabalu (based on coordinates obtained from <https://mapcarta.com/15883030>, accessed 19th February 2017; similar web-based services give similar coordinates); assuming that this information is accurate, it is possible that Pendlebury's route to Mount Kinabalu took him through or near present day Kabayau village, so the type locality might be in its vicinity. The specimens on which I have based my descriptions are from locations on the Kinabalu massif, so are reasonably close to topotypical if present day Kabayau is assumed to be the true type locality, and even closer if Pendlebury's location is actually somewhere on Mount Kinabalu.

Drepanosticta actaeon typically occurs at small, usually high gradient, forest streams in hilly terrain, from near sea level to at least 1200 m a.s.l. It is widely distributed in the north of Borneo (Fig. 56), occurring across Sabah and most of Sarawak, but has not, to date, been found west of the Lupar River. In Sarawak it becomes more common in the hilly and mountainous interior of the state. It can be expected to occur in Kalimantan, and is likely to occur in Brunei's Temburong District.

***Drepanosticta kosterini* sp. nov.**

(Figs. 1, 3, 5, 9, 13, 18, 19, 24, 25, 29, 32, 37, 41, 42, 46, 52, 53, 56)

Drepanosticta new species cf *actaeon*; — Dow 2012a: 3, 5; — Dow et al. 2016: 3.

Etymology: The species is named *kosterini*, a noun in the genitive case, after Oleg Kosterin, in recognition of his contributions to odonatology in south-east Asia.

Type material: Holotype. ♂ (SAR11_12_PST211, RMNH.INS.506815), small forest streams crossed by trail, Borneo Highlands Resort, Gunung Penrissen, Kuching Division, Sarawak, 22 vii 2012, leg. RAD, in RMNH. Paratypes. All from Borneo Highlands Resort,

Gunung Penrissen, Kuching Division, Sarawak, currently in collection RAD unless otherwise noted, others to be deposited in RMNH (those with an RMNH number already in RMNH), BMNH and the Sarawak Museum at a later date: ♂ (SAR11_12_PST255), small forest stream running onto golf course, 21 vii 2012, leg. RAD; ♂ (SAR13_14_PST233), same location, 28 vi 2014, leg. RAD; 1 ♂ (SAR15_PST109), 1 ♀ (SAR15_PST110), same location, 17 vii 2015, leg. RAD; 4 ♂ (SAR11_12_PST272-275; SAR11_12_PST209, RMNH.INS.506814), 1 ♀ (SAR11_12_PST276), location and date as holotype, leg. RAD; 1 ♂ (SAR11_12_PST14), 1 ♀ (SAR11_12_PST215), same location, 25 vii 2012, leg. RAD; 4 ♂ (SAR13_14_PST218-221), 2 ♀ (SAR13_14_PST222-223), same location, 29 vi 2014, leg. RAD; 3 ♂ (SAR11_12_PST277-279), 2 ♀ (SAR11_12_PST210, RMNH.INS.506817; SAR11_12_PST280), large forest stream running onto golf course, and its tributaries, 23 vii 2012, leg. RAD; 2 ♂ (SAR16_PST11-2), same location, 3 iii 2016, leg. RAD; 4 ♂ (SAR11_12_PST225-228), boulder-strewn high gradient forest stream, 24 vii 2012, leg. RAD; 1 ♂ (SAR13_14_PST224, RMNH.5008-433), forest stream below peak of Gunung Penrissen at 950-1100m, 2 vii 2014, leg. RAD; 1 ♂ (SAR15_PST38), small forest stream below peak of Gunung Penrissen, 14 vii 2015, leg. RAD; 1 ♀ (SAR15_PST32), same location, 15 vii 2015, leg. G.T. Reels.

Description of holotype male.

Head (Fig. 3): Labium pale except end hooks which are brown. Labrum pale orange, narrowly black along free margin. Anteclypeus and mandible bases pale orange, postclypeus black with poorly defined brownish areas centrally and to each side. Vertex and frons bronzy black, occiput and underside of head shining black. Ratio of width of compound eye to width of vertex measured at level of lateral ocelli ca 0.75. Transverse occipital carina with lateral extremities angulated, prominent. Ocelli whitish. Antenna with scape and pedicel brown, remainder missing.

Thorax: Propleuron almost entirely yellow. Anterior pronotal lobe black centrally, yellow to rear and lower laterally. Middle pronotal lobe almost entirely yellow except small darker area centrally at rear. Posterior lobe black, free margin rather abruptly raised to rear and laterally (Fig. 13). Synthorax: Mesepisternum entirely bronzy black. Antealar triangles black. Mesepimeron almost entirely black. Metepisternum black with a yellow band evenly narrowing from legs to antealar carina (Fig. 24), a small indistinct pale area in lower corner by antealar carina. Metepimeron yellow with poorly defined brown area centrally below metepleurale suture. Venter of synthorax yellow. Legs (left posterior and middle legs absent below trochanter, right posterior leg entirely absent): each with coxa and trochanter yellow, femur yellow adjacent to trochanter, becoming dirty yellow brown below, black around joint with tibia, tibia and tarsi mostly pale brownish. Wings: 14 Px in Fw, 13 in Hw. Right Fw with 3 Ax, basal Ax strongly slanted in all wings. Vein Ab present, joined to vein Ac at base. Arculus slightly distal to Ax2. R4 arising distal to subnodus, IR3 joined to it by a short stalk. Pterostigma trapezoidal with costal side shorter than anal side, strongly reddish brown with narrow pale border, covering slightly more than one underlying cell.

Abdomen: S1 mostly yellow laterally, brownish above. S2 brown above, yellowish below. S3-6 dark brown to black above, pale lower laterally on S3-4, all with narrow pale basal annulus, poorly defined dorsally. S7-9 dark brown with indistinct reddish

brown areas (Fig. 32 shows S8–10). S10 dark brown and black, paler brown lower laterally. Anal appendages (Figs. 41, 42, 46) largely dark brown and black, paler areas interiorly on cerci apically. Cerci ca 2.5 times length of S10, in lateral view (Fig. 41) broad at base then abruptly narrowing but then broadening slightly to form a small arch along lower margin, long dorsal spine present at ca one-third length from base, directed upwards and rearwards. Apices of cerci shallowly bifurcated. Small apical dorsal interior projection present, just visible in lateral view, continued interiorly as a ridge running towards lower arm of bifurcated apex. Paraprocts slightly longer than cerci, broad at base, narrowing over their length, apical part strap-like (Fig. 46), robust spine arising at base of strap-like section, directed inwards, upwards and slightly rearwards. Genital ligula (Fig. 29) with terminal segment deeply divided into a pair of arms from ca the level of the internal fold, arms expanded at apex.

Measurements (mm): abdomen without anal appendages 33, cercus ca 1, Hw 20.

Female. Based on SAR13_14_PST223, but illustrations made using SAR11_12_PST210 (identical in all significant respects), Figs. 18, 19 and 25 show the thorax, Fig. 53 the habitus of the female used for illustration. As male except as noted below.

Head (Fig. 5): Pale markings yellowish cream rather than orange, pale marking on labrum same in basal one third but then dark brown to free margin.

Wings: R4 at subnodus in 2 wings, 14 Px in Fw, 12 Px in Hw.

Abdomen: S3–6 with indistinct yellowish lateral areas in place of basal annuli, S7 brown, darkening to rear, S8–9 pale lower laterally in basal two-thirds, rest dark brown, S10 without paler area lower laterally. Cerci ca same length as S10, ovipositor extending distinctly further than tips of cerci, pale, styles dark brown, indistinct dark area lower centrally (Fig. 37).

Measurements (mm): abdomen without anal appendages or ovipositor 29, Hw 21.

Variation in paratypes. There is little variation apart from in size. In males the colouration of the postclypeus varies between completely dark brown/black to basally black with the remainder orange, R4 occasionally arises at the subnodus in one or more wings, in some individuals S7 has the same colouration as S3–6, S10 is sometimes completely dark. In females the extent of pale colour on the labrum varies from that seen in the male to just a pair of central marks in the basal one quarter, R4 is usually at least slightly distal to the subnodus in all wings and S3–6 are often paler brown. In males the strap-like terminal part of the paraprocts is curled to varying degrees, so that it appears variable.

Measurements (mm): Males: 13–14 Px in Fw, 11–13 Px in Hw, abdomen without anal appendages 30.5–36, Hw 20–22.5; females 13–14 Px in Fw, 11–13 Px in Hw, abdomen without anal appendages or ovipositor 29.5–31.5, Hw 21–22.

Diagnosis. The male of *D. kosterini* is easily separated from all other Bornean Platystictidae apart from *D. actaeon* and *D. rufostigma* by the following combination of characters: posterior pronotal lobe black or almost entirely black, without horns or lateral hanging lobes, synthorax without antehumeral markings, vein Ab present, reddish

pterostigma, terminal abdominal segments without blue dorsal markings, cerci without a tuft of long setae in their apical half, paraprocts with strap-like terminal parts. It is separated from *D. rufostigma* by the colour of the labrum (predominantly blue or bluish white in *D. rufostigma*), details of the anal appendages, e.g. the much less pronounced ventral basal arch of the cerci (compare Figs. 41 and 43), the longer dorsal spine and the shape of the apical part, and by the structure of the genital ligula, where the terminal segment is deeply divided in *D. kosterini*, but much less so in *D. rufostigma*. It is separated from *D. actaeon* by the longer dorsal spines on the cerci and, most convincingly, by the structure of the genital ligula, where it differs from *D. actaeon* in the same manner that it differs from *D. rufostigma* (compare the illustrations in Figs 28–30).

The female is separated from that of most other species (where the female is known) by the same combination of characters (where they apply to females) as the males. It is most easily separated from *D. rufostigma* by the colour of the labrum and clypeus, with pale markings yellowish cream (Fig. 5) rather than blue or bluish in *D. rufostigma* (Fig. 7). Separation from *D. actaeon* females, except by location, is problematic. Separation from the female of *D. forcifcula* Kimmins, 1936 is also problematic at present.

Remarks. *Drepanosticta kosterini* is clearly the sister species of *D. actaeon*, with which it shares similar colouration, prothorax structure and male anal appendages. The most notable difference between the two species is in the genital ligula; this was examined in three of the paratypes of *D. kosterini* as well as the holotype, and found to be identical in all. The known ranges of the two species are allopatric, and females of the two are difficult to separate except on the basis of location. However the two species are well separated in the COI marker (Fig. 1), so that identification using DNA barcoding should be straightforward.

At present *D. kosterini* is only known from Gunung Penrissen in south-west Sarawak, where it has been found at forest streams above 750m a.s.l (Fig. 56). Sampling has been conducted at the foot of Gunung Penrissen, at Annah Rais, without finding *D. kosterini* but no sampling at altitudes between Annah Rais and ca 750m a.s.l. has yet been conducted, and it is not known if the species is confined to higher altitudes. It should be looked for in the Bungo Range in Sarawak, which is close to Gunung Penrissen, and over the border with Indonesia on Gunung Niut in north-west Kalimantan.

***Drepanosticta rufostigma* (Selys, 1886)**

(Figs. 1, 6, 7, 10, 11, 14, 15, 20, 21, 26, 27, 30, 33, 34, 35, 38, 43, 44, 47, 54, 55, 57)

Platysticta rufostigma Selys Longchamps 1886: 155–156 (original description of holotype male from Labuan); — Laidlaw 1913: 79, plate IV, fig. 9 (Lawas).

Drepanosticta rufostigma (Selys, 1886); — Laidlaw 1920: 340; — Laidlaw 1924: 306 (discussion); — Hincks 1930: 52 (“Mt. Poi. Sarawak”); — Lieftinck 1933: 292–296, fig. 4 (description both sexes from material from north west Kalimantan, illustration of

male appendages); — Kimmins 1936: 98 (Mount Dulit); — Lieftinck 1954: 35, 177; — van Tol 1992: 198; — Matsuki & Kitagawa 1993: 3–4 (Mount Serapi); — Thompson & van Tol 1993: 59, 64, 69 (Sungai Ingei, Brunei); — Donnelly 1994: 126; — Kitagawa 1997: 5 (Sarawak); — Kitagawa et al. 1999: 81 (Tabin Wildlife Reserve, Sabah); — Orr 2001: 189 (Brunei); — Orr 2003: 21, 30, 31, 38, 70, 71, 72, 148, Figs. 23a, 24a, 88, Plate 6b (discussed, illustrations); — Dow 2005: 11; — Kalkman 2005: 14; — van Tol 2006: 13; — Dow & Reels 2008: 3; — Dow & Reels 2009: 13; — van Tol et al. 2009: 26, 27, 36, 64–65, 66, 67, 69, 70, Figs. 45–55; — Dow & Reels 2010: 15, 16, 17; — Norma-Rashid et al. 2010: 327; — Dow 2012a: 6, 9; — Dow 2012b: 9, 18, 20; — Dow & Ngiam 2012: 10, Fig. 10; — Dow & Reels 2013: 15; — Dow, Reels & Butler 2013a: 10; — Dow, Reels & Butler 2013b: 6, Fig. 7; — Dijkstra et al. 2014: Figs. 2, 3, Table S2; — Dow & Ngiam 2014: 26, 42, 43, 44; — Dow & Ngiam 2015: 13; — Dow, Reels & Ngiam 2015a: 4, 19; — Dow, Reels & Ngiam 2015b: 9; — Dow 2016a: 4; — Dow, Butler & Reels 2016: 4; — Luke et al. 2017: Table S2 (south-east Sabah).

Material examined. 1 ♂ (SAR11_12_PST374), stream at ca 200m on Gunung Pueh, Kuching Division, Sarawak, Malaysia, 4 x 2012, leg. R.A. Dow, in RMNH; 1 ♀ (SAR13_14_PST385), small streams accessed from trail up from Nattaran't Camp, same area, 700–920m, 31 vii 2013, leg. R.A. Dow, in collection Dow; 1 ♂ (SAR09_10_PST179), stream south of main peak of Gunung Kalulong, ca 750–930m, upper Baram, Miri Division, Sarawak, Malaysia, 7 x 2009, leg. RAD; 1 ♂ (SAR09_10_PST421), stream on lower slopes of Gunung Seludong, same area, 20 vii 2010, leg. W. Keding, in RMNH; 1 ♂ (SAB12_PST58), stream running into Bamboo Garden, Poring Hot Springs, Mount Kinabalu National Park, Sabah, Malaysia, 10 ix 2012, leg. R.A. Dow, in RMNH. Specimens listed in Dow 2012a, 2012b, 2016a, Dow, Butler & Reels 2016, Dow & Reels 2013, Dow, Reels & Butler 2013a, 2013b, Dow & Ngiam 2012, 2014, 2015, Dow, Reels & Ngiam 2015a, 2015b. Additional material, not previously published, is listed in the appendix.

Remarks. *Drepanosticta rufostigma* was described from a male labelled as from Labuan (Selys Longchamps 1886). However, since Labuan sometimes appears as the collecting locality on labels of specimens collected elsewhere in Borneo but shipped back to Europe from Labuan, it cannot be regarded as the true type locality with certainty. Lieftinck (1933) provided a redescription of the male, and a first description of the female, from specimens from the north-west of Kalimantan. Here I do not attempt a comprehensive treatment of this species, but provide a full set of illustrations and some brief notes on variation, habitat and distribution.

Drepanosticta rufostigma is rather variable in some features of its colouration, particularly in the male. Specimens from the western populations in Sarawak's Kuching and Samarahan Divisions, and north-west Kalimantan (based on the description in Lieftinck (1933)) often have blue marks laterally on abdominal segment 9 (Fig. 33), an extensive blue to bluish white area lower laterally on S8 and blue dorsally beyond the posterior carina on S8–9 (not apparent on the male illustrated in Fig. 33), whereas those from further east in Sarawak never have any blue on the abdomen (as in Fig. 35). However some specimens from Sabah have the area behind the posterior carina

of S9 bluish (as in Fig. 34) and a very few have lateral blue marks on S9. The extent of brown colour on the propleuron is variable (compare Figs 10 and 11) in all populations studied, although extensive brown here may be more common in the southwestern populations than others. The males studied by me have Hw 18–21mm, and abdomen without anal appendages 31–35mm; the females, correspondingly, Hw 19–22.5mm, abdomen with appendages or ovipositor 27–32mm. Variation in this species needs a more detailed analysis, but that is beyond the scope of this paper.

Lieftinck (1933) states that "it [*D. rufostigma*] is a rare and very local insect but apparently more frequently met with than any other member of the subfamily, in Borneo". The latter part of this statement is correct, at least in Sarawak, but this is generally a common species on streams in hilly and mountainous terrain in mixed and hill dipterocarp forest in Sarawak, and is more often encountered on low gradient streams and wider, less shaded streams than most other Bornean Platystictidae. Its apparent rarity was clearly an artefact of under-collecting and the fact that most collectors did not know where to look for Platystictidae until relatively recently. However, the rather limited data available does suggest that it might be scarcer in Sabah than in Sarawak; there is not enough data from Kalimantan to make any judgement about its scarcity or otherwise there. Orr (2001) states that it is "Common on small tributaries in primary mixed dipterocarp forest" in Brunei. It occurs to an altitude of at least 1100m. The known distribution of *D. rufostigma* is illustrated in Fig. 57.

Discussion

The *D. rufostigma*-group of species are not closely related to the true *Drepanosticta*, whose type species is the Himalayan *D. carmichaeli* (Laidlaw, 1915). The problems with the current taxonomy of the old world Platystictidae have been commented on elsewhere (for instance van Tol et al. 2009, Dow & Orr 2012 and Dijkstra et al. 2014) and need not be expanded upon here. A short discussion of the relationships of the *D. rufostigma*-group to the rest of the Platystictidae is warranted here, but this subject will be dealt with in greater depth elsewhere.

Recognising the issues with the classification of the Platystictidae, Orr (2003) divided the Bornean species into three or four groups, largely on the basis of colouration, independently of the genus that each was placed in at the time. *D. actaeon* and *D. rufostigma* were placed in his third group, which also included *D. forficula* and (implicitly) *D. attala* Lieftinck, 1934, *D. barbatula* Lieftinck, 1940 and *D. drusilla* Lieftinck, 1934; the latter three species are closely related to each other. Later Dow & Orr (2012a) considered that the closest relatives of *Telosticta* are *D. actaeon* and *D. rufostigma*, and *D. dulitensis* Kimmins, 1936, on the basis of the structure of the anal appendages of the male; the close relationship of the first two species to each other was also noted. *Drepanosticta barbatula* and its allies were considered more distantly related to *Telosticta* and *D. forficula* to be even more distantly related, but nothing was stated directly on their relationships to the *D. rufostigma*-group. Subsequently Dow & Orr (2012b) considered *D. attala*, *D. barbatula*, *D. drusilla* and *D. simuni* Dow & Orr, 2012, to form a natural grouping with *D. lestoides* (Brauer, 1868) from the Philippines. The molecular analyses presented in Dijkstra et al. (2014: Figs. 2 and 3)

suggest a closer relationship between the *D. rufostigma*-group and *D. lestoides* plus its close allies, than between the *D. rufostigma*-group and *Telosticta* plus *D. dulitensis*. In my view these molecular analyses are likely to reflect the true situation and the *D. rufostigma*-group is the sister of *D. lestoides* plus its allies from Borneo; this whole grouping is the sister of *Telosticta* plus *D. dulitensis*. The recently described *D. burbachi* is clearly the sister species of *D. dulitensis* (see Dow 2013), and so belongs in the *Telosticta* plus *D. dulitensis* group. Note that in Fig. 1, *D. attala* clusters with *D. dulitensis* rather than the *D. rufostigma*-group; this is due to the non-phylogenetic analysis method employed and the few taxa involved.

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Appendix: additional material of *Drepanosticta actaeon* and *Drepanosticta rufostigma* examined.

The author's name is abbreviated as RAD in the lists below, and specimens are currently in collection Dow unless otherwise noted. The code CUMZ is used for The University Museum of Zoology, Cambridge.

Drepanosticta actaeon

Sarawak, Malaysia: 3 ♂, tributaries to Sungai Engkari, Ulu Engkari, Lanjak Entimau Wildlife Sanctuary, Sri Aman Division, 14 vii 2016, leg. RAD; 1 ♀, same location, 15 vii 2016, leg. RAD; 2 ♂, tributary to Sungai Jela, same area, 18 vii 2016, leg. RAD; 2 ♂, stream below Ubah Ribu, Bukit Lanjak, same area, 19 vii 2016, leg. RAD; 3 ♂, Sungai Jik and tributaries, Nanga Bloh, Lanjak Entimau Wildlife Sanctuary, Kapit Division, 21 viii 2013, leg. RAD; 1 ♂, Sungai Satap and tributaries, same area, 23 viii 2013, leg. RAD; 4 ♂, 2 ♀, tributary to stream crossed by logging road at ca 900m, Gunung Melatai, Kapit Division, 8 ix 2015, leg. RAD; 1 ♂, stream crossed by logging road at ca 1000m, same mountain, 1000–1260m, 10 ix 2015, leg. M. Budi; 1 ♀, same location, 11 ix 2015, leg. RAD; 2 ♂, same location, 12 ix 2015, leg. M. Budi; 1 ♂, small hillside stream, Kastima Logging area, Belaga, Kapit Division, 450–540m, 23 vi 2016, leg. RAD; 4 ♂, ♀, stream on lower slopes Bukit Kana, Bintulu Division, 26 iii 2012, leg. RAD, 1 in RMNH (RMNH.INS.506253); 1 ♂, same location and date, leg. O. Tateh; 4 ♂, ♀, same location, 27 iii 2012, leg. RAD; 1 ♂ (RMNH.INS.506863), same location and date, leg. B. Gimán & N. Megom, in RMNH; 4 ♂, 1 ♀, same location and date, leg. O. Tateh; 3 ♂, stream south of main peak of Gunung Kalulong, upper Baram, Miri Division, ca 750–930m, 18 xii 2007, leg. RAD; 1 ♂, same data but leg. G.T. Reels; 1 ♂ (RMNH.INS.228955, in ethanol), same location, 19 xii 2007, leg. G.T. Reels, in RMNH; 4 ♂, 2 ♀, same location, 7 x 2009, leg. RAD; 1 ♂ (RMNH.INS.503664, in ethanol), same location, 8 x 2009, leg. RAD, in RMNH; 9 ♂, 1 ♀, same location and date, leg. L. Southwell; 4 ♂, 10 x 2009, leg. L. Southwell; 1 ♀, stream southeast of main peak of Gunung Kalulong, same area, ca 600–700m, 6 x 2009, leg. RAD; 2 ♂, stream east of main peak of Gunung Kalulong, same area, ca 750–800m, 17 vii 2010, leg. RAD, 1 in RMNH (RMNH.INS.503453); 3 ♂, stream northeast of Gunung Kalulong, same area, ca 310m, 20 vii 2010, leg. RAD; 1 ♂, same data but leg. L. Southwell; 1 ♀, stream at foot of Gunung Kalulong, same area, 21 vii 2010, leg. RAD; 1 ♂ (RMNH.INS.503455), same location and date, leg. W. Keping, in RMNH; 1 ♂, stream southeast of Lio Mato, upper Baram, Miri Division, 13 x 2009; leg. RAD; 1 ♂, stream in disturbed forest, Sungai Lamah, mid Baram, Miri Division, 9 ii 2015, leg. RAD; 1 ♂, Stream below Camp 1, foot of Gunung Mulu, Gunung Mulu National Park, Miri Division, 1 v 2014, leg. P.O.M. Steinhoff, in collection Steinhoff; 2 ♂, Camp 2 stream system, same area, 22 iv 2005, leg. RAD; 1 ♂, 1 ♀, same location, 6 i 2008, leg. RAD; 2 ♂, 1 ♀ (in tandem with one of the males), same location, 11 ix 2008, leg. RAD; 1 ♂, same location, 18 vi 2014, leg. P.O.M. Steinhoff, in collection Steinhoff.

Sabah, Malaysia: 1 ♂, Kipungit stream system, Poring Hots Springs, Kinabalu National Park, 11 ix 2012, leg. RAD; 1 ♂, Langanan stream system, same area, 12 ix 2012, leg.

RAD; 2 ♂, stream running into Bamboo Garden, same area, 10 ix 2012, leg. RAD, 1 in RMNH (RMNH.INS.507659); 3 ♂, 1 ♀, Sungai Kemantis and tributaries, Sayap Station, Mount Kinabalu, same national park, 14 ix 2012, leg. RAD; 1 ♂ (RMNH.INS.507719), same data but in RMNH; 2 ♂, same location, 15 ix 2012, leg. RAD; 2 ♂, Sungai Lumotok Besar, same area, 15 ix 2012, leg. RAD; 2 ♂, Sungai Lumotok Kecil, same area, 16 ix 2016, leg. RAD; 1 ♂, stream near Maliau Basin Field Centre, 8 viii 2014, leg. RAD, to be deposited in CUMZ; 1 ♂, same location and date, leg. S. Luke, to be deposited in CUMZ; 2 ♂, stream, SAFE project, 13 viii 2014, leg. RAD, to be deposited in CUMZ; 3 ♂, 2 ♀, stream in "virgin forest" reserve, same project, 14 viii 2014, leg. RAD, to be deposited in CUMZ; 3 ♂, same location and date, leg. Siun, to be deposited in CUMZ; 1 ♂, 1 ♀, upstream on stream at SAFE camp, same project, 15 viii 2014, leg. RAD, to be deposited in CUMZ.

Drepanosticta rufostigma

Sarawak, Malaysia: 1 ♂, water pipe stream, Pueh Ranger Post, foot of Gunung Pueh, Samunsam Wildlife Sanctuary, Kuching Division, 8 viii 2016, leg. RAD; 1 ♂, Nattaran't Camp stream, Gunung Pueh range, Kuching Division, 29 vii 2013, leg. RAD; 1 ♂, 1 ♀, same location, 1 viii 2013, leg. RAD; 1 ♂, same location and date, leg. R.W.J. Ngiam; 5 ♂, 1 ♀, same location and date, leg. J. Sujang; 3 ♂, same location and date, leg. R. Sujang; 3 ♂, small streams accessed from trail up from Nattaran't Camp, same area, 700-920m, 31 vii 2013, leg. RAD; 1 ♂, same location and date, leg. Gidi; 3 ♂, same location and date, leg. R.W.J. Ngiam; 2 ♂, same location and date, leg. J. Sujang; 2 ♂, stream by View Point Trail, Gunung Gading National Park, Kuching Division, 31 vii 2016; leg. RAD; 1 ♀, trailside on View Point Trail, same area and date, leg. RAD; 2 ♂, stream accessed from Summit Trail on far side of summit to park headquarters, same area, ca 650m, 1 viii 2016, leg. RAD; 4 ♂, streams crossed by Lintang Trail, same area, 2 viii 2016, leg. RAD; 3 ♂, 1 ♀ (found dead in spider web), last stream crossed by Summit Trail, ca 320-420m, same area, 3 viii 2016, leg. RAD; 2 ♂, small streams at waterfall 3, same area, 4 viii 2016, leg. RAD; 1 ♂, tributary to Sungai Rayu, Matang Wildlife Center, Kubah National Park, Kuching Division, 4 i 2015, leg. RAD; 1 ♀, stream on Mount Matang, Matang Range, same area, 5 vii 2015, leg. RAD; 3 ♂, forest streams on Gunung Santubong, Gunung Santubong National Park, Damai Peninsula, Kuching Division, 25 vii 2013, leg. RAD; 8 ♂, hillside stream, Ulu Sebuyau area, Samarahan Division, 7 vii 2015, leg. RAD; 6 ♂, same location, 9 vii 2015, leg. G.T. Reels; 2 ♂, same location and date, leg. L. Southwell; 1 ♂, tributaries to Sungai Engkari, Ulu Engkari, Lanjak Entimau Wildlife Sanctuary, Sri Aman Division, 14 vii 2016, leg. RAD; 2 ♂, same location and date, leg. G.T. Reels; 1 ♂, same location, 15 vii 2016, leg. RAD; 3 ♂, same location and date, leg. G.T. Reels; 2 ♂, tributary to Sungai Segerak, same area, 17 vii 2016, leg. RAD; 3 ♂, 1 ♀, same location, 21 vii 2016, leg. G.T. Reels; 1 ♂, Sungai Jela and tributaries, same area, 18 vii 2016, leg. RAD; 1 ♂, 1 ♀, same location and date, leg. G.T. Reels; 2 ♂, same location, 19 vii 2016, leg. G.T. Reels; 1 ♂, stream below Ubah Ribu, ca 650-700m, Bukit Lanjak, same area, 19 vii 2016, leg. RAD; 2 ♂, Sungai Segak Mit, Ulu Mujok, Lanjak Entimau Wildlife Sanctuary, Sarikei Division, 30 vii 2015, leg. RAD; 1 ♂, same location, 17 viii 2016, leg. B. Megong &

N. Mengiring; 1 ♂, Sungai Segak Besai, same area, 14 viii 2016, leg. RAD; 1 ♂, Sungai Selabi, same area, 1 viii 2015, leg. RAD; 1 ♂, Sungai Sengkadan, same area, 16 viii 20116, leg. R.W.J. Ngiam; 2 ♂, same location, 19 viii 2016, leg. RAD; 1 ♂, Sungai Sepulau Mit, same area, 18 viii 2016, leg. R.W.J. Ngiam; 1 ♂, streams at Bukit Tanggan, same area, 19 viii 2016, leg. R.W.J. Ngiam; 1 ♂, 1 ♀, Sungai Ju and tributaries, same area but outside of Lanjak Entimau Wildlife Sanctuary, 2 viii 2015, leg. RAD; 1 ♂, Sungai Lingga, same area, 5 viii 2015, leg. RAD; 1 ♂, small stream at Nanga Bloh Field Station, Lanjak Entimau Wildlife Sanctuary, Kapit Division, 20 viii 2013, leg. J. Awan, M. Adu & A. Pasang; 3 ♂, same location and date, leg. RAD; 4 ♂, same location, 12 iii 2016, leg. RAD; 1 ♂, Sungai Jik and tributaries, same area, 21 viii 2013, leg. RAD; 3 ♂, Sungai Satap and tributaries, same area, 23 viii 2013, leg. RAD; 2 ♂, same location, 16 iii 2016, leg. RAD; 2 ♂, Sungai Kelimau and tributaries, same area, 24 viii 2013, leg. RAD; 1 ♂, Sungai Pemanca, same area, 24 viii 2013, leg. J. Awan & M. Adu; 1 ♂, same location, 13 iii 2016, leg. RAD; 1 ♂, Sungai Gindi and tributaries, same area, 9 iii 2016, leg. RAD; 2 ♂, Sungai Nyungan and tributaries, same area, 14 iii 2016, leg. RAD; 2 ♂, Sungai Menyarin and tributaries, same area, 15 iii 2016, leg. RAD; 3 ♂, tributary to Sungai Bloh, 25 viii 2013, leg. RAD; 1 ♂, small streams, Nanga Gaat area, Kapit Division, 5 ix 2015, leg. M. Budi; 2 ♂, stream in same area, 5 ix 2015, leg. RAD; 2 ♂, stream reached using junction on main logging road near to Nanga Gaat gate, same area, 6 ix 2015, leg. RAD; 1 ♂, stream crossed by logging road at ca 1000m, Gunung Melatai, Kapit Division, 1000–1260m, 12 ix 2015, leg. RAD; 1 ♂, stream near camp site, same area, 13 ix 2015, leg. RAD; 1 ♂, Sungai Kayan and tributaries, Kastima Logging area, Belaga, Kapit Division, 21 vi 2016, leg. RAD; 1 ♂, Sungai Pesun and tributaries, same area, 22 vi 2016, leg. RAD; 2 ♂, 1 ♀, small hillside stream, 450–540m, same area, 23 vi 2016, leg. RAD; 3 ♂, tributaries to Sungai Sawih, Anap Muput, Bintulu Division, 17 xi 2010, leg. RAD, one in RMNH; 2 ♂, stream in Anap Muput area, 18 xi 2010, leg. RAD; 1 ♂, Sungai Sebalang, same area, 19 xi 2010, leg. RAD; 1 ♂, same location, 20 xi 2010, leg. RAD; 1 ♂, Bukit Setiam, Bintulu Division, 31 i 2008, leg. RAD; 1 ♂, stream on lower slopes Bukit Kana, Bintulu Division, 26 iii 2012, leg. RAD; 2 ♂, same location, 27 iii 2012, leg. RAD; 2 ♂, same location and date, leg. B. Gimán & N. Megom; 1 ♂, same location and date, leg. O. Tateh; 1 ♂, stream system in block A1M, Sarawak Planted Forest Project, Bintulu Division, 25 iii 2012, leg. RAD; 1 ♂, same location and date, leg. O. Tateh; 3 ♂, 1 ♀, stream system in Block T1F, Samarakan area, Sarawak Planted Forest Project, Bintulu Division, 21 viii 2009, leg. RAD; 1 ♂, same location, 5 v 2011, leg. RAD; 2 ♂, same location and date, leg. L. Joseph; 2 ♂, same location and date, leg. O. Tateh; 1 ♂, stream in block K2L, Sarawak Planted Forest Project, Bintulu Division, 26 x 2010, leg. RAD; 1 ♂, same location and date, leg. S. Stone; 4 ♂, stream system on Bukit Mina, Bukit Mina Wildlife Corridor, Sarawak Planted Forest Project, Bintulu Division, 23 i 2008, leg. RAD; 3 ♂, 2 ♀, same location, 23 x 2008, leg. RAD; 1 ♂, same location and date, leg. B. Gimán & N. Megom; 7 ♂, same location, 1 v 2011, leg. L. Joseph; 3 ♂, same location and date, leg. O. Tateh; 1 ♂, 20 iii 2014, leg. RAD; 1 ♀, same location and date, leg. O. Tateh; 1 ♂, stream on steep ridge in block T2C in Bukit Mina Wildlife Corridor, Sarawak Planted Forest Project, Bintulu Division, 22 iii 2014, leg. RAD; 3 ♂, same location and date, leg. O. Tateh; 3 ♂, high gradient stream system in Bukit Mina Wildlife Corridor, Sarawak Planted

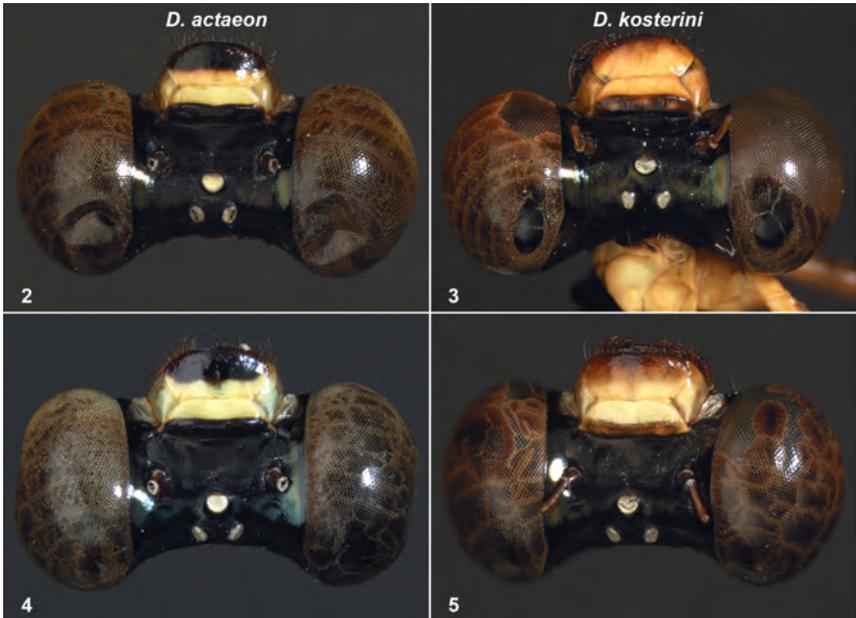
Forest Project, Bintulu Division; 26 iii 2014, leg. RAD; 1 ♂, same location and date, leg. B. Gimán; 1 ♂, same location and date, leg. O. Tateh; 1 ♂, same location, 28 iii 2014, leg. RAD; 6 ♂, 1 ♀, same location and date, leg. B. Gimán; 1 ♂, same location, 3 ix 2014, leg. RAD; 2 ♂, same location and date, leg. B. Gimán; 1 ♂, same location and date, leg. N. Megom; 1 ♂, Bukit Jugam, Bukit Mina Wildlife Corridor, Sarawak Planted Forest Project, Bintulu Division, 24 viii 2009, leg. RAD; 1 ♂, same location, 4 ix 2014, leg. B. Gimán; 3 ♂, stream system near Kemena Camp, Tubau, Sarawak Planted Forest Project, Bintulu Division, 19 i 2008, leg. RAD; 2 ♂, same location, 18 x 2008, leg. RAD; 5 ♂, stream system in disturbed forest, same area, 17 viii 2009, leg. RAD, one in RMNH; 3 ♂, same location and date, leg. O. Tateh & S. Stone; 3 ♂, streams in block E2N, Tubau, Sarawak Planted Forest Project, Bintulu Division, 19 x 2008, leg. RAD; ♂, same location, 20 x 2008, leg. O. Tateh; 2 ♂, 1 ♀, same location, 16 viii 2009, leg. RAD; 3 ♂, 1 ♀, same location, 31 viii 2009, leg. RAD; 2 ♂, same location and date, leg. O. Tateh; 3 ♂, same location, 2 ix 2009, leg. O. Tateh; 1 ♂, same location, 10 vi 2010, leg. RAD; 2 ♂, same location, 12 vi 2010, leg. O. Tateh; 3 ♂, 1 ♀, same location, 15 vi 2010, leg. RAD; 5 ♂, same location and date, leg. O. Tateh; 1 ♂, stream system close to last location, same area, 14 vi 2010, leg. RAD; 1 ♂, same location, 16 vi 2010, leg. RAD; 1 ♂, same location and date, leg. O. Tateh; 1 ♂, Sungai Segan and tributaries, Bintulu Division, 21 iii 2014, leg. B. Gimán; 1 ♂, stream on Circular Trail, Similajau National Park, Bintulu Division, 2 ii 2008, leg. RAD; 1 ♂, same location and date, leg. G.T. Reels; 1 ♂, Sungai Suan, Samling Timber Company road between Lapok and Samling Baram Base Camp, mid Baram, Miri Division, 11 xii 2007, leg. G.T. Reels; 1 ♂, stream south of main peak of Gunung Kalulong, upper Baram, Miri Division, ca 750–930m, 17 xii 2007, leg. RAD; 4 ♂, same location, 18 xii 2007, leg. RAD; 1 ♂, same location and date, leg. G.T. Reels; 5 ♂, same location, 19 xii 2007, leg. G.T. Reels; 1 ♂, same location, 7 x 2009, leg. RAD; 3 ♂, 1 ♀ (in tandem with one of the males), same location, 8 x 2009, leg. RAD; 4 ♂, 1 ♀, same location and date, leg. L. Southwell; 6 ♂, 2 ♀, stream east of main peak of Gunung Kalulong, same area, 700–800m, 17 vii 2010, leg. RAD; 2 ♂, same location and date, leg. M. Kibi; 1 ♂, stream west of main peak of Gunung Kalulong, same area, ca 700–900m, 18 vii 2010, leg. RAD; 4 ♂, stream in Gunung Kalulong area, 21 vii 2010, leg. RAD; 1 ♂, same location and date, leg. W. Kebin; 7 ♂, same location and date, leg. M. Kibi; 2 ♂, 1 ♀, same location and date, leg. L. Southwell; 7 ♂, stream on lower slopes of Gunung Seludong, same area, 20 vii 2010, leg. RAD; 1 ♂, same location and date, leg. L. Southwell; 2 ♂, stream system on north face Batu Uro', same area, 16 vii 2010, leg. RAD; 1 ♂, stream north of Gunung Kalulong, same area, 14 vii 2010, leg. RAD; 3 ♂, Sungai Tamdoh and tributaries, same area, 15 vii 2010, leg. RAD; 3 ♂, small tributary of Sungai Silat, near confluence with Baram River, same area, 9 vii 2014, leg. RAD; 2 ♂, 1 ♀, mini hydro stream system near Lio Mato, upper Baram, Miri Division, 12 x 2009, leg. RAD; 1 ♂, stream southeast of Lio Mato, same area, 13 x 2009; leg. RAD; 1 ♂, tributary of Sungai Tudan just above confluence with Baram River not far upstream from Lio Mato, same area, 7 vii 2012, leg. L. Southwell; 6 ♂, tributary to Sungai Aro Lano above waterfall, Long Banga Water Catchment area, upper Baram, Miri Division, 16 xii 2007, leg. RAD; 1 ♂, same location and date, leg. G.T. Reels; 2 ♂, same location and date, leg. L. Southwell; 3 ♂, Sungai Lamah and tributaries, mid Baram, Miri Division, 9 ii 2015, leg. RAD; 3 ♂,

1 ♀, same location, 10 ii 2015, leg. RAD; 3 ♂, 1 ♀, small streams near Pantu waterfall, Lambir Hills National Park, 11 v 2005, leg. RAD; 1 ♂, same location, 15 v 2005, leg. RAD; 3 ♂, 1 ♀, same location, 1 ii 2006, leg. RAD; 1 ♂, same location and date, leg. G.T. Reels; 4 ♂, stream system beyond Pantu system on main trail, same area, 2 ii 2006, leg. RAD; 2 ♂, stream below Nibong waterfall, same national park, 22 xii 2007, leg. RAD; 4 ♂, stream on Oil Well Trail, same national park, 22 iv 2011. Leg. RAD; 2 ♂, Latak stream, same national park, 24 iv 2011, leg. L. Southwell; 1 ♂, tributary to Sungai Liku, Lambir Hills National Park Extension, same area, 16 vii 2012, leg. L. Southwell; 1 ♂, Bat Observatory stream, Gunung Mulu National Park, Miri Division, 16 iv 2005, leg. RAD; 1 ♂, same location, 5 ii 2006, leg. G.T. Reels; 1 ♂, same location, 24 xii 2007, leg. RAD; 1 ♂, stream at Camp 1, foot of Gunung Mulu, same national park, 21 iv 2005, leg. RAD; 1 ♂, stream system in "Garden of Eden", same national park, 6 ii 2006, leg. RAD; 2 ♂, first stream system on old trail to Sarawak Chamber, same national park, 11 i 2008, leg. RAD; 2 ♂, second stream system on old trail to Sarawak Chamber, same national park, 7 i 2008, leg. RAD; 6 ♂, 1 ♀, same location and date, leg. L. Southwell; 2 ♂, same location, 13 i 2008, leg. L. Southwell; 3 ♂, same location, 10 ix 2008, leg. J. Simun; 1 ♀, trickle beside Summit Trail near Camp 1, same national park, 4 i 2008, leg. RAD; 1 ♂, 1 ♀, streams off trail system below Camp 2, lower slopes of Gunung Mulu, same national park, 5 i 2008, leg. L. Southwell; 2 ♂, 1 ♀, Camp 2 stream system, lower slopes of Gunung Mulu, same national Park, 22 iv 2005, leg. RAD; 1 ♂, same location, 19 ii 2006, leg. RAD; 1 ♂, same location and date, leg. L. Southwell; 1 ♀, 6 i 2008, leg. RAD; 1 ♂, same location, 12 i 2008, leg. RAD; 1 ♂, 11 ix 2008, leg. J. Simun; 6 ♂, 1 ♀, stream and tributaries, Long Lansat, same national park, 19 iv 2005, leg. RAD; 5 ♂, same location, 8 ii 2006, leg. RAD; 2 ♂, same location and date, leg. G.T. Reels; 3 ♂, same location, 26 xii 2007, leg. RAD; 2 ♂, same location, 9 i 2008, leg. RAD; 1 ♂ (feneral), same location and date, leg. L. Southwell.

Sabah, Malaysia: 2 ♂. Kibambangan waterfall stream system, Inobong, Crocker Range National Park, 18 ix 2012, leg. RAD; 2 ♂, 1 ♀, same location, 19 ix 2012, leg. RAD; 2 ♂, same location, 21 ix 2012, leg. RAD; 2 ♂, 1 ♀, Batu Dinding stream system, same area, 20 ix 2012, leg. RAD; 2 ♂, small streams on Langanan waterfall trail, Poring Hot Springs, Mount Kinabalu National Park, 11 ix 2012, leg. RAD.

Brunei: 1 ♂, Wasai Tanai stream system, Labi Hills, Belait District, 28 v 2013, leg. RAD; 1 ♂, Sungai Ingei Kiri and tributaries, Sungai Ingei, Belait District, 2 iii 2014, leg. RAD.

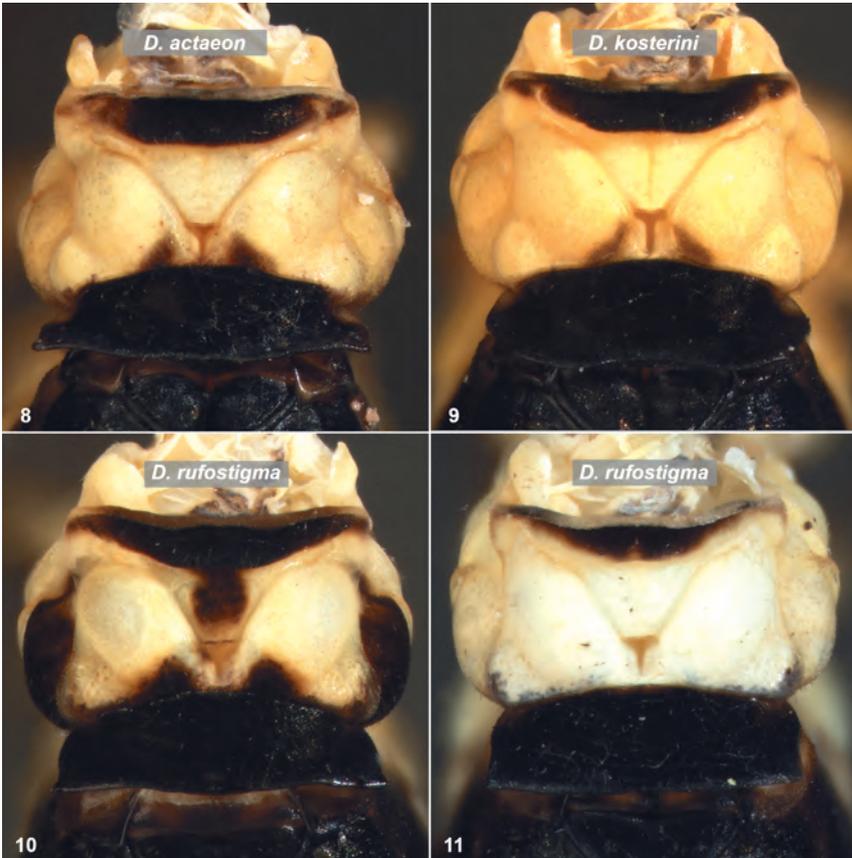
Figures



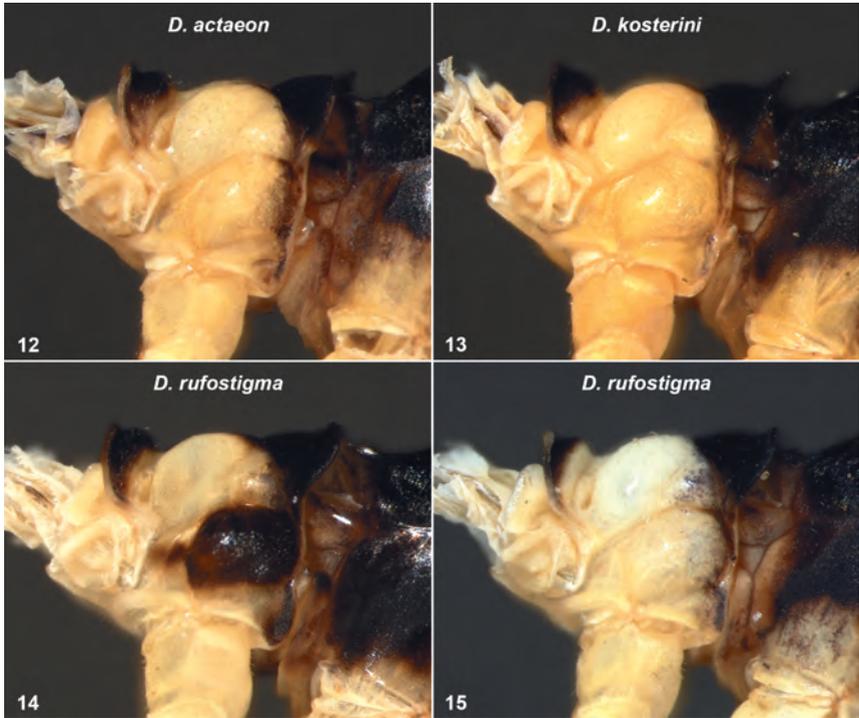
Figures 2–5. Male head dorsal-frontal: (2) *D. actaeon* SAB12_PST81, Poring; (3) *D. kosterini* holotype male. Female head dorsal-frontal: (4) *D. actaeon* SAB12_PST17, Sayap; (5) *D. kosterini* paratype SAR11_12_PST210.



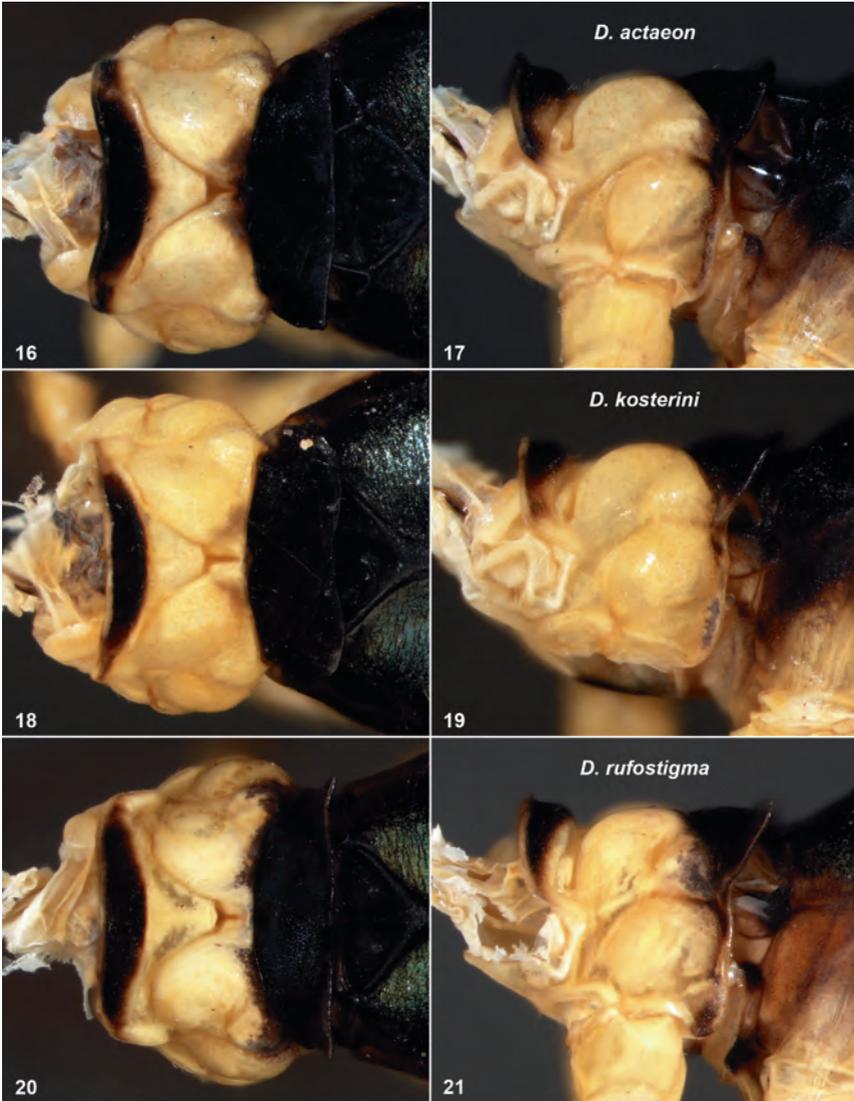
Figures 6–7. Dorsal view of head of *D. rufostigma*: (6) male SAR11_12_PST374, Gunung Pueh; (7) female SAR13_14_PST385, Gunung Pueh.



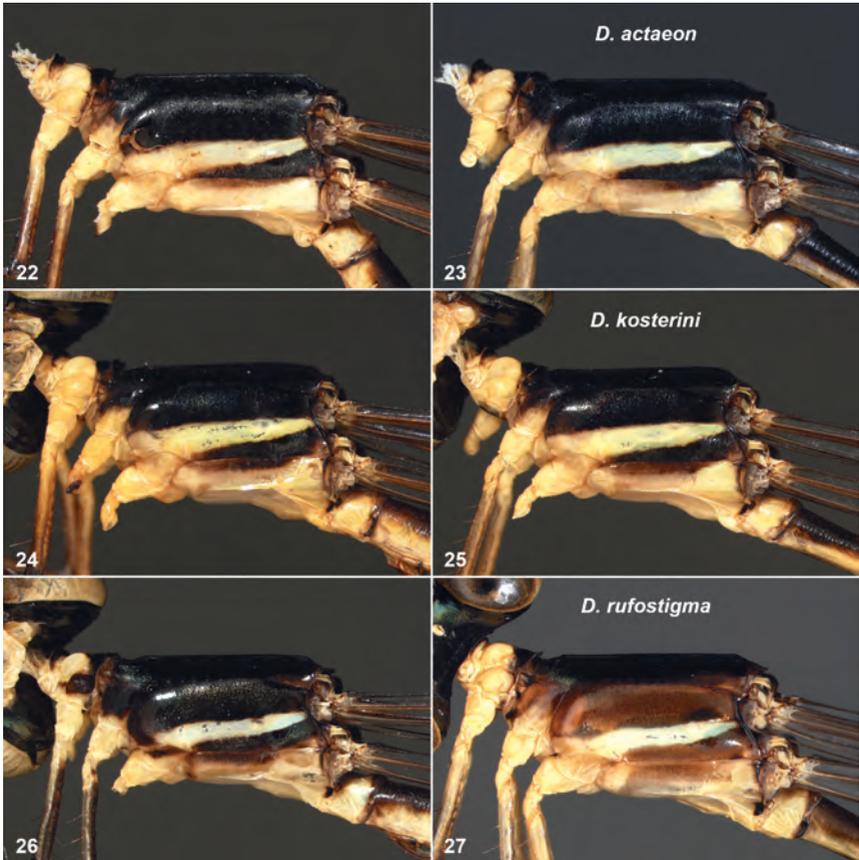
Figures 8–11. Male prothorax dorsal: (8) *D. actaeon* SAB12_PST81, Poring; (9) *D. kosterini* holotype male; (10) *D. rufostigma* SAR11_12_PST374, Gunung Pueh; (11) *D. rufostigma* SAB12_PST58, Poring.



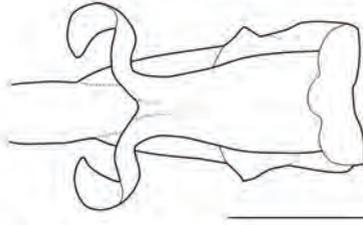
Figures 12–15. Male prothorax lateral: (12) *D. actaeon* SAB12_PST81, Poring; (13) *D. kosterini* holotype male; (14) *D. rufostigma* SAR11_12_PST374, Gunung Pueh; (15) *D. rufostigma* SAB12_PST58, Poring.



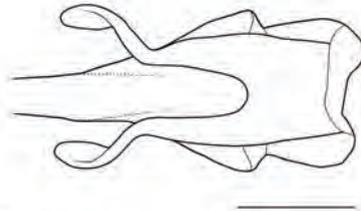
Figures 16–21. Female prothorax. *D. actaeon* SAB12_PST17, Sayap: (16) dorsal; (17) lateral. *D. kosterini* paratype SAR11_12_PST210: (18) dorsal; (19) lateral. *D. rufostigma* SAR13_14_PST385, Gunung Pueh (20) dorsal; (21) lateral.



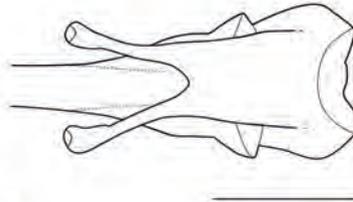
Figures 22–27. Synthorax lateral (males on the left, females on the right): (22) *D. actaeon* male SAB12_PST81, Poring; (23) *D. actaeon* female SAB12_PST17, Sayap; (24) *D. kosterini* holotype male. (25) *D. kosterini* female paratype SAR11_12_PST210; (26) *D. rufostigma* male SAR11_12_PST374, Gunung Pueh; (27) *D. rufostigma* female SAR13_14_PST385, Gunung Pueh.

D. actaeon

28

D. kosterini

29

D. rufostigma

30

Figures 28–30. Genital ligula, ventral view, all scale bars 0.2mm: (28) *D. actaeon* SAR-07_8_PST196, Gunung Mulu; (29) *D. kosterini* holotype male; (30) *D. rufostigma* SAR11_12_PST374, Gunung Pueh.

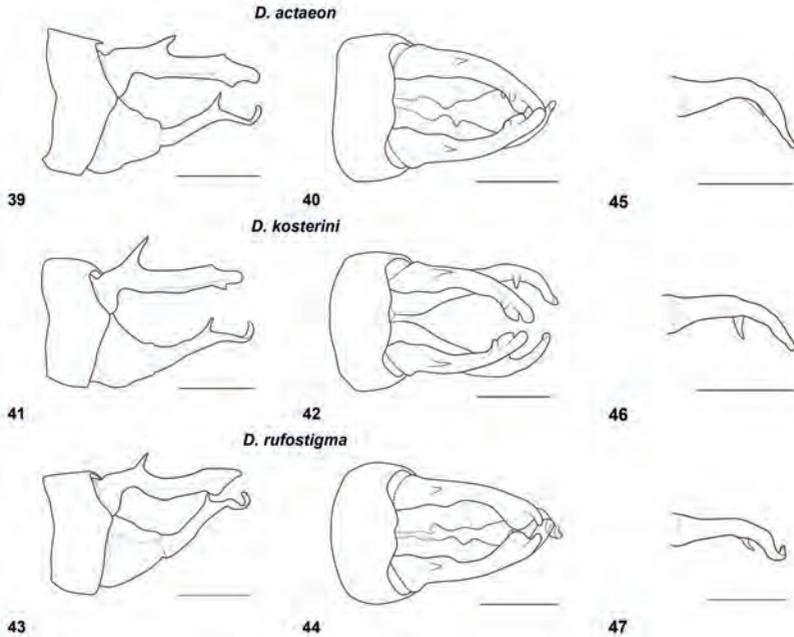


Figures 31–32. Male terminal abdominal segments lateral: (31) *D. actaeon* SAB12_PST81, Poring; (32) *D. kosterini* holotype male.



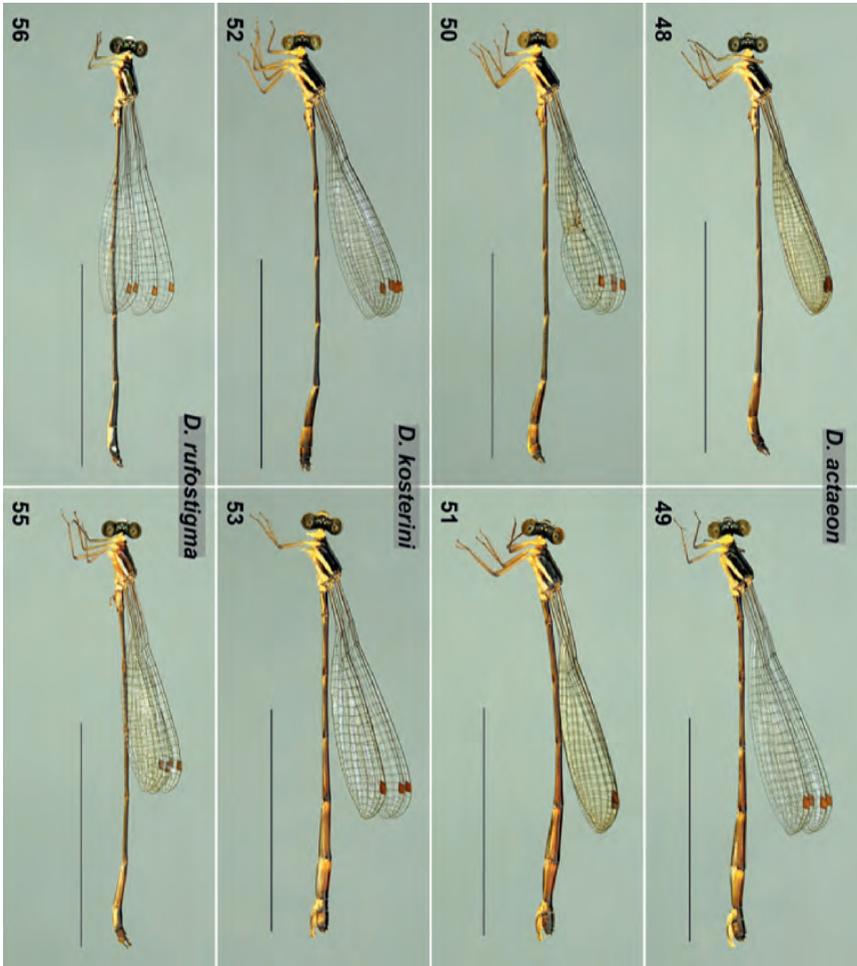
Figures 33–35. Male terminal abdominal segments of *D. rufostigma*: (33) SAR11_12_PST374, Gunung Pueh, lateral view; (34) *D. rufostigma*, SAB12_PST17, Sayap; (35) SAR09_10_PST179, paratype SAR11_12_PST210; Gunung Kalulong, dorsal view.

Figures 36–38. Female terminal abdominal segments lateral: (36) *D. actaeon* Gunung Pueh, lateral view; (37) *D. kosterini* Poring, lateral view; (38) *D. rufostigma* SAR13_14_PST385, Gunung Pueh.



Figures 39–44. Male anal appendages, all scale bars 0.5mm. *D. actaeon* SAB-12_PST12, Poring; (39) lateral; (40) dorsal. *D. kosterini* holotype: (41) lateral; (42) dorsal. *D. rufostigma* SAR11_12_PST374, Gunung Pueh; (43) lateral; (44) dorsal.

Figures 45–47. Apical part left male paraproct in ventral view, all scale bars 0.5mm (45) *D. actaeon* SAB12_PST80, Poring; (46) *D. kosterini* holotype; (47) *D. rufostigma* SAR11_12_PST374, Gunung Pueh.



Figures 48–55. Habitus of *D. rufostigma*-group species; all scale bars 20mm. (48) *D. actaeon* male SAR07_8_PST130, Kapit, Sarawak; (49) *D. actaeon* female SAB12_PST68, Sayap, Sabah; (50) *D. actaeon* red-eyed male SAR07_8_PST231, Gunung Mulu, Sarawak; (51) *D. actaeon* red-eyed female SAR09_10_PST158, Gunung Kalulong, Sarawak; (52) *D. kosterini* paratype male SAR13_14_PST233; (53) *D. kosterini* paratype female SAR12_12_PST210; (54) *D. rufostigma* male SAR11_12_PST374, Gunung Pueh, Sarawak; (55) *D. rufostigma* male SAR09_10_PST421, Gunung Kalulong, Sarawak.

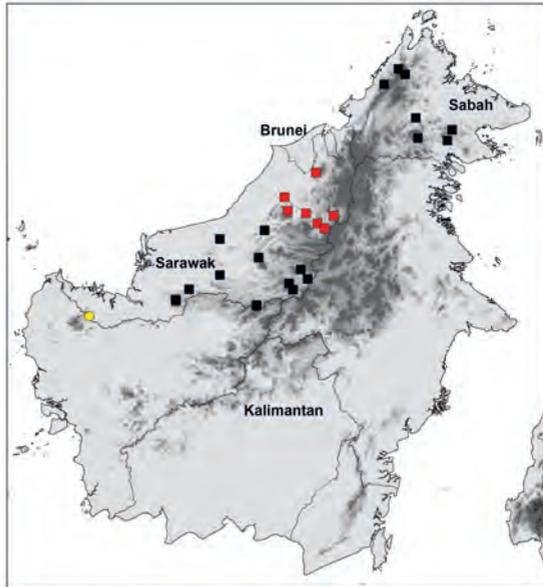


Figure 56. Distributions of *Drepanosticta actaeon* and *D. kosterini*. Squares: *D. actaeon*; black squares are typical populations, red squares the red-eyed populations. Yellow circle: *D. kosterini*.

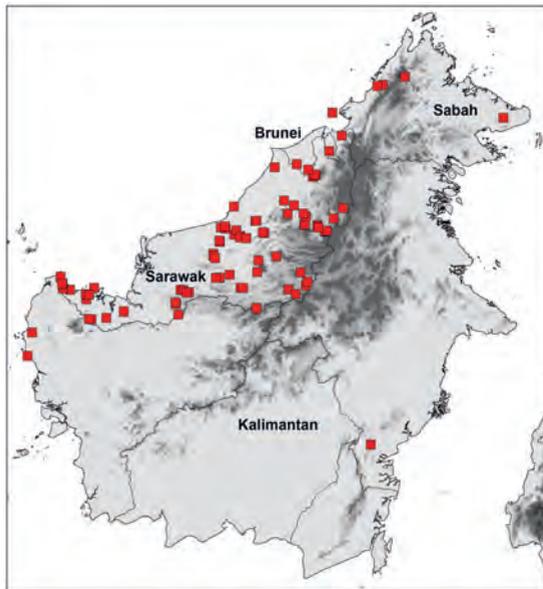


Figure 57. Distribution of *Drepanosticta rufostigma*.

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