

## Dragonflies and damselflies (Odonata) from Flores Island, Lesser Sunda Archipelago: New occurrences in extreme environments and an island-level checklist of this group

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### Abstract

Although the Odonata are common inhabitants of various extreme environments such as geothermal springs, brackish wetlands, mangroves, and volcanic lakes, the assemblages of this group associated with extreme habitats in Australasia are rather poorly known. Here, we combine museum collection data and published reports on Odonata from extreme habitats on Flores Island, Lesser Sunda Archipelago. The highly acidic Sano Nggoang Crater Lake (mean pH = 3.17) on Flores houses seven species as follows: *Agriocnemis pygmaea*, *Xiphiagrion cyanomelas* (Coenagrionidae), *Neurothemis ramburii*, *Orthetrum pruinatum pruinatum*, *O. sabina*, *O. testaceum soembanum* (Libellulidae), and *Anax gibbosulus* (Aeshnidae). A coastal marsh site with slightly brackish water on Flores harbors at least five dragonfly species as follows: *Diplacodes trivialis*, *Neurothemis intermedia excelsa*, *N. terminata*, *Pantala flavescens*, and *Rhyothemis phyllis ixias* (Libellulidae). The migratory dragonfly *Pantala flavescens* was a single species recorded on the waterless Kanawa Island near the western edge of Flores. Our findings suggest that extreme habitats in eastern Indonesia primarily colonized by widespread generalist Odonata species. Finally, an updated checklist of Odonata species recorded from Flores Island was compiled. Our survey of museum specimens recovered two species not found on existing species lists for Flores: *Neurothemis intermedia excelsa* and *Pantala flavescens*.

**Key words:** Odonata; acidic lake; coastal marsh; waterless island; Flores Island; East Nusa Tenggara Islands, Wallacea; island biogeography; checklist.

### Introduction

The order Odonata (dragonflies and damselflies) contains not less than 5,900 species globally (Kalkman *et al.* 2008; Van Tol 2020). These insects are able to colonize a wide array of extreme environments such as hot springs, acidic, alkaline, sulfide, and hypoxic water bodies, salt-water wetlands and mangroves, and ephemeral wetlands and pools (Brues 1924; Corbet 2004).

Odonata was considered one of the four insect orders (the others being Diptera, Coleoptera, and Hemiptera) that commonly occur in hot springs around the World (Pritchard 1991). There is a large body of

literature on various dragonfly and damselfly species inhabiting geothermal habitats in North America (Brues 1924), South America (Brues 1924), Siberia (Borisov 2016), Central Asia (Borisov 2015), Sumatra (Brues 1939), Java and Sulawesi (Lieftinck 1934, 1936), and other regions. Several species at the northern and altitudinal extents of their ranges are exclusively exploit hot springs, e.g. *Argia vivida* Hagen, 1865 (Coenagrionidae) and *Hetaerina americana* (Fabricius, 1798) (Lestidae) in North America (Leggott & Pritchard 1986; Pritchard 2008), *Orthetrum albistylum* (Selys, 1848) (Libellulidae) in Siberia (Borisov 2017), *Anotogaster sieboldii* (Selys, 1854) (Cordulegastridae) on Kunashir Island (Aksenova *et al.* 2020), and *Sympetrum haritonovi* Borisov, 1983 (Libellulidae) in the Tien-Shan, Pamir-Alai and Kopetdagh mountain ranges (Haritonov & Borisov 2013).

Although a wide array of dragonfly species is associated with coastal habitats such as brackish pools and marshes in North America and Europe (Wright 1943; McCreddie *et al.* 2005; Catling *et al.* 2006, Catling 2009; Uboni *et al.* 2020), only a few species can breed in marine water (Osburn 1906; Dunson 1980; Dunson & Travis 1994; Dow & Choong 2015; Wilson 2020). Ephemeral water bodies and seasonal lakes in semi-arid (savanna) and desert areas of Africa house diverse Odonata assemblages (e.g. Weir 1974; Suhling *et al.* 2003; Damm & Hadrys 2012). The larvae of dragonfly *Cordulegaster dorsalis* Hagen, 1858 (Cordulegastridae) can successfully develop in episodically drying headwater streams in British Columbia, Canada (Marczak *et al.* 2006).

The damselfly species *Proischnura subfurcata* (Selys, 1876) (Coenagrionidae) inhabits continuous papyrus swamps of East and Central Africa, being adapted to the extreme and chronic hypoxic stress (Apodaca & Chapman 2004). Several other Odonata taxa are known to tolerate moderately acidified water bodies, e.g. *Coenagrion lunulatum* (Charpentier, 1840) (Coenagrionidae) (Dolmen & Pedersen 2018), while a few species were recorded from extremely acidic water bodies (Rodrigues & Scharf 2001; Rychla *et al.* 2011). The skimmer species *Orthetrum boumiera* Watson & Arthington, 1978 exclusively inhabits brown-water, acidic dune lakes in eastern Australia (Watson & Arthington 1978).

In dense tropical forests, a few Odonata taxa adapted to breed in the leaf axils of trees and epiphytes filled by rainwater. The *Papuagrion* larvae (Coenagrionidae) use the leaf axils of pandanus trees in New Guinea (Kalkman & Orr 2016), while the larvae of two *Erythrodiplax* species (Libellulidae) are associated with bromeliads in Costa Rica, Cuba, and Jamaica (Haber *et al.* 2015). The larvae of the African East Coast giant damselfly, *Coryphagrion grandis* Morton, 1924 (Coenagrionidae) develop in tree holes and coconut shells filled by rainwater (Clausnitzer & Lindeboom 2002).

Our brief overview of the body of literature reveals that numerous species of Odonata can tolerate and successfully colonize various extreme environments in Europe, North America, Central America, Africa, New Guinea, and Australia. However, data on Odonata from extreme habitats of Southeast Asia and the Indonesian Archipelago is very limited (e.g. Lieftinck 1936; Brues 1939). This study (1) reports on the novel occurrences of dragonflies and damselflies in extreme environments such as a highly acidic crater lake, a coastal marsh, and a small waterless islet in eastern Indonesia; (2) discusses these findings in a broader biogeographic context; and (3) compiles an updated checklist of Odonata species from Flores Island.

## Materials & Methods

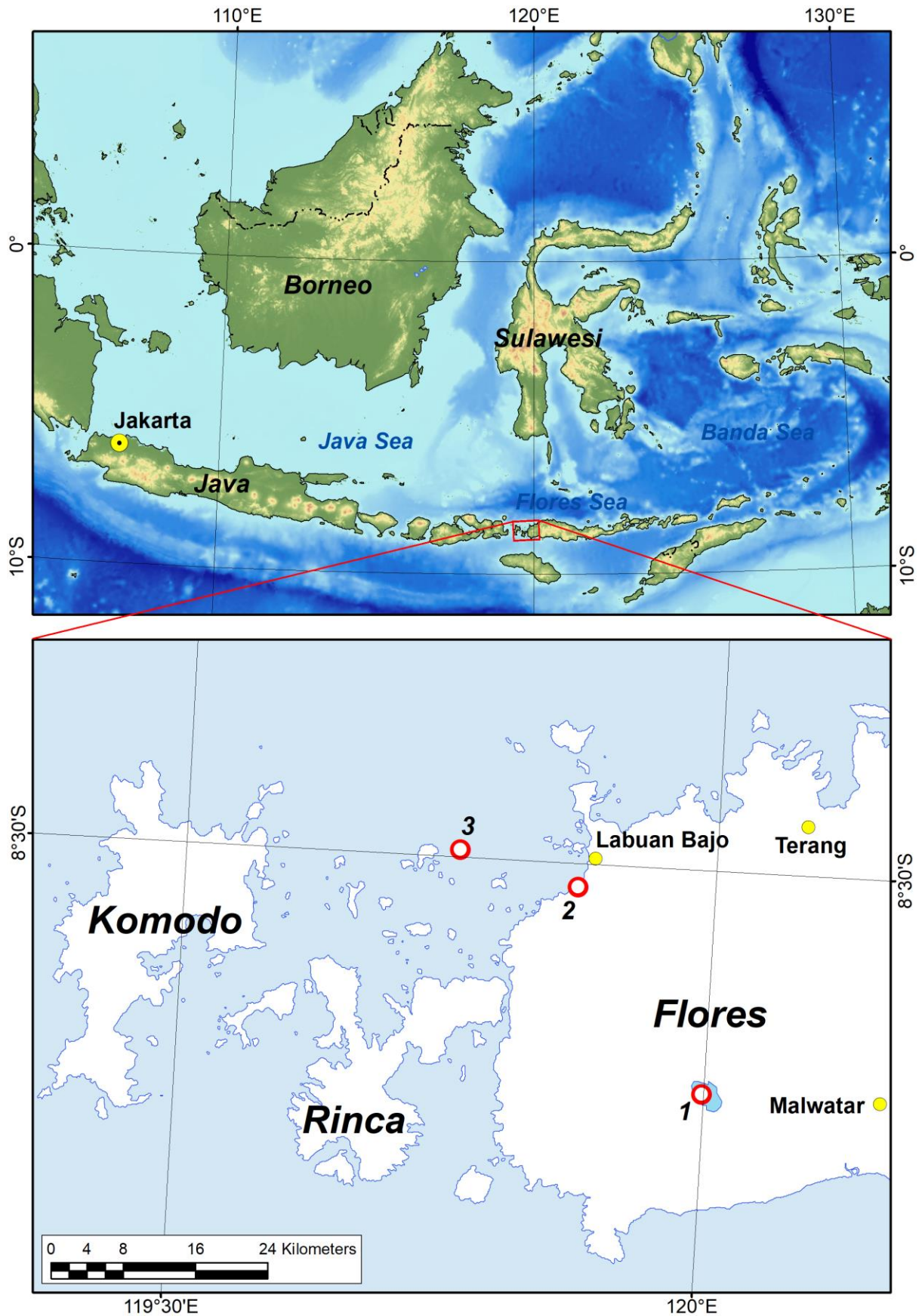
### Studied museum lots, morphological research, and published records

Samples of dragonflies and damselflies from extreme environments of Flores were studied in the Russian Museum of Biodiversity Hotspots [RMBH], N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia. Samples were examined using a research stereomicroscope (SteREO Discovery.V8, Carl Zeiss, Germany). Specimens and morphological details were photographed using a Canon EOS 60D camera with Canon EF 100 mm f/2.8L Macro IS USM Lens (Canon Inc., Tokyo, Japan).

Published records of Odonata on Flores were taken from the available literature (Lieftinck 1936, 1939, 1953, 1960).

### Locality data of available museum lots

The geographic localization and environmental characteristics of the localities are presented below (Figs 1-2).



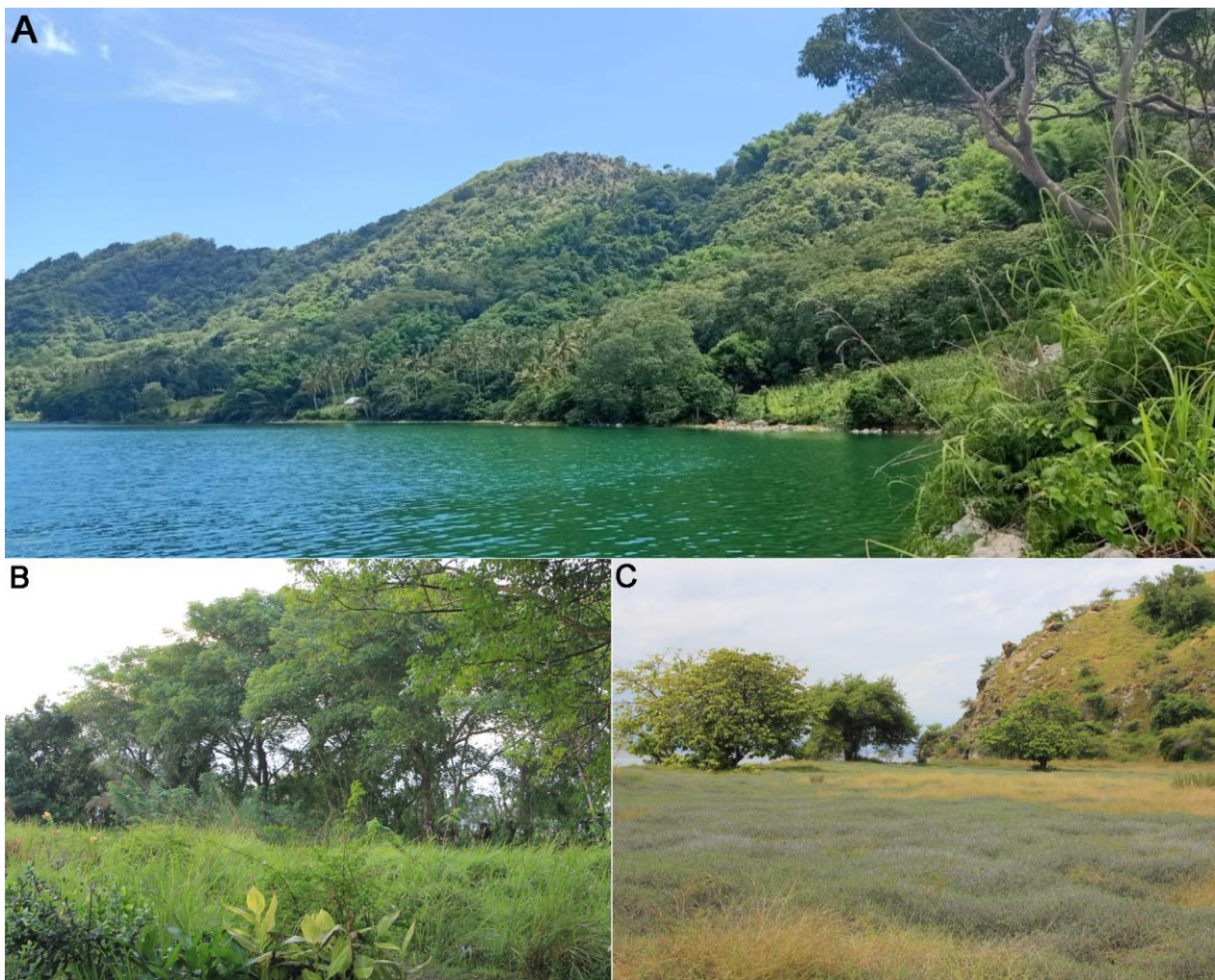
**Figure 1.** Map of the localities with extreme habitats on Flores and Kanawa islands (Lesser Sunda Archipelago, Indonesia), from which available museum lots were sampled: Sano Nggoang Lake (1); coastal marsh near Labuan Bajo on Flores Island (2); and Kanawa Island (3).



**Site 1.** Sano Nggoang Lake [8.7093°S, 119.9975°E]. This is a large crater lake (size of 3.3×2.2 km) situated in the center of the Waesano Stratovolcano, West Flores (Fig. 2A). It has a maximum depth of 500 m, being the deepest volcanic lake in eastern Indonesia (ESIA 2019). Based on a published report, the lake's waters are highly acidic (mean  $pH = 3.17$ ; range 2.81–3.85;  $N = 4$ ) (ESIA 2019). The surface waters in this lake are characterized by the following parameters (mean and min-max in  $mg \times L^{-1}$ ;  $N = 4$ ):  $TDS$ : 1582 [1500–1635];  $BOD$  (5 days 20°C): 223.8 [220.7–227.2];  $COD$ : 687.9 [524.1–750.3];  $NO_3^-$ : 0.19 [0.10–0.24];  $NH_4^+$ : 0.77 [0.37–0.93];  $Cl^-$ : 611.0 [566.2–631.4];  $SO_4^{2-}$ : 725.8 [704.0–750.1];  $H_2S$ : 0.56 [0.06–0.73] (ESIA 2019).

**Site 2.** Small coastal marsh [8.5220°S, 119.8704°E] near Labuan Bajo on Flores. This site contained a shallow reed marsh of 100×100 m in size having a slightly brackish water and situated ca. 30 m away from the shoreline (Fig. 2B). This marsh was destroyed due to the reconstruction of Bajo Komodo Ecolodge in 2018 (I. Bolotov, pers. observ.).

**Site 3.** Kanawa Island [8.4926°S, 119.7575°E]. This is a small island, 500×730 m, situated 9 km away from the western edge of Flores. The maximum altitude is 60 m. The island is covered by dry grass savanna with Indian jujube (*Ziziphus mauritiana*) and tamarind (*Tamarindus indica*) (Bolotov *et al.* 2018a). It does not house permanent water bodies but small seasonal marshes are present in its western and northern parts during the rainy season (Fig. 2C).



**Figure 2.** Examples of extreme habitats on Flores and Kanawa islands (Lesser Sunda Archipelago, Indonesia). (A) Sano Nggoang Lake on Flores Island. This highly acidic, slightly brackish lake supports viable populations of *Orthetrum sabina*, *Agriocnemis pygmaea*, and *Xiphiagrion cyanomelas*. (Photo: Wiwin Windari Petersen). (B) Coastal marsh near Labuan Bajo on Flores Island. Habitat of *Diplacodes trivialis*, *Neurothemis intermedia excelsa*, *N. terminata*, *Pantala flavescens*, and *Rhyothemis phyllis ixias*. (Photo: Yulia S. Kolosova). (C) Dry grass savanna with Indian jujube (*Ziziphus mauritiana*) and tamarind (*Tamarindus indica*) near the foothill on Kanawa Island (waterless during dry season). Site of *Pantala flavescens* occurrence (vagrant specimen). (Photo: Yulia S. Kolosova).

## Results

### Preliminary checklist of the Odonata fauna on Flores

Altogether 46 species of odonates were recorded from Flores, including 16 Zygopteran and 30 Anisopteran taxa (Table 1). Based on available museum collections, we added two species new to the fauna of this island: *Neurothemis intermedia excelsa* and *Pantala flavescens*.

**Table 1.** Checklist of Odonata species from Flores Island, Lesser Sunda Archipelago, Indonesia

Suborder/Family	Genus	Species	Range*	Reference to occurrence on Flores Island
<b>ZYGOPTERA</b>				
Euphaeidae	<i>Allophaea</i> Fraser, 1929	<i>A. lara lombokensis</i> (McLachlan, 1898)	Lombok, Sumbawa, Flores, Groot Bastaard, Pantar, Alor	Lieftinck (1936, 1953)
Chlorocyphidae	<i>Libellago</i> Selys, 1840	<i>L. naia</i> Lieftinck, 1932	Flores, Sumba	Lieftinck (1936, 1953)
Chlorocyphidae	<i>Rhinocypha</i> Rambur, 1842	<i>R. pagenstecheri pagenstecheri</i> Förster, 1897	Lombok, Sumbawa, Flores	Lieftinck (1936, 1953)
Platynemididae	<i>Copera</i> Kirby, 1890	<i>C. marginipes</i> (Rambur, 1842)	Oriental Region	Lieftinck (1936, 1953)
Platynemididae	<i>Nososticta</i> Hagen, 1860	<i>N. emphylla</i> (Lieftinck, 1936)	Lombok, Sumbawa, Flores	Lieftinck (1936, 1953)
Platynemididae	<i>Nososticta</i> Hagen, 1860	<i>N. selysii</i> (Förster, 1896)	Komodo, Flores, Sumba, Sawu, Timor	Lieftinck (1936, 1953); Seehausen (2017)
Coenagrionidae	<i>Argiocnemis</i> Selys, 1877	<i>A. femina</i> (Brauer, 1868)	Oriental Region	Lieftinck (1936, 1953)
Coenagrionidae	<i>Argiocnemis</i> Selys, 1877	<i>A. pygmaea</i> (Rambur, 1842)	Oriental and Australian regions	Lieftinck (1953); this study
Coenagrionidae	<i>Argiocnemis</i> Selys, 1877	<i>A. rubescens</i> Selys, 1877	Oriental and Australian regions	Lieftinck (1936, 1953)
Coenagrionidae	<i>Pseudagrion</i> Selys, 1876	<i>P. microcephalum</i> (Rambur, 1842)	Oriental and Australian regions	Lieftinck (1936, 1953)
Coenagrionidae	<i>Pseudagrion</i> Selys, 1876	<i>P. pilidorsum declaratum</i> Lieftinck, 1936	Lombok, Flores, Sawu, Alor	Lieftinck (1936, 1953)
Coenagrionidae	<i>Pseudagrion</i> Selys, 1876	<i>P. rubriceps</i> Selys, 1876	Oriental Region	Lieftinck (1936, 1953)
Coenagrionidae	<i>Xiphiagrion</i> Selys, 1876	<i>X. cyanomelas</i> (Selys, 1876)	Indonesia, Timor, the Philippines, and New Guinea	Lieftinck (1936, 1953); this study
Platystictidae	<i>Drepanosticta</i> Laidlaw, 1917	<i>D. floresiana</i> Lieftinck, 1939	Flores	Lieftinck (1939, 1953)
Lestidae	<i>Indolestes</i> Fraser, 1922	<i>I. floresianus</i> Lieftinck, 1960	Flores	Lieftinck (1960)
Lestidae	<i>Lestes</i> Leach, 1815	<i>L. concinnus</i> Hagen, 1862	Oriental and Australian regions	Lieftinck (1953)
<b>ANISOPTERA</b>				
Libellulidae	<i>Acisoma</i> Rambur, 1842	<i>A. panorpoides</i> Rambur, 1842	Oriental Region	Lieftinck (1936, 1953)
Libellulidae	<i>Agrionoptera</i> Brauer, 1864	<i>A. insignis insignis</i> (Rambur, 1842)	Oriental Region	Lieftinck (1936, 1953)
Libellulidae	<i>Brachydiplax</i> Brauer, 1868	<i>B. duivenbodei</i> (Brauer, 1866)	Oriental and Australian regions	Lieftinck (1936, 1953)
Libellulidae	<i>Crocothemis</i> Brauer, 1868	<i>C. servilia</i> (Drury, 1773)	Oriental and Australian regions	Lieftinck (1936, 1953)
Libellulidae	<i>Diplacodes</i> Kirby, 1889	<i>D. trivialis</i> (Rambur, 1842)	Seychelles Islands, Oriental and Australian regions	Lieftinck (1936, 1953); this study
Libellulidae	<i>Lathrecista</i> Kirby, 1889	<i>L. asiatica asiatica</i> (Fabricius, 1798)	Oriental and Australian regions	Lieftinck (1953)
Libellulidae	<i>Neurothemis</i> Brauer, 1867	<i>**N. intermedia excelsa</i> Lieftinck, 1934	Java, Kangean Islands, Flores, and Sumba	This study

...continued on the next page

*DRAGONFLIES AND DAMSELFLIES FROM FLORES ISLAND*

Suborder/Family	Genus	Species	Range*	Reference to occurrence on Flores Island
Libellulidae	<i>Neurothemis</i> Brauer, 1867	<i>N. ramburii</i> (Brauer, 1866)	Indonesia and the Philippines	Lieftinck (1936, 1953)
Libellulidae	<i>Neurothemis</i> Brauer, 1867	<i>N. terminata</i> Ris, 1911	Indonesia, Timor, and the Philippines	Lieftinck (1936, 1953); this study
Libellulidae	<i>Orthetrum</i> Newman, 1833	<i>O. glaucum</i> (Brauer, 1865)	Oriental Region	Lieftinck (1936, 1953)
Libellulidae	<i>Orthetrum</i> Newman, 1833	<i>O. pruinsum pruinsum</i> (Burmeister, 1839)	Indonesia	Lieftinck (1936, 1953)
Libellulidae	<i>Orthetrum</i> Newman, 1833	<i>O. sabina</i> (Drury, 1773)	Nearly cosmopolitan	Lieftinck (1936, 1953); this study
Libellulidae	<i>Orthetrum</i> Newman, 1833	<i>O. testaceum soembanum</i> Förster, 1903	Lombok, Sumbawa, Flores, Alor, Wetar	Lieftinck (1936, 1953)
Libellulidae	<i>Pantala</i> Hagen, 1861	** <i>P. flavescens</i> (Fabricius, 1798)	Nearly cosmopolitan	This study
Libellulidae	<i>Rhodothemis</i> Ris, 1909	<i>R. rufa</i> (Rambur, 1842)	Oriental and Australian regions	Lieftinck (1936, 1953)
Libellulidae	<i>Rhyothemis</i> Hagen, 1867	<i>R. phyllis ixias</i> Lieftinck, 1953	Flores, Sumba, ?Rote	Lieftinck (1936, 1953); Seehausen <i>et al.</i> (2018); this study
Libellulidae	<i>Potamarcha</i> Karsch, 1890	<i>P. congener</i> (Rambur, 1842)	Oriental and Australian regions	Lieftinck (1953)
Libellulidae	<i>Tetrathemis</i> Brauer, 1868	<i>T. irregularis hyalina</i> Brauer, 1868	Malaysia, Indonesia, Timor, and New Guinea	Lieftinck (1936, 1953); Seehausen (2017)
Libellulidae	<i>Tholymus</i> Hagen, 1867	<i>T. tillarga</i> (Fabricius, 1798)	Oriental, Australian, and Afrotropical regions	Lieftinck (1936, 1953)
Libellulidae	<i>Tramea</i> Hagen, 1861	<i>T. eurybia</i> Selys, 1878	Andaman Islands, Indonesia, New Guinea, eastern Australia, and Fiji	Lieftinck (1953)
Libellulidae	<i>Trithemis</i> Brauer, 1868	<i>T. aurora</i> (Burmeister, 1839)	Oriental Region	Lieftinck (1936, 1953)
Libellulidae	<i>Trithemis</i> Brauer, 1868	<i>T. festiva</i> (Rambur, 1842)	From Southern Europe via Oriental Region to New Guinea	Lieftinck (1936, 1953)
Libellulidae	<i>Trithemis</i> Brauer, 1868	<i>T. lilacina</i> Förster, 1899	Bali, Lombok, Sumbawa, Flores, Sumba, Timor	Lieftinck (1936, 1953); Seehausen (2017); Seehausen <i>et al.</i> (2018)
Libellulidae	<i>Zyxomma</i> Rambur, 1842	<i>Z. obtusum</i> Albarda, 1881	Oriental and Australian regions	Lieftinck (1953)
Corduliidae	<i>Hemicordulia</i> Selys, 1870	<i>H. australiae</i> (Rambur, 1842)	Lesser Sundas, Lord Howe, Norfolk, Australia, and New Zealand	Lieftinck (1953)
Corduliidae	<i>Procordulia</i> Martin, 1907	<i>P. sambawana</i> (Förster, 1899)	Sumbawa, Flores	Lieftinck (1936)
Aeshnidae	<i>Anax</i> Leach, 1815	<i>A. gibbosulus</i> Rambur, 1842	Sumatra, Java, Flores, Sumba, Sawu, Kei, New Guinea, and Australia	Lieftinck (1936, 1953)
Aeshnidae	<i>Anax</i> Leach, 1815	<i>A. guttatus</i> (Burmeister, 1839)	Oriental and Australian regions	Lieftinck (1953)
Aeshnidae	<i>Gynacantha</i> Rambur, 1842	<i>G. musa</i> Karsch, 1892	Java and Flores	Lieftinck (1936, 1953)
Gomphidae	<i>Paragomphus</i> Cowley, 1934	<i>P. flavohamatus</i> (Martin, 1921)	Lombok, Sumbawa, Flores	Lieftinck (1936, 1953)

\*Based on the world's catalogue (Steinmann 1997a, b) with some additions (Lieftinck 1936, 1939, 1953, 1960; Seehausen & Günther 2016; Seehausen & Theischinger 2017). \*\*New records for Flores (this study).

### Occurrences of Odonata from extreme environments on Flores

The extreme habitats on Flores Island support species-poor Odonata assemblages. Based on available museum lots, three species were recorded on the shore of the Sano Nggoang Lake [site 1], i.e. the dragonfly *Orthetrum sabina*, and damselflies *Agriocnemis pygmaea* and *Xiphiagrion cyanomelas* (Figs 3-5). Historically, four additional species were also recorded from this crater lake, i.e. *Orthetrum pruinosum pruinosum*, *O. testaceum soembanum*, *Neurothemis ramburii*, and *Anax gibbosulus* (see below taxonomic accounts of these species for detail and references).

Five dragonfly species were found in adult stage near the edge of permanent coastal marsh [site 2], i.e. *Diplacodes trivialis*, *Neurothemis intermedia excelsa*, *N. terminata*, *Pantala flavescens*, and *Rhyothemis phyllis ixias* (Figs 6-10).

Finally, one *Pantala flavescens* male was recorded on the waterless island of Kanawa [site 3] (Fig. 9).

### Taxonomic overview of Odonata species recorded from extreme environments on Flores

#### Coenagrionidae

*Agriocnemis pygmaea* (Rambur, 1842)

Fig. 3A-D

Material examined: INDONESIA: Flores Island, Sano Ngoang Lake, lake shore, camp site, edge of secondary mountain forest on the caldera slope, 8.7093°S, 119.9975°E [site 1], 24.i.2015, 1♂, 4♀ [RMBH: sample in 96% ethanol], Bolotov leg.

Earlier records from Flores: This species was mentioned for Flores without exact material and locality data (Lieftinck 1953: 128, Table 2).

Distribution: Seychelles, India, Sri Lanka, Taiwan, mainland Southeast Asia, the Philippines, Indonesian Archipelago, New Guinea, Solomon Islands, and Australia (Steinmann 1997a).

*Xiphiagrion cyanomelas* Selys, 1876

Fig. 4A-F

Material examined: INDONESIA: Flores Island, Sano Ngoang Crater Lake, lake shore, camp site, edge of secondary mountain forest on the caldera slope, 8.7093°S, 119.9975°E [site 1], 24.i.2015, 3♂ [RMBH: sample in 96% ethanol], Bolotov leg.

Earlier records from Flores: “1♂, W. Flores, Rana Mese, 12-1300 m [Rana Mese Lake, approx. 8.6393°S, 120.5610°E, alt. 1220 m], 24.ix.1932, R. Woltereck leg.; 46♂, 21♀, W. Flores, Laboean Badjo [Labuan Bajo], 100 m (5♂, 1♀), Naga, 220 m (1♀, 12.xi.1929), Wai Sano, Kratersee [Sano Ngoang Crater Lake], 650 m (41♂, 19♀), xi.1929, J. K. de Jong leg.; ausserdem zahlreiche Larven aus dem Kratersee Wai Sano [also numerous larvae from the Sano Ngoang Crater Lake]” (Lieftinck 1936: 134). “Many specimens, W. Flores, Mborong, 100 m, 8.xi.1949, Lerang, 1300 m, 15-16.xi.1949, and Rana Mese, 1300 m, 18-21.xi.1949, E. Sutter (Sumba Exped.); 2♂, Labuan Badjo, vi.1937, J. K. de Jong (MB); 1♂, Munang, 500 m, 25.v.1951, J. M. A. van Groenendael (MB).” (Lieftinck 1953: 165).

Distribution: The Philippines (Palawan, Siargao, and Mindanao), Simalur, Enggano, Sumatra, Java, Borneo, Sulawesi, Flores, Sumba, Wetar, Sula, Buru, Ambon, Ceram, New Guinea, Aru, New Britain, and New Ireland (Lieftinck 1953; Steinmann 1997a; Villanueva 2011a, b).

#### Libellulidae

*Diplacodes trivialis* (Rambur, 1842)

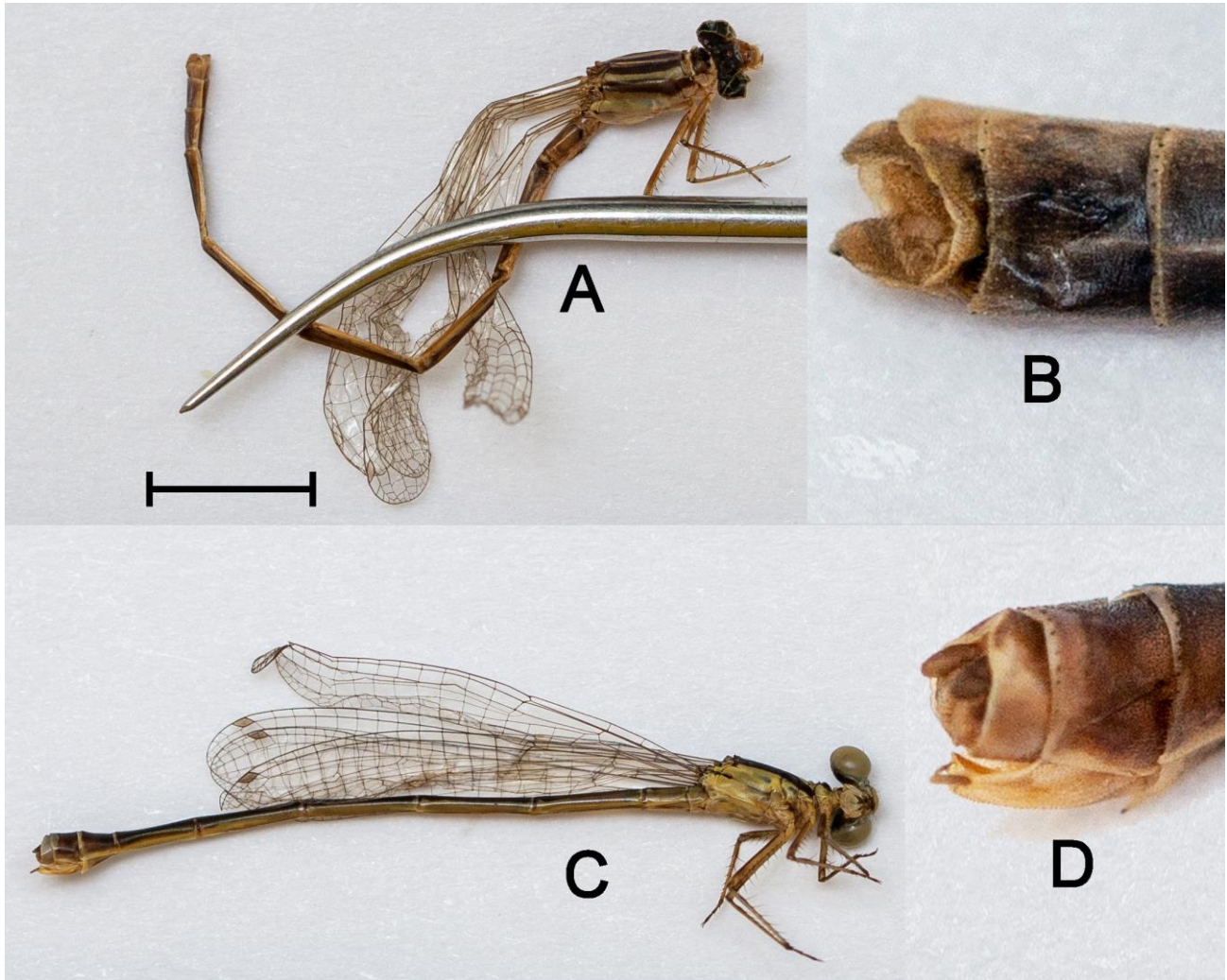
Fig. 6A-D

Material examined: INDONESIA: Flores Island, near Labuan Bajo, Bajo Komodo Ecological, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 01.v.2011, 2♀ [RMBH: dried specimens on cotton layer], Bolotov leg.



Earlier records from Flores: “1♂, W. Flores, Wai Radjang, 18.xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 141). “Numerous specimens from <...> Komodo (MB), Flores (MB)...” (Lieftinck 1953: 211).

Distribution: Seychelles, India, Sri Lanka, mainland Southeast Asia, China, Japan, Indonesian Archipelago, the Philippines, New Guinea, Solomon Islands, Australia, and the Fiji Islands (Steinmann 1997b).



**Figure 3.** *Agriocnemis pygmaea* from Sano Ngoang Lake, Flores Island, Lesser Sunda Archipelago, Indonesia: (A) teneral male, and (C) adult female (RMBH: ethanol-preserved specimens; scale bar = 5 mm); (B) anal appendages of the male (dorsal view); and (D) tip of the female abdomen (lateral view).

*Neurothemis intermedia excelsa* Lieftinck, 1934

Fig. 7A-B

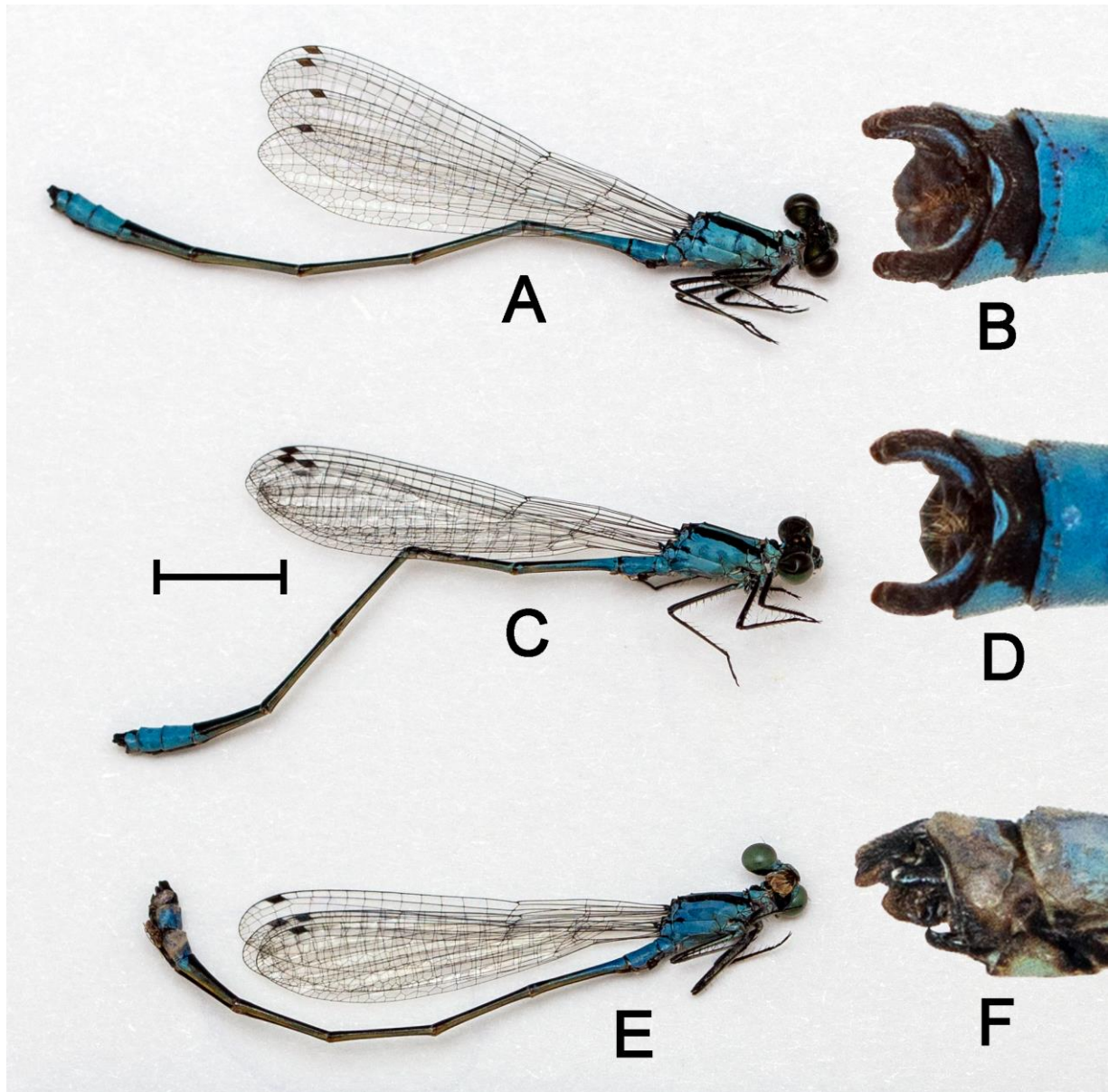
Material examined: INDONESIA: Flores Island, near Labuan Bajo, Bajo Komodo Ecological Reserve, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 13.i.2012, 1♀ [RMBH: dried specimen on cotton layer], Bolotov leg.

Earlier records from Flores: Unknown. To the best of our knowledge, the present study reports on the first record of *Neurothemis intermedia excelsa* from this island.

Distribution: Java, Kangean Islands, Sumba (Lieftinck 1953; Seehausen & Günther 2016), and Flores (this study).

Comments: This subspecies can be distinguished from other geographic races by the combination of the following characters: coloration of the wing base does not reach triangle in the forewing and extends to triangle in the hindwing (male); coloration of the wing base restricted to innermost cells (female) (Seehausen & Günther 2016).





**Figure 4.** *Xiphiagrion cyanomelas* from Sano Ngoang Lake, Flores Island, Lesser Sunda Archipelago, Indonesia: (A, C) male, and (E) female (RMBH: ethanol-preserved specimens; scale bar = 5 mm); (B, D) anal appendages of the males (dorsal view); and (F) tip of the female abdomen (lateral view).

*Neurothemis ramburii* (Brauer, 1866)

Material examined: Not available.

Earlier records from Flores: “Wai Sano (Kratersee) [Sano Ngoang Crater Lake] <...> xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 142).

Distribution: Indonesia, and the Philippines (Lieftinck 1936, 1953; Seehausen & Dow 2016).

*Neurothemis terminata* Ris, 1911

Fig. 8A-D

Material examined: INDONESIA: Flores Island, near Labuan Bajo, Bajo Komodo Ecological Reserve, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 01.v.2011, 1♂, 1♀ [RMBH: dried specimens on cotton layer], Bolotov leg.

Earlier records from Flores: 1♂ (Lieftinck 1936: 143). “Numerous specimens from <...> W. and C. Flores (MB)” (Lieftinck 1953: 213).

Distribution: Philippines, Borneo across Flores and Timor to Java and around central Sumatra (Lieftinck 1936; Seehausen & Dow 2016).

*Orthetrum pruinsum pruinsum* (Burmeister, 1839)

Material examined: Not available.

Earlier records from Flores: “Wai Sano, Kratersee [Sano Ngoang Crater Lake], 650 m (3♀), xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 138).

Distribution: Indonesia (Steinmann 1997b).

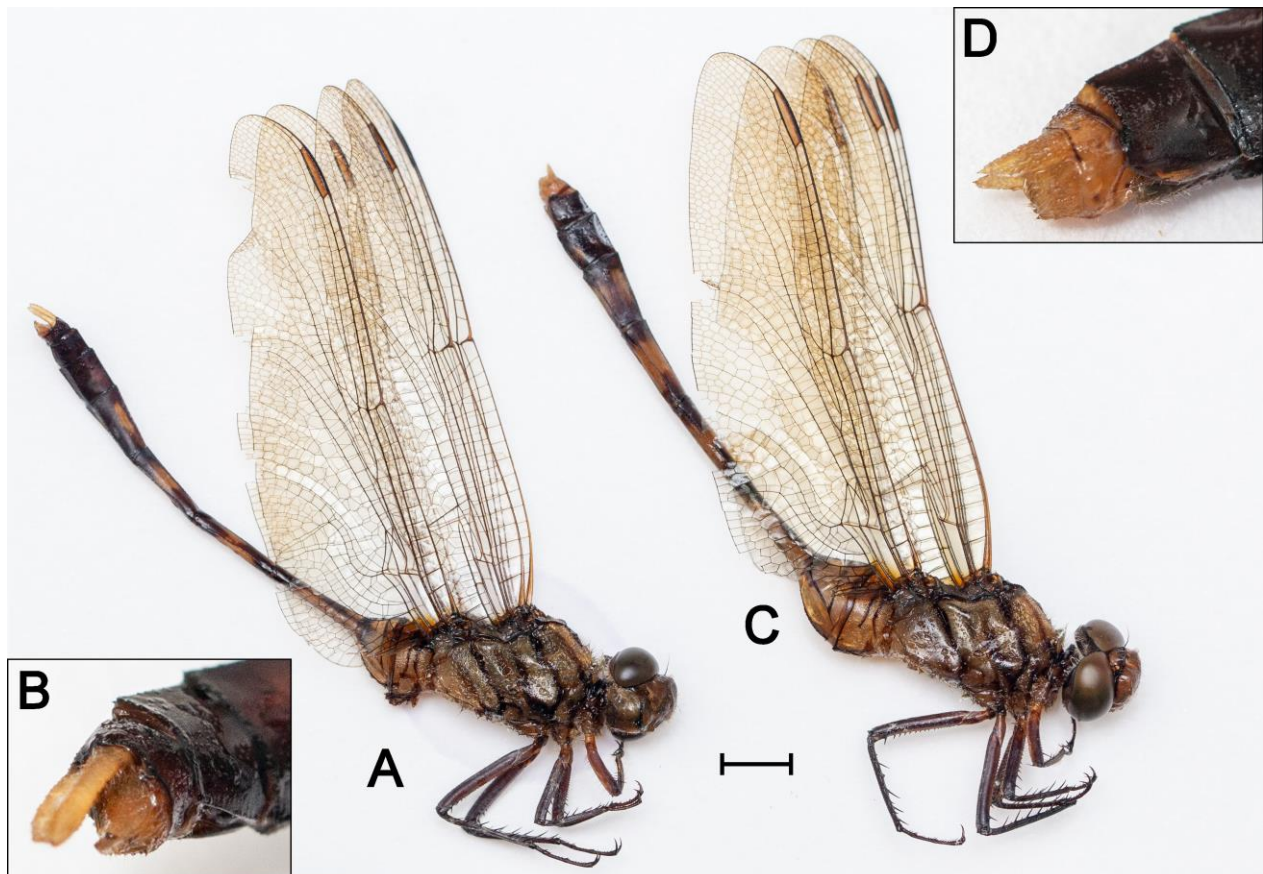
*Orthetrum sabina* (Drury, 1770)

Fig. 5A-D

Material examined: INDONESIA: Flores Island, Sano Ngoang Lake, lake shore, camp site, edge of secondary mountain forest on the caldera slope, 8.7093°S, 119.9975°E [site 1], 23.i.2015, 2♂, 1♀ [RMBH: sample in 96% ethanol], Bolotov leg.

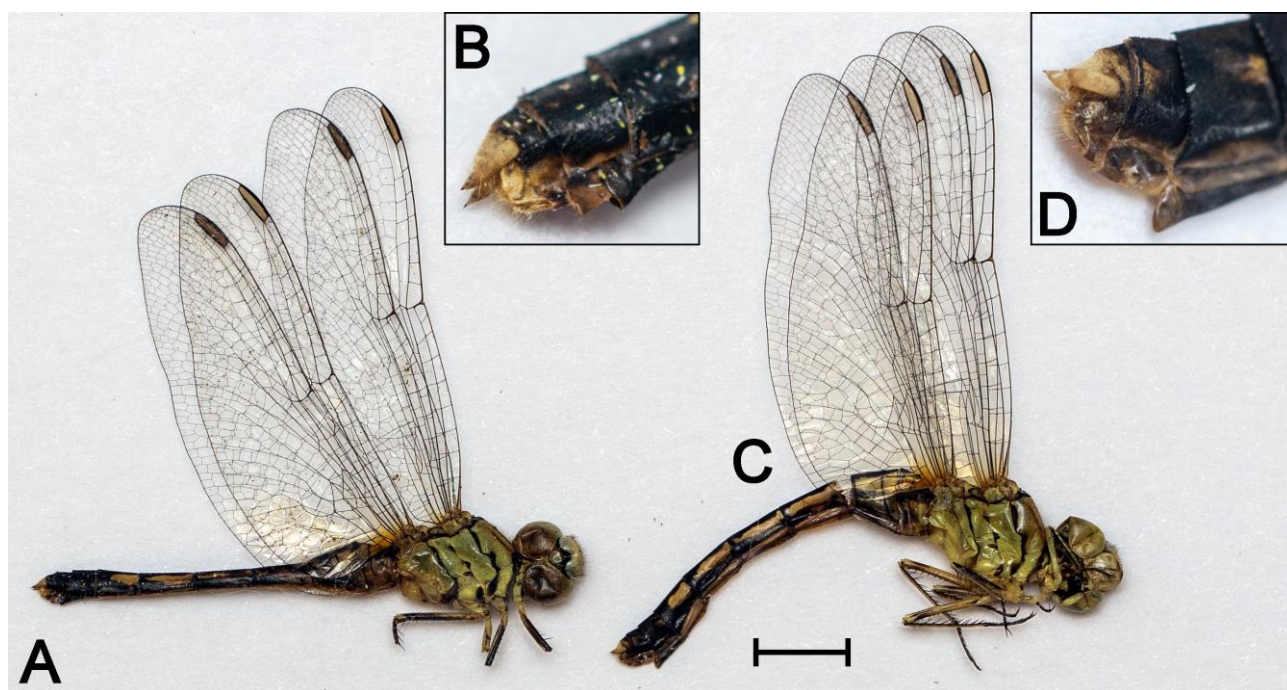
Earlier records from Flores: “5♂, 1♀, W. Flores, Naga, 220 m, und Kratersee Wai Sano [Sano Ngoang Crater Lake], 650 m, xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 138). “4♂, W. Flores, Labuan Badjo and Reo, vi.1937, J. K. de Jong (MB)” (Lieftinck 1953: 207).

Distribution: Africa, Middle East, China, India, Sri Lanka, Southeast Asia, Australasia, and Australia (Steinmann 1997b).



**Figure 5.** *Orthetrum sabina* from Sano Ngoang Lake, Flores Island, Lesser Sunda Archipelago, Indonesia: (A) male, and (C) female (RMBH: ethanol-preserved specimens; scale bar = 5 mm); (B) anal appendages of the male (lateral view); and (D) tip of the female abdomen (lateral view).





**Figure 6.** *Diplacodes trivialis* from coastal marsh site near Labuan Bajo, Flores Island, Lesser Sunda Archipelago, Indonesia: (A, C) females (RMBH: dried specimens; scale bar = 5 mm); and (B, D) tip of abdomen of the females.

*Orthetrum testaceum soembanum* Förster, 1903

Material examined: Not available.

Earlier records from Flores: “Kratzersee Wai Sano [Sano Ngoang Crater Lake], 650 m (7♂), xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 140).

Distribution: Lombok, Sumbawa, Flores, Alor, Wetar (Lieftinck 1936, 1953).

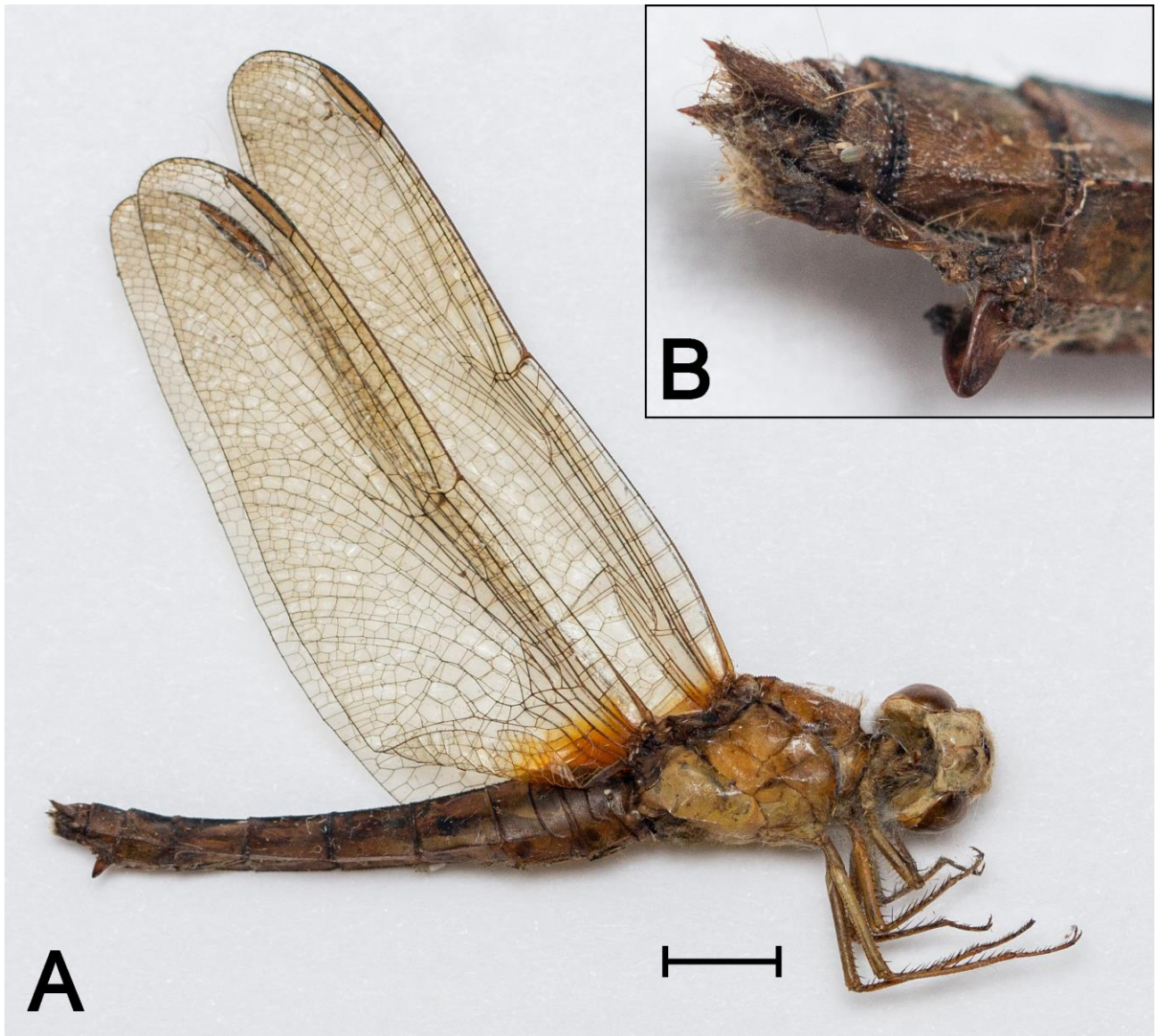
*Pantala flavescens* (Fabricius, 1798)

Fig. 9A-D

Material examined: INDONESIA: Flores Island, near Labuan Bajo, Bajo Komodo Ecological, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 01.v.2011, 1♂ [RMBH: dried specimen on cotton layer], Bolotov leg.; Kanawa Island, dry savanna with Indian jujube (*Ziziphus mauritiana*) near the foothill, 8.4926°S, 119.7575°E [site 3], 25.iv.2011, 1♂ [RMBH: dried specimen on cotton layer], Bolotov leg.

Earlier records from Flores: Unknown. To the best of our knowledge, the present study reports on the first record of *Pantala flavescens* from this island. Lieftinck (1936: 146) noted that “...diese überall häufige und kosmopolitische Libelle noch nie von der Inselkette erwähnt worden. Sie kommt aber zweifellos auf allen Kleinen Sunda-Inseln vor [...this ubiquitous and cosmopolitan dragonfly has never been mentioned for this island chain but it undoubtedly inhabits all the Lesser Sunda Islands]”. There are historical and recent records from Timor (Lieftinck 1936; Seehausen 2017), and historical records from Komodo, Roti, Wetar, and Kisar (Lieftinck 1953).

Distribution: Migratory species, which is widespread throughout tropical, subtropical, and temperate areas globally (Steinmann 1997b). It can reach Southern Siberia, the Russian Far East, and the Baltic Sea in the North, and Australia and New Zealand in the South (Corbet 1979; Hawking & Ingram 1994; Buczyński *et al.* 2014; Borisov & Malikova 2019).



**Figure 7.** *Neurothemis intermedia excelsa* from coastal marsh site near Labuan Bajo, Flores Island, Lesser Sunda Archipelago, Indonesia: (A) female (RMBH: dried specimen; scale bar = 5 mm); and (B) tip of abdomen of the female.

*Rhyothemis phyllis ixias* Lieftinck, 1953  
Fig. 10A-F

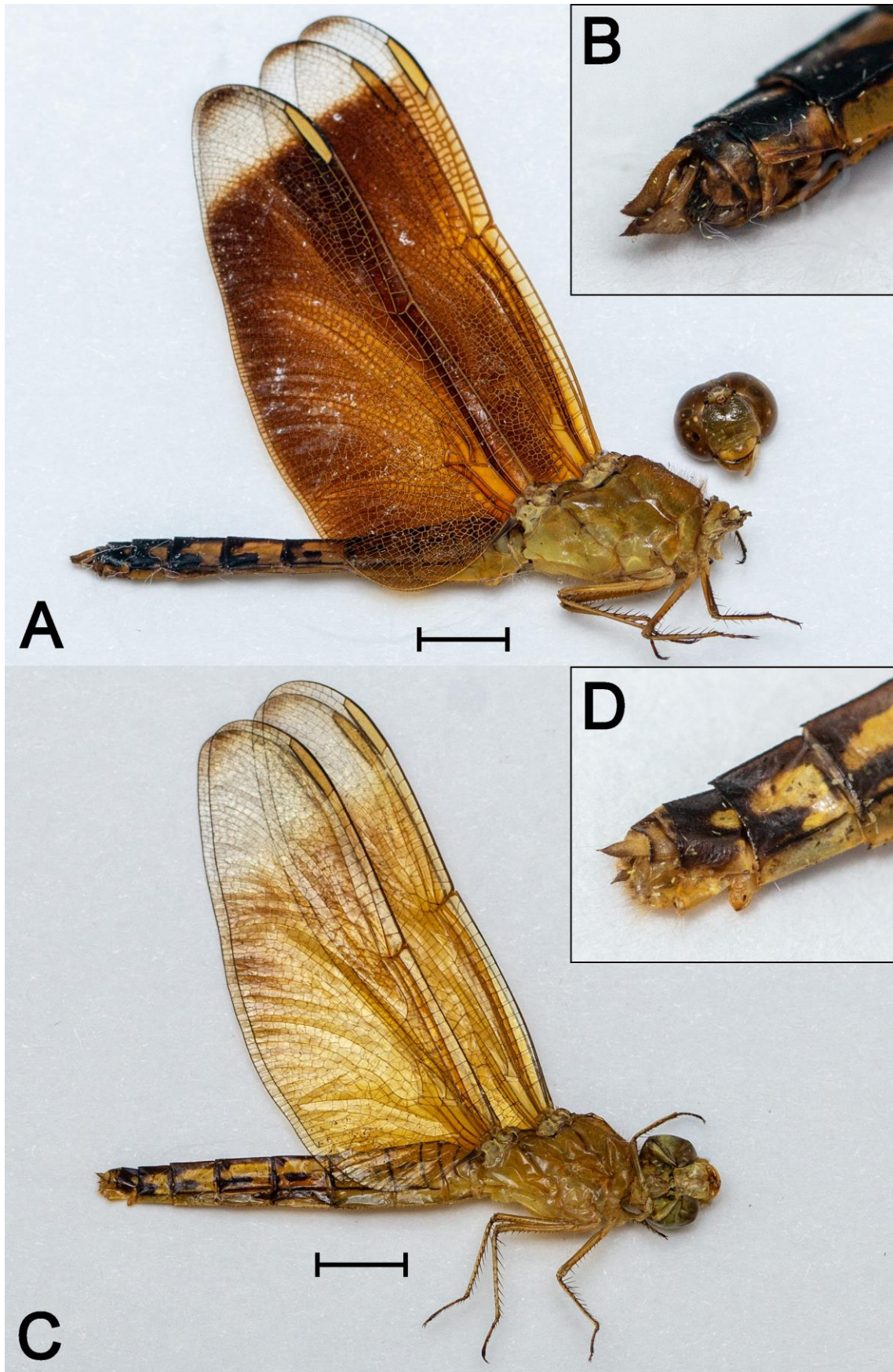
Material examined: INDONESIA: Flores Island, near Labuan Bajo, Bajo Komodo Ecolodge, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 01.v.2011, 2♀ [RMBH: dried specimens on cotton layer], Bolotov leg.

Earlier records from Flores: “1♀, W. Flores, Mboera, 35 m, x.1929, J. K. de Jong leg.” (Lieftinck 1936: 146). “3♂, 11♀, W. Flores, Labuan Badjo and Mbura, vi.1937, J. K. de Jong (MB)” (Lieftinck 1953: 221).

Distribution: This subspecies is known to occur on Flores and Sumba (Lieftinck 1953), and, probably, on Rote (Seehausen *et al.* 2018).

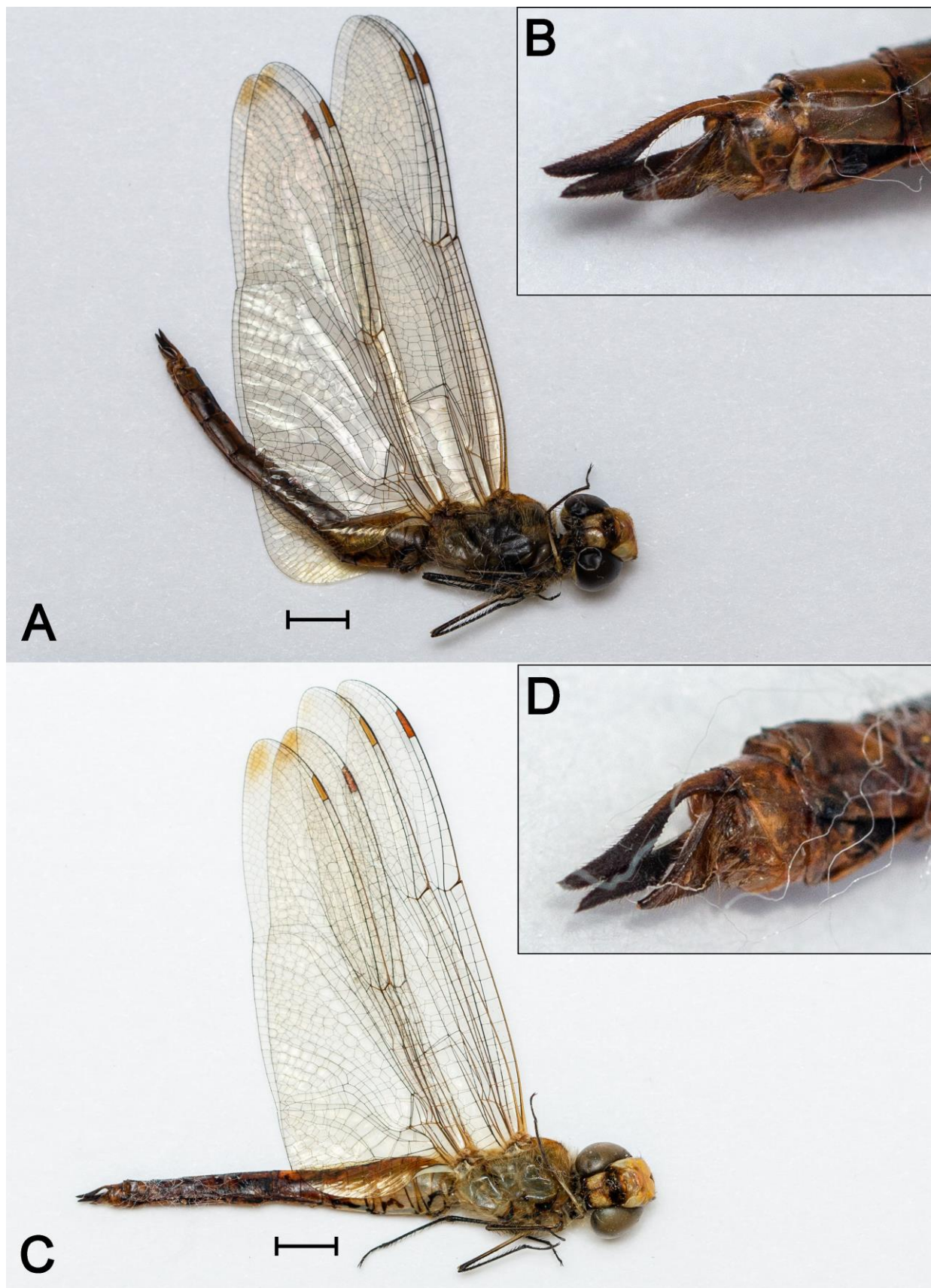
Comments: The primary diagnostic feature of this subspecies is the darker face and blackish labium (Fig. 10C, 10F) (vs almost yellow in the nominate subspecies) (Seehausen *et al.* 2018).





**Figure 8.** *Neurothemis terminata* from coastal marsh site near Labuan Bajo, Flores Island, Lesser Sunda Archipelago, Indonesia: (A) male, and (C) female (RMBH: dried specimens; scale bar = 5 mm); (B) anal appendages of the male (lateral view); and (D) tip of the female abdomen (lateral view).





**Figure 9.** *Pantala flavescens* from Flores and Kanawa islands, Lesser Sunda Archipelago, Indonesia: (A) male from dry seasonal marsh site on Kanawa Island near the western edge of Flores Island (RMBH: dried specimen; scale bar = 5 mm); (B) its anal appendages (lateral view); (C) male from coastal marsh near Labuan Bajo on Flores Island (RMBH: dried specimen; scale bar = 5 mm); and (D) its anal appendages (lateral view).



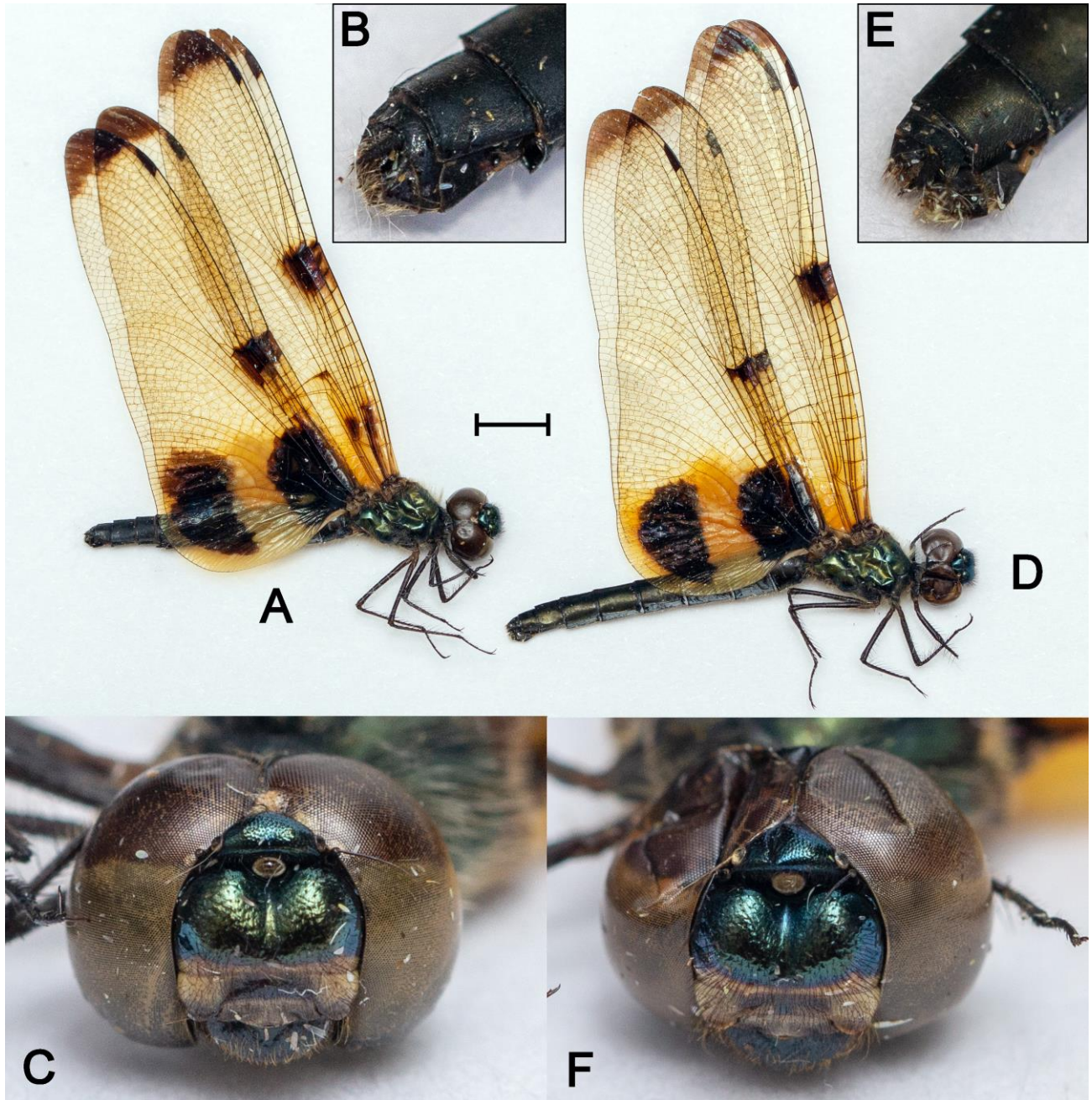
## Aeshnidae

*Anax gibbosulus* Rambur, 1842

Material examined: Not available.

Earlier records from Flores: adults “2♀, W. Flores, Kratersee Wai Sano [Sano Ngoang Crater Lake], 6.xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 151); and larvae “6 Exemplare (ult), W. Flores, Kratersee Wai Sano [Sano Ngoang Crater Lake], 650 m, xi.1929, J. K. de Jong leg.” (Lieftinck 1936: 158).

Distribution: Sumatra, Java, Flores, Sumba, Sawu, Kei, New Guinea, and Australia (Lieftinck 1936, 1953; Steinmann 1997b).



**Figure 10.** *Rhyothemis phyllis ixias* from coastal marsh site near Labuan Bajo, Flores Island, Lesser Sunda Archipelago, Indonesia: (A, D) females (RMBH: dried specimens; scale bar = 5 mm); (B, E) tip of abdomen of the females; and (C, F) head of the females (frontal view).

## Discussion

### Brief review of the Odonata fauna on Flores

This study brings the total Odonata fauna of Flores Island to 46 species (16 Zygopteran and 30 Anisopteran taxa) (Table 1). Two species recovered on Flores for the first time, i.e. *Neurothemis intermedia excelsa* and *Pantala flavescens*. The dragonfly species richness on Flores is similar to that on Timor (approximately 40 species) (Seehausen *et al.* 2018), but much less than that on Sumba, which has more than 70 species (Lieftinck 1953).

Most Odonata taxa in the fauna of Flores are widespread species sharing clear affinities to the Oriental Region (30 species, 65% of the total species richness), while 15 species and subspecies (32%) can be considered endemic to the region (Table 1). The ranges of the latter group expand throughout the Lesser Sunda Islands (two species are also known to occur on Java) or restricted to the eastern insular group of this archipelago (i.e. the East Nusa Tenggara Region). Among these endemic taxa, two species are unknown beyond Flores, i.e. *Drepanosticta floresiana* and *Indolestes floresianus*, although their distribution needs further study (Lieftinck 1939, 1953, 1960). Finally, *Hemicordulia australiae* represents the single species of probably Papuan-Australian origin on Flores (2%) (Kalkman *et al.* 2008).

Similar biogeographic patterns with the high prevalence of Oriental taxa and low proportion of Australian species were recovered in other insect groups on the Lesser Sunda Archipelago, e.g. Lepidoptera (Zolotukhin & Witt 2005; Spitsyn *et al.* 2016, 2018, 2019; Bolotov *et al.* 2017, 2018b, 2019; Spitsyn & Bolotov 2018, 2020a, b, c; Spitsyn & Potapov 2020), and Coleoptera (Mohamedsaid 2009).

### Odonata populations in extremely acidic water bodies in Indonesia and beyond

The Sano Nggoang Lake represents a deep, acidic, and brackish water body enriched by nitrogen and sulphur (see Material and methods). Available museum collections indicate that the shallow coastal areas of this crater lake (pH below 3.9) house viable populations of *Orthetrum sabina*, *Agriocnemis pygmaea*, and *Xiphiagrion cyanomelas*. Additionally, *Orthetrum pruinatum pruinatum*, *O. testaceum soembanum*, *Neurothemis ramburii*, and *Anax gibbosulus* were recorded from this lake based on published data (Lieftinck 1936). In summary, the Odonata fauna of this acidic lake on Flores contains seven widespread, generalist species. The damselfly *Xiphiagrion cyanomelas* and the skimmer *Orthetrum sabina* were common species in this caldera in 1929 and 2015. *Agriocnemis pygmaea* did not occur in 1929, but this diminutive species may have been overlooked, as it was on Timor (Seehausen *et al.* 2018). The other species were not rediscovered in 2015. It should be mentioned that the larvae of *Xiphiagrion cyanomelas* and *Orthetrum pruinatum* were also found in Lake Linow, an acidic, geothermal water body in northern Sulawesi (temperature 27.8°C, pH 4.0; 05.vi.1932) (Lieftinck 1936).

The Sano Nggoang and Linow lakes in eastern Indonesia are rather unusual examples of successful colonization of highly acidic environments by dragonflies. Typically, these insects cannot colonize extremely acidic water bodies. This is most likely associated with negative effects of low pH (below 4.0) on the survivorship, predation, respiration rate, and fitness of dragonfly nymphs (Gorham & Vodopich 1992), although the eggs of dragonflies seem to be resistant to acidic waters and can tolerate pH 3.5 without significant shifts in the development times and hatching success (Hudson & Berrill 1986; Rychla *et al.* 2011). Only chironomids were recorded in the acidic Banyupahit-Banyuputih River (pH below 3.5) flowing from the Kawah Ijen Crater Lake in East Java, Indonesia (Löhr *et al.* 2006). Odonata were absent in highly acidic (pH below 3.0) mining lakes in the Muskau Arch area at the Germany–Poland border (Rychla *et al.* 2011), while *Coenagrion mercuriale* (Charpentier, 1840) was found in such a lake (pH 3.0) near Grünewalde in eastern Germany (Rodrigues & Scharf 2001). However, water bodies with a slightly higher pH can host dragonfly assemblages with several acid-tolerant species, e.g. the Adirondack lakes in North America (pH 4.0–6.0) (Frolich Strong & Robinson 2004) and small forest lakes in Europe (pH 4.2–5.0) (Mossberg & Nyberg 1979). It was shown that pH is a primary environmental filter of dragonfly assemblages controlling site-to-site shifts in their phylogenetic structure across biomes (Arrowsmith *et al.* 2018).

### Dragonflies in coastal marshes and on small waterless islands

The coastal marsh site near Labuan Bajo on Flores supported at least five species, i.e. *Diplacodes trivialis*, *Neurothemis intermedia excelsa*, *N. terminata*, *Pantala flavescens*, and *Rhyothemis phyllis ixias*. The majority of these taxa represent widespread generalist species, a pattern consistent with findings from coastal wetlands in North America (Wright 1943; McCreadie *et al.* 2005; Catling *et al.* 2006, Catling 2009) and



Europe (Uboni et al. 2020). In particular, diverse assemblages of odonates exploit brackish pools and salt marshes from Quebec and New Brunswick in Canada to the deltas of the Mississippi and Mobile rivers/Tensaw on the Gulf of Mexico (Wright 1943; McCreadie *et al.* 2005; Catling *et al.* 2006, Catling 2009). It was shown that at least 15 widespread Odonata species inhabit brackish wetlands in Europe (Uboni *et al.* 2020). Saline inland lakes in North America can also support rather species-poor Odonata assemblages, comprising a few common, generalist species (Schwarz 1891; Osburn 1906; Cannings & Cannings 1987). The dragonfly *Erythrodiplax berenice* (Drury, 1773) (Libellulidae) can breed in seawater and is a common inhabitant of salt-water marches and ponds in eastern North America (Osburn 1906; Dunson 1980; Dunson & Travis 1994). The mangrove skimmer *Orthetrum poecilops* Ris, 1919 (Libellulidae) is another coastal specialist from East Asia that can breed in salt water (Wilson 2020). Recently, *Mortonagrion megabinluyog* Dow & Choong, 2015 (Coenagrionidae), a possible example of coastal species with restricted range, was described from coastal mangroves of Brunei on Borneo (Dow & Choong 2015).

Record of *Pantala flavescens* from the Kanawa Island in April (dry season) aligns with available data on high migratory abilities of this dragonfly. This migratory species was recorded repeatedly on islands, which lack surface fresh water, e.g. Beihuang Island in China (Cao *et al.* 2018), Ngulu Atoll in Micronesia (Buden 2010), and Maldives (Hobson *et al.* 2012). It was shown that arrival of *Pantala flavescens* to Maldives and Seychelles is a part of its annual migration through the western Indian Ocean from India to East Africa (Anderson 2009; Hobson *et al.* 2012). Conversely, small waterless islands can support dragonfly development during the rainy season when seasonal marshes and pools emerge in various depressions. It was shown that dragonflies and other aquatic invertebrates rapidly colonized even small temporary pools such as rainwater-filled elephant footprints in the Kibale National Park, Uganda, East Africa (Remmers *et al.* 2017).

## Conclusion

- The Odonata colonizing extreme environments such as acidic lakes and seaside habitats in eastern Indonesia are primarily widespread generalist species.
- Species-poor dragonfly assemblages were recovered from extreme habitats in eastern Indonesia for the first time. The highly acidic Sano Nggoang Crater Lake on Flores supported seven species, while a small coastal marsh site on the shore of this island harbored five species. One migratory species was found on a waterless islet near the eastern edge of Flores.
- The Odonata fauna of Flores Island contains 46 species, with 16 Zygopteran and 30 Anisopteran taxa. Our research of museum specimens recovered two species new to the fauna of Flores: *Neurothemis intermedia excelsa* and *Pantala flavescens*. The Odonata species richness estimate on Flores is comparable with that on Timor but much lower than that on Sumba.

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