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 prunosum prunosum, 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 (Lief tinck 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 *Sympecrum haritonovi* Borisov, 1983 (Libellulidae) in the Tien-Shan, Pamir-Alai and Kopetdag 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; McCreadie 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; Rychła 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. Lief tinck 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 (Lief tinck 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]; $BOD (5 \text{ days} 20^\circ C): 223.8$ [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 Xiphagrion 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               |
|-----------------|---------------------|------------------------------|-----------------------------|--------------------------------------------------------|
| **ZYGOPTERA**   |                     |                              |                             |                                                        |
| Euphaeidae      | *Allophaea* Fraser, 1929 | *A. lara lombokensis* (McLachlan, 1898) | Lombok, Sumbuwa, Flores, Groot Bastaard, Pantar, Alor | Lieftinck (1936, 1953)                                  |
| Chlorocyphidae  | *Libellago* Selys, 1840 | *L. naias* Lieftinck, 1932  | Flores, Sumba               | Lieftinck (1936, 1953)                                  |
| Chlorocyphidae  | *Rhinocypha* Rambur, 1842 | *R. pagenstecheri pagenstecheri* Förster, 1897 | Lombok, Sumbawa, Flores, Sumba | Lieftinck (1936, 1953)                                  |
| Platycnemididae | *Copera* Kirby, 1890 | *C. marginipes* (Rambur, 1842) | Oriental Region             | Lieftinck (1936, 1953)                                  |
| Platycnemididae | *Nososticta* Hagen, 1860 | *N. emphyla* (Lieftinck, 1936) | Lombok, Sumbawa, Flores, Sumba, Sawu, Timor | Lieftinck (1936, 1953); Seehausen (2017)               |
| Platycnemididae | *Nososticta* Hagen, 1860 | *N. selysii* ( Förster, 1896) | Komodo, Flores, Sumba, Sawu, Timor | Lieftinck (1936, 1953); Seehausen (2017)               |
| Coenagrionidae  | *Argiocnemis* Selys, 1877 | *A. femina* (Brauer, 1868) | Oriental Region             | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Argiocnemis* Selys, 1877 | *A. pygmaea* (Rambur, 1842) | Oriental and Australian regions | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Argiocnemis* Selys, 1877 | *A. rubescens* Selys, 1877 | Oriental and Australian regions | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Pseudagrion* Selys, 1876 | *P. microcephalum* (Rambur, 1842) | Oriental and Australian regions | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Pseudagrion* Selys, 1876 | *P. ptilidorsum declaratum* Lieftinck, 1936 | Lombok, Flores, Sawu, Alor | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Pseudagrion* Selys, 1876 | *P. rubriceps* Selys, 1876 | Oriental Region             | Lieftinck (1936, 1953)                                  |
| Coenagrionidae  | *Xiphiagrion* Selys, 1876 | *X. cyanomelas* (Selys, 1876) | Indonesia, Timor, the Philippines, and New Guinea | Lieftinck (1936, 1953); this study                      |
| Platystictidae  | *Drepanosticta* Laidlaw, 1917 | *D. floresiana* Lieftinck, 1939 | Flores | Lieftinck (1939, 1953)                                  |
| Lestidae        | *Indolestes* Fraser, 1922 | *I. floresianus* Lieftinck, 1960 | Flores | Lieftinck (1960)                                      |
| Lestidae        | *Lestes* Leach, 1815 | *L. concinnus* Hagen, 1862 | Oriental and Australian regions | Lieftinck (1953)                                      |
| **ANISOPTERA**  |                     |                              |                             |                                                        |
| Libellulidae    | *Acisoma* Rambur, 1842 | *A. panorpoide* Rambur, 1842 | Oriental Region             | Lieftinck (1936, 1953)                                  |
| Libellulidae    | *Agrionoptera* Brauer, 1864 | *A. insignis insignis* (Rambur, 1842) | Oriental Region             | Lieftinck (1936, 1953)                                  |
| Libellulidae    | *Brachydiplax* Brauer, 1868 | *B. duivenbodei* (Brauer, 1866) | Oriental and Australian regions | Lieftinck (1936, 1953)                                  |
| Libellulidae    | *Crocothemis* Brauer, 1868 | *C. servilia* (Drury, 1773) | Oriental and Australian regions | Lieftinck (1936, 1953)                                  |
| Libellulidae    | *Diplacodes* Kirby, 1889 | *D. trivialis* (Rambur, 1842) | Seychelles Islands, Oriental and Australian regions | Lieftinck (1936, 1953); this study                      |
| Libellulidae    | *Lathrecista* Kirby, 1889 | *L. asiatica asiatica* (Fabricius, 1798) | Oriental and Australian regions | Lieftinck (1953)                                      |
| Libellulidae    | *Neurothemis* Brauer, 1887 | *N. intermedia excelsa* Lieftinck, 1934 | Java, Kangean Islands, Flores, and Sumba | This study                                           |

...continued on the next page...
| Suborder/Family | Genus | Species | Range* | Reference to occurrence on Flores Island |
|----------------|-------|---------|--------|------------------------------------------|
| Libellulidae   | Neurothemis Brauer, 1867 | N. ramburii (Brauer, 1866) | Indonesia and the Philippines | Lief tinck (1936, 1953) |
| Libellulidae   | Neurothemis Brauer, 1867 | N. terminata Ris, 1911 | Indonesia, Timor, and the Philippines | Lief tinck (1936, 1953); this study |
| Libellulidae   | Orthetrum Newman, 1833 | O. glaucum (Brauer, 1865) | Oriental Region | Lief tinck (1936, 1953) |
| Libellulidae   | Orthetrum Newman, 1833 | O. pruinosum pruinosum (Burmeister, 1839) | Indonesia | Lief tinck (1936, 1953) |
| Libellulidae   | Orthetrum Newman, 1833 | O. sabina (Drury, 1773) | Nearly cosmopolitan | Lief tinck (1936, 1953); this study |
| Libellulidae   | Orthetrum Newman, 1833 | O. testaceum soembanum Förster, 1903 | Lombok, Sumbawa, Flores, Alor, Wetar | Lief tinck (1936, 1953) |
| Libellulidae   | Pantala Hagen, 1861 | **P. flavescens (Fabricius, 1798) | Nearly cosmopolitan | This study |
| Libellulidae   | Rhodothemis Ris, 1909 | R. rufa (Ram bur, 1842) | Oriental and Australian regions | Lief tinck (1936, 1953); Seehausen et al. (2018) |
| Libellulidae   | Rhyothemis Hagen, 1861 | T. aurora (Burmeister, 1839) | Oriental Region | Lief tinck (1936, 1953) |
| Libellulidae   | Trithemis Brauer, 1868 | T. festiva (Ram bur, 1842) | From Southern Europe via Oriental Region to New Guinea | Lief tinck (1936, 1953); Seehausen (2017) |
| Libellulidae   | Trithemis Brauer, 1868 | T. lilacina Förster, 1899 | Bali, Lombok, Sumbawa, Flores, Sumba, Timor | Lief tinck (1936, 1953); Seehausen et al. (2018) |
| Libellulidae   | Zyxomma Ram bur, 1842 | Z. obtusum Albarda, 1881 | Oriental and Australian regions | Lief tinck (1953) |
| Corduliidae    | Hemicordulia Selys, 1870 | H. australiae (Ram bur, 1842) | Lesser Sundas, Lord Howe, Norfolk, Australia, and New Zealand | Lief tinck (1953) |
| Corduliidae    | Procordulia Martin, 1907 | P. sambawana (Förster, 1899) | Sumbawa, Flores | Lief tinck (1936) |
| Aeshnidae      | Anax Leach, 1815 | A. gibbosulus Ram bur, 1842 | Sumatra, Java, Flores, Sumba, Sawu, Kei, New Guinea, and Australia | Lief tinck (1936, 1953) |
| Aeshnidae      | Anax Leach, 1815 | A. guttatus (Bur meister, 1839) | Oriental and Australian regions | Lief tinck (1936, 1953) |
| Aeshnidae      | Gynacantha Ram bur, 1842 | G. musa Karsch, 1892 | Java and Flores | Lief tinck (1936, 1953) |
| Gomphidae      | Paragomphus Cowley, 1934 | P. flavohamatus (Martin, 1921) | Lombok, Sumbawa, Flores | Lief tinck (1936, 1953) |

*Based on the world’s catalogue (Steinmann 1997a, b) with some additions (Lief tinck 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 ixioides* (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 1936: 134). "Many specimens, W. Flores, Mborong, 100 m, 8.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: 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 Bajo, 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 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, 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 Ecolodge, small permanent marsh on the sea coast, 8.5220°S, 119.8704°E [site 2], 13.1.2012, 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 be 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 Ecolodge, 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 pruinosum pruinosum (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).
Orthetrum testaceum soembanum Förster, 1903

Material examined: Not available.

Earlier records from Flores: “Kratersee 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 Ecolodge, 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♂, 1♀, 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).

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**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 florestiana* 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 *Xiphiaigrion cyanomelomias*. Additionally, *Orthetrum pruinosum pruinosum*, *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 *Xiphiaigrion cyanomelomias* 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 *Xiphiaigrion cyanomelomias* and *Orthetrum pruinosum* 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; Rychła et al. 2011). Only chironomids were recorded in the acidic Banyupahit-Banyuputh 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 (Rychła 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 ixiuas*. 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; McCreddie 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.

Acknowledgments

We are grateful to Mr. Mikel Albarran Valle (Indonesia) for his great help during this study. Special thanks go to Wiwin Windari Petersen (Indonesia) who kindly provided a photo of the Sano Nggoang Lake for this paper. The Ministry of Science and Higher Education of Russia supported this work as follows: project AAAA-A17-117033010132-2 to Y.S.K., project AAAA-A18-118012390161-9 to M.Y.G. and I.N.B., and project AAAA-A18-118011690221-0 to G.S.P.

References

Aksenova, O. V., Potapov, G. S., Bespalaya, Y. V., Kolosova, Y. S., Vikhrev, I. V., Kondakov, A. V., Gofarov, M. Y. & Bolotov, I. N. (2020) Dragonflies from hot springs in Russia with a country-level checklist of species known to occur in geothermal environments. *Ecologica Montenegrina*, 34, 49–63. http://dx.doi.org/10.37828/em.2020.34.6

Anderson, R. C. (2009) Do dragonflies migrate across the western Indian Ocean? *Journal of Tropical Ecology*, 25(4), 347–358. https://www.jstor.org/stable/25562628

Apodaca, C. K. & Chapman, L. J. (2004) Larval damselflies in extreme environments: behavioral and physiological response to hypoxic stress. *Journal of Insect Physiology*, 50(9), 767–775.
https://doi.org/10.1016/j.jinsphys.2004.05.007
Arrowsmith, J., Shivaprakash, K. N., Larrivée, M., Turgeon, J. & Lessard, J. P. (2018) Environmental filtering along a broad-scale acidity gradient shapes the structure of odonate communities. *Ecosphere*, 9(12), e02473. https://doi.org/10.1002/ecs2.2473

Bolotov, I. N., Kondakov, A. V., Spitsyn, V. M., Gofarov, M. Yu. & Kolosova, Yu. S. (2017) *Leptocneria vinarskii* sp. nov. (Lepidoptera: Erebidae: Lymantriinae), an overlooked Wallacean lineage of the Australian genus. *Scientific Reports*, 7, 1–7. https://doi.org/10.1038/s41598-017-12797-3

Bolotov, I. N., Gofarov M. Y., Kolosova, Y. S. & Spitsyn, V. M. (2018a) Bird fauna of the small island Kanawa, Flores Sea, Indonesia. *Russian Journal of Ornithology*, 27(1668), 4459–4467.

Bolotov, I. N., Kondakov, A. V. & Spitsyn V. M. (2018b) A review of tiger moths (Lepidoptera: Erebidae: Arctiinae: Arctiini) from Flores Island, Lesser Sundas Archipelago, with description of a new species and new subspecies. *Ecológica Montenegrina*, 16, 1–15. https://doi.org/10.37828/em.2018.16.1

Bolotov, I. N., Spitsyn, V. M., Kondakov, A. V. & Tomilova, A. A. (2019) A review of *Barsine* (Lepidoptera: Erebidae: Arctiinae: Lithosiini) from the East Nusa Tenggara Islands, Indonesia, with description of a new genus. *Ecológica Montenegrina*, 20, 207–214. https://doi.org/10.37828/em.2019.20.17

Borisov, S. N. (2015) Dragonflies (Odonata) of thermal springs in Central Asia. *Entomological Review*, 95(9), 1203–1211. https://doi.org/10.1134/S0013873815090080

Borisov, S. N. & Malikova, E. I. (2019) Distribution and migration strategy of *Pantala flavescens* (Fabricius, 1798) (Odonata, Libellulidae) near the northern limit of its range in Transbaikalia and in the Far East of Russia. *Euroasian Entomological Journal*, 18(3), 155–162. https://doi.org/10.15298/euroasenjt.18.3.01

Borisov, S. N. (2016) Dragonflies (Odonata) of the Barguzinskaya depression and of the Svyatoi Nos Peninsula (North-Eastern Baikal region, Russ.). *Euroasian Entomological Journal*, 15(4), 339–348.

Borisov, S. N. (2017) Distribution of *Orthetrum albistylum* (Selys, 1848) (Odonata, Libellulidae) in thermal springs of the Baikal rift zone, Russia. *Euroasian Entomological Journal*, 16(4), 299–303.

Brues, C. T. (1924) Observations on animal life in the thermal waters of Yellowstone Park, with a consideration of the thermal environment. *Proceedings of the American Academy of Arts and Sciences*, 59(15), 371–438. http://www.jstor.org/stable/20026104

Brues, C. T. (1939) Studies on the fauna of some thermal springs in the Dutch East Indies. *Proceedings of the American Academy of Arts and Sciences*, 73(4), 71–95. http://www.jstor.org/stable/25130154

Buczyński, P., Shapoval, A. P. & Buczyńska, E. (2014) *Pantala flavescens* at the coast of the Baltic Sea (Odonata: Libellulidae). *Odonatologica*, 43(1/2), 3–11.

Buden, D. W. (2010) *Pantala flavescens* (Insecta: Odonata) rides west winds into Ngulu Atoll, Micronesia: Evidence of seasonality and wind-assisted dispersal. *Pacific Science*, 64(1), 141–143. https://doi.org/10.2984/64.1.141

Cannings, R. A. & Cannings, S. G. (1987) The Odonata of some saline lakes in British Columbia, Canada: ecological distribution and zoogeography. *Advances in Odonatology*, 3(1), 7–21.

Cao, L. Z., Fu, X. W., Hu, C. X. & Wu, K. M. (2018) Seasonal migration of *Pantala flavescens* across the Bohai Strait in Northern China. *Environmental Entomology*, 47(2), 264–270. https://doi.org/10.1093/ee/nvy017

Catling, P. M. (2004) Dragonflies (Odonata) emerging from brackish pools in saltmarshes of Gaspé, Quebec. *Canadian Field-Naturalist*, 123(2), 176–177. http://dx.doi.org/10.22621/cfn.v123i2.932

Catling, P. M., Hutchinson, R. & Brunelle, P. M. (2006) Use of saltmarsh by dragonflies (Odonata) in the Baie des Chaleurs region of Quebec and New Brunswick in late summer and autumn. *Canadian Field-Naturalist*, 120(4), 413–420. http://dx.doi.org/10.22621/cfn.v120i4.348

Clausnitzer, V. & Lindeboom, M. (2002) Natural history and description of the dendrolimnetic larva of *Coryphagrion granids* (Odonata). *International Journal of Odonatology*, 5(1), 29–44. http://dx.doi.org/10.1080/13887890.2002.9748175

Corbet, P. S. (1979) *Pantala flavescens* (Fabricius) in New Zealand (Anisoptera: Libellulidae). *Odonatologica*, 8(2), 115–121.

Corbet, P. S. (2004) *Dragonflies: behavior and ecology of Odonata*. Revised Edition. Harley Books, Colchester, 829 pp.
Damm, S. & Hadrys, H. (2012) A dragonfly in the desert: genetic pathways of the widespread *Trithemis arteriosa* (Odonata: Libellulidae) suggest male-biased dispersal. *Organisms Diversity & Evolution*, 12(3), 267–279. http://dx.doi.org/10.1007/s13127-012-0079-1

Dolmen, D. & Pedersen, J. (2018) *Coenagrion hastulatum* and *C. lunulatum* – their responses to the liming of acidified lakes and the release of fish. *Odonatologica*, 47(1/2), 100–120. http://dx.doi.org/10.5281/zenodo.1239949

Dow, R. A. & Choong, C. Y. (2015) *Mortonagrion megabiniuyag* spec. nov. from Brunei (Odonata: Zygoptera: Coenagrionidae). *Zootaxa*, 3914(1), 89–93. http://dx.doi.org/10.11646/zootaxa.3914.1.8

Dunson, W. A. (1980) Adaptations of nymphs of a marine dragonfly, *Erythrodilax herencis*, to wide variations in salinity. *Physiological Zoology*, 53(4), 445–452. http://dx.doi.org/10.1086/physzool.53.4.30157882

Dunson, W. A. & Travis, J. (1994) Patterns in the evolution of physiological specialization in salt-marsh animals. *Estuaries*, 17(1A), 102–110. http://dx.doi.org/10.2307/1552338

ESIA (2019) Indonesia - Geothermal Energy Upstream Development Program Project (GEUDP): Environmental and Social Impact Assessment for Waesano Geothermal Project (ESIA). Indonesia, 295 pp. http://documents.worldbank.org/curated/en/262681556011595144

Frolich Strong, K. & Robinson, G. (2004) Odonate communities of acidic Adirondack Mountain lakes. *Journal of the North American Benthological Society*, 23(4), 839–852.

Gorham, C. T. & Vodopich, D. S. (1992) Effects of acidic pH on predation rates and survivorship of damselfly nymphs. *Hydrobiologia*, 242(1), 51–62. https://doi.org/10.1007/BF00017643

Haber, W. A., Wagner, D. L. & De La Rosa, C. (2015) A new species of *Erythrodilax* breeding in bromeliads in Costa Rica (Odonata: Libellulidae). *Zootaxa*, 3947(3), 386–396. http://dx.doi.org/10.11646/zootaxa.3947.3.5

Haritonov, A. Y. & Borisov, S. N. (2013) Distribution and habitat characteristics of Sympetrum haritonovi Borisov, 1983 (Odonata, Libellulidae) in Central Asia mountains Tien-Shan, Pamir-Alai and Kopetdag. *Euroasiatic Entomological Journal*, 12(3), 213–216.

Hawking, J. H. & Ingram, B. A. (1994) Rate of larval development of *Pantala flavescens* (Fabricius) at its southern limit of range in Australia (Anisoptera: Libellulidae). *Odonatologica*, 23(1), 63–68.

Hobson, K. A., Anderson, R. C., Soto, D. X. & Wassenaar, L. I. (2012) Isotopic evidence that dragonflies (*Pantala flavescens*) migrating through the Maldives come from the northern Indian subcontinent. *PLoS ONE*, 7(12), e52594. https://doi.org/10.1371/journal.pone.0052594

Hudson, J. & Berrill, M. (1986) Tolerance of low pH exposure by the eggs of Odonata (dragonflies and damselflies). *Hydrobiologia*, 140(1), 21–25. https://doi.org/10.1007/BF00006725

Kalkman, V.J., Clausnitzer, V., Dijkstra, K.B. Orr, A.G., Paulson, D.R. & van Tol, J. (2008) Global diversity of dragonflies (Odonata) in freshwater. *Hydrobiologia*, 595, 351–363. https://doi.org/10.1007/s10750-007-9029-x

Kalkman, V. J. & Orr, A. G. (2016) A description of the larva and discussion of radiation in the phytotelm breeding damselfly genus *Papuagrion* in New Guinea (Odonata: Zygoptera: Coenagrionidae). *International Journal of Odonatology*, 19(3), 169–182. https://doi.org/10.1080/13887890.2016.1203363

Leggott, M. & Pritchard, G. (1986) Thermal preference and activity thresholds in populations of Argia vivida (Odonata: Coenagrionidae) from habitats with different thermal regimes. *Hydrobiologia*, 140(1), 85–92. https://doi.org/10.1007/BF00006730

Lief tinck, M. A. (1934) An annotated list of the Odonata of Java, with notes on their distribution, habits and life-history. *Treubia*, 14, 377–462. https://doi.org/10.14203/treubia.v14d.2454

Lief tinck, M. A. (1936) Die Odonaten der Kleinen Sunda Inseln. *Revue Suisse de Zoologie*, 43, 99–160.

Lief tinck, M.A. (1939) Sur quatre especes nouvelles de Platystictidae de l’Inde orientale. *Revue Francaise d’Entomologie*, 6, 144–154.

Lief tinck, M. A. (1953) The Odonata of the island Sumba with a survey of the dragonfly fauna of the Lesser Sunda Islands. *Verhandlingen der Naturforschenden Gesellschaft in Basel*, 64, 118–228.

Lief tinck, M.A. (1960) Considerations on the genus *Lestes* Leach with notes on the classification and descriptions of new Indo-Australian species and larval forms (Odonata, Lestidae). *Nova Guinea*, *Zoology*, 8, 127–171.

Löhr, A. J., Sluik, R., Olaveson, M. M., Ivorra, N., Van Gestel, C. A. & Van Straalen, N. M. (2006) Macroinvertebrate and algal communities in an extremely acidic river and the Kawah Ijen crater lake
DRAGONFLIES AND DAMSELFIES FROM FLORES ISLAND

(nPH< 0.3), Indonesia. Archiv für Hydrobiologie, 165(1), 1–21. https://doi.org/10.1127/0003-9136/2006/0165-0001

Marczak, L. B., Richardson, J. S. & Classen, M. C. (2006) Life history phenology and sediment size association of the dragonfly Cordulegastrus dorsalis (Odonata: Cordulegastridae) in an ephemeral habitat in southwestern British Columbia. Canadian Field Naturalist, 120(3), 347–350.

http://dx.doi.org/10.22621/cfn.v120i3.327

McCreadie, J. W., Ihle, D. T. & Adler, P. H. (2005) Biodiversity of larval damselflies and dragonflies (Insecta: Odonata) in the lower Mobile/Tensaw Delta, Alabama. Southeastern Naturalist, 4(2), 321–334. https://doi.org/10.1656/1528-7092(2005)004[0321:BOLDAD]2.0.CO;2

Mohamedsaid, M. S. (2009) Chrysomelidae of the Lesser Sunda Islands: Wallace’s Line and the crossing of worlds. Research on Chrysomelidae, 2, 57–104. https://doi.org/10.1163/9789004169470.1–299.21

Mossberg, P. & Nyberg, P. (1979) Bottom fauna in brackish water. Report: Institute of Fresh-water Research, Drottningholm, 58, 1–87.

Osburn, R. C. (1906) Observations and experiments on dragon-flies in brackish water. The American Naturalist, 40(474), 395–399. https://www.jstor.org/stable/2455367

Pritchard, G. (1991) Insects in thermal springs. The Memoirs of the Entomological Society of Canada, 123(S155), 89–106. https://doi.org/10.4039/entm123155089-1

Pritchard, G. (2008) The life history of a temperate zone dragonfly living at the edge of its range with comments on the colonization of high latitudes by Neotropical genera of Zygoptera (Odonata). International Journal of Odonatology, 11(2), 209–223. https://doi.org/10.1080/13887890.2008.9748324

Remmers, W., Gameiro, J., Schaberl, I. & Clausnitzer, V. (2017) Elephant (Loxodonta africana) footprints as habitat for aquatic macroinvertebrate communities in Kibale National Park, south-west Uganda. African Journal of Ecology, 55(3), 342–351. https://doi.org/10.1111/aje.12358

Rodrigues, G. G. & Scharf, B. W. (2001) Review of benthic invertebrate fauna in extremely acidic environments (pH< 3). Mine Water and the Environment, 20(3), 114–121.

Rychla, A., Benndorf, J. & Buczyński, P. (2011) Impact of pH and conductivity on species richness and community structure of dragonflies (Odonata) in small mining lakes. Fundamental and Applied Limnology, 179(1), 41–50. https://doi.org/10.1127/1863-9135/2011/0179-0041

Schwarz, E. A. (1891). Preliminary remarks on the insect fauna of the Great Salt Lake, Utah. The Canadian Entomologist, 23(11), 235–248. https://doi.org/10.4039/Ent23235

Seehausen, M. (2017) Survey of Odonata from Timor Island, with description of the female of Anax georgius (Odonata: Aeshnidae). Faunistic Studies in Southeast Asian and Pacific Island Odonata, 20, 1–34.

Seehausen, M. & Günther, A. (2016) Records of Neurothemis nesaea from Sulawesi, with taxonomic annotations on the N. intermedia-group (Odonata: Libellulidae). Odonatologica, 45(3/4), 271–290.

Seehausen, M. & Dow, R. A. (2016) Morphological studies and taxonomic considerations on the ‘reddish-brown-winged’ group of Neurothemis Brauer, 1867 with the description of N. taiwanensis sp. nov. (Odonata: Libellulidae). International Dragonfly Fund Report, 93, 1–101.

Seehausen, M. & Theischinger, G. (2017) Nososticta impercepta sp. nov. (Odonata: Platycnemididae) from Timor, with a key to the Sundac species. Zootaxa, 4250(3), 262–274. https://doi.org/10.11646/zootaxa.4250.3.4

Seehausen, M., da Silva Pinto, R. M., Trainor, C. R. & Lopes, J. P. (2018) Further records of Odonata from Timor Island, with the first photographs of living Nososticta impercepta (Odonata: Platycnemididae) and additional records from Rote and Romang Islands. Faunistic Studies in Southeast Asian and Pacific Island Odonata, 25, 1–73.

Spitsyn, V. M. & Bolotov, I. N. (2018) Barsine podbolotskayae sp. n. from Flores Island, Lesser Sunda Archipelago, Indonesia (Lepidoptera, Erebidiae, Arctiinae). ZooKeys, 768, 105–111. https://doi.org/10.3897/zookeys.768.24345

Spitsyn, V. M. & Bolotov, I. N. (2020) Euapterote elisavetae sp. nov. from Flores Island, Indonesia (Lepidoptera: Eupterotidae). Ecologica Montenegrina, 29, 51–55. https://doi.org/10.37828/em.2020.29.8

Spitsyn, V. M. & Bolotov, I. N. (2020) Teuloma bajawica sp. nov. from Flores Island, Indonesia (Lepidoptera: Erebidiae: Arctiinae: Lithosiini). Ecologica Montenegrina, 31, 35–39. https://doi.org/10.37828/em.2020.31.7
Spitsyn, V. M. & Bolotov, I. N. (2020c) Theretra makhrovi sp. nov. from Flores Island, Indonesia (Lepidoptera: Sphingidae). *Ecologica Montenegrina*, 31, 1–5. https://doi.org/10.37828/em.2020.31.1

Spitsyn, V. M. & Potapov, G. S. (2020) A new species of the genus Odonestis from the Flores Island, Indonesia (Lepidoptera: Lasiocampidae). *Ecologica Montenegrina*, 29, 47–50. https://doi.org/10.37828/em.2020.29.7

Spitsyn, V. M., Bolotov, I. N., Gofarov, M. Y. & Bolotov, N. I. (2016) First record of the genus Aethalida Walker, 1865 (Lepidoptera: Erebidae: Arctiinae) from Flores Island, East Nusa Tenggara, Indonesia. *Ecologica Montenegrina*, 6, 56–60.

Spitsyn, V. M., Kondakov, A. V., Bolotov, N. I., Pham, N. T., Gofarov, M. Y. & Bolotov, I. N. (2018) DNA barcoding unravels contrasting evolutionary history of two widespread Asian tiger moth species during the Late Pleistocene. *PLoS ONE*, 13(4), 1–15. https://doi.org/10.1371/journal.pone.0194200

Spitsyn, V. M., Bolotov, I. N., Kondakov, A. V. & Tomilova, A. A. (2019) Estigena wallacei sp. nov. from West Flores, Indonesia (Lepidoptera: Lasiocampidae). *Ecologica Montenegrina*, 22, 27–33. https://doi.org/10.37828/em.2019.22.2

Steinmann, H. (1997a) World Catalogue of Odonata, Vol. 1: Zygoptera. *Das Tierreich*, 110, 1–500.

Steinmann, H. (1997b) World Catalogue of Odonata. Vol. 2: Anisoptera. *Das Tierreich*, 111, 1–636.

Suhling, F., Jödicke, R. & Schneider, W. (2003) Odonata of African arid regions – are there desert species? *Cimbebasia*, 18, 207–224.

Uboni, C., Jugovic, J., Tordoni, E., Pizzul, E., Riservato, E. & Bacaro, G. (2020) Dragonfly (Odonata) diversity patterns in mixohaline coastal wetlands. *Estuaries and Coasts*, 43(2), 375–386. https://doi.org/10.1007/s12237-019-00687-y

Van Tol, J. (2020) Odonata: Global Species Database of Odonata (version Dec 2011). Species 2000 & ITIS Catalogue of Life, 2020-08-01 Beta, Naturalis, Leiden, the Netherlands. www.catalogueoflife.org/col

Villanueva, R. J. T. (2011a) Odonata fauna of Diomabok Lake and its surroundings, Davao Oriental, Mindanao Island, Philippines. *International Dragonfly Fund Report*, 38, 1–29.

Villanueva, R. J. T. (2011b) Odonata of Siargao and Bucas Grande islands, the Philippines. *International Dragonfly Fund Report*, 34, 1–25.

Watson, J. A. L. & Arthington, A. H. (1978) A new species of Orthetrum Newman from dune lakes in eastern Australia (Odonata: Libellulidae). *Australian Journal of Entomology*, 17(2), 151–157. https://doi.org/10.1111/j.1440-6055.1978.tb02223.x

Weir, J. S. (1974) Odonata collected in and near seasonal pools in Wankie National Park, Rhodesia, with notes on the physico-chemical environments in which nymphs were found. *Journal of the Entomological Society of Southern Africa*, 37(1), 135–145. https://hdl.handle.net/10520/AJA000128789_2846

Wilson, K. D. P. (2020) Marine dragonfly under threat at Lantau, Hong Kong (Odonata: Orthetrum poecilops). *Agrion*, 24(2), 162–168.

Wright, M. (1943) A comparison of the dragonfly fauna of the lower delta of the Mississippi River with that of the marshes of the Central Gulf Coast. *Ecological Monographs*, 13(4), 481–497. https://doi.org/10.2307/1948592

Zolotukhin, V. V. & Witt, T. J. (2005) Contribution to the knowledge of Indonesian Lasiocampidae (Lepidoptera). *Tinea*, 19(1), 59–68.