Dragonflies from mainland Yemen and the Socotra Archipelago – additional records and novelties

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Abstract

The odonatological results of two field trips to mainland Yemen carried out mainly in summer 2005 and winter 2007, and to Socotra in winter 1999 are put on record. At 30 localities, 33 dragonfly species were collected, respectively observed (3). One species, *Azuragrion somalicum* is new for mainland Yemen, and a second, *Pseudagrion niloticum*, is new for mainland Yemen and the Arabian Peninsula. Three species, *Azuragrion somalicum, Orthetrum julia*, and *Sympetrum fonscolombii* are new records for Socotra.

Kurzfassung

Die odonatologischen Ergebnisse zweier Feldaufenthalte auf dem jemenitischen Festland hauptsächlich im Sommer 2005 und Winter 2007 und auf Socotra im Winter 1999 werden mitgeteilt. An 30 Fundorten wurden 33 Libellenarten gesammelt oder beobachtet (3). *Azuragrion somalicum* ist neu für das jemenitische Festland, *Pseudagrion niloticum*, ist neu für das jemenitische Festland und die Arabische Halbinsel. *Azuragrion somalicum, Orthetrum julia* und *Sympetrum fonscolombii* sind Neunachweise für Socotra.

Introduction

The southwest of Arabia, comprising the Asir Mountains in Saudi Arabia and the high mountains of Yemen, is one of three biological hotspots of the peninsula, the other two being Dhofar (Oman) and Hadhramout (Yemen). These are considered relict pockets from more humid spells of the late Pleistocene and Holocene (Samraoui et al. 1993). With more than 40 taxa the southwest exhibits the highest species richness.

Although the three regions seem to differ slightly in species composition, this may turn out as an artifact once the odonate fauna of the Mahri and al-Hawf regions close to Dhofar become better known. Compared to other oceanic islands and taking into account its large size, Socotra has an impoverished odonate fauna with only one endemic.

Abbreviations

Collectors and/or illustrators: E.F.: Eva Feldkamp (Frankfurt a.M., Germany). – A.K.N.: Abdul Karim Nasher (University of Sana'a, Yemen). – H.P.: Hans Pohl (Phyletisches Museum, University of Jena, Germany). – W.S.: Wolfgang Schneider (Senckenberg Museum, Frankfurt a.M., Germany). – K.v.D.: Kay van Damme (University of Birmingham, UK).

List of localities with species present

Yemen mainland (localities 1-16) (Figure 1)

1. Wadi al-Khun (Hadhramout): 03.06.2005, 16°09'45"N 49°04'46"E, 689 m a.s.l.: *Arabicnemis caerulea, Ischnura evansi, Trithemis annulata, T. arteriosa*

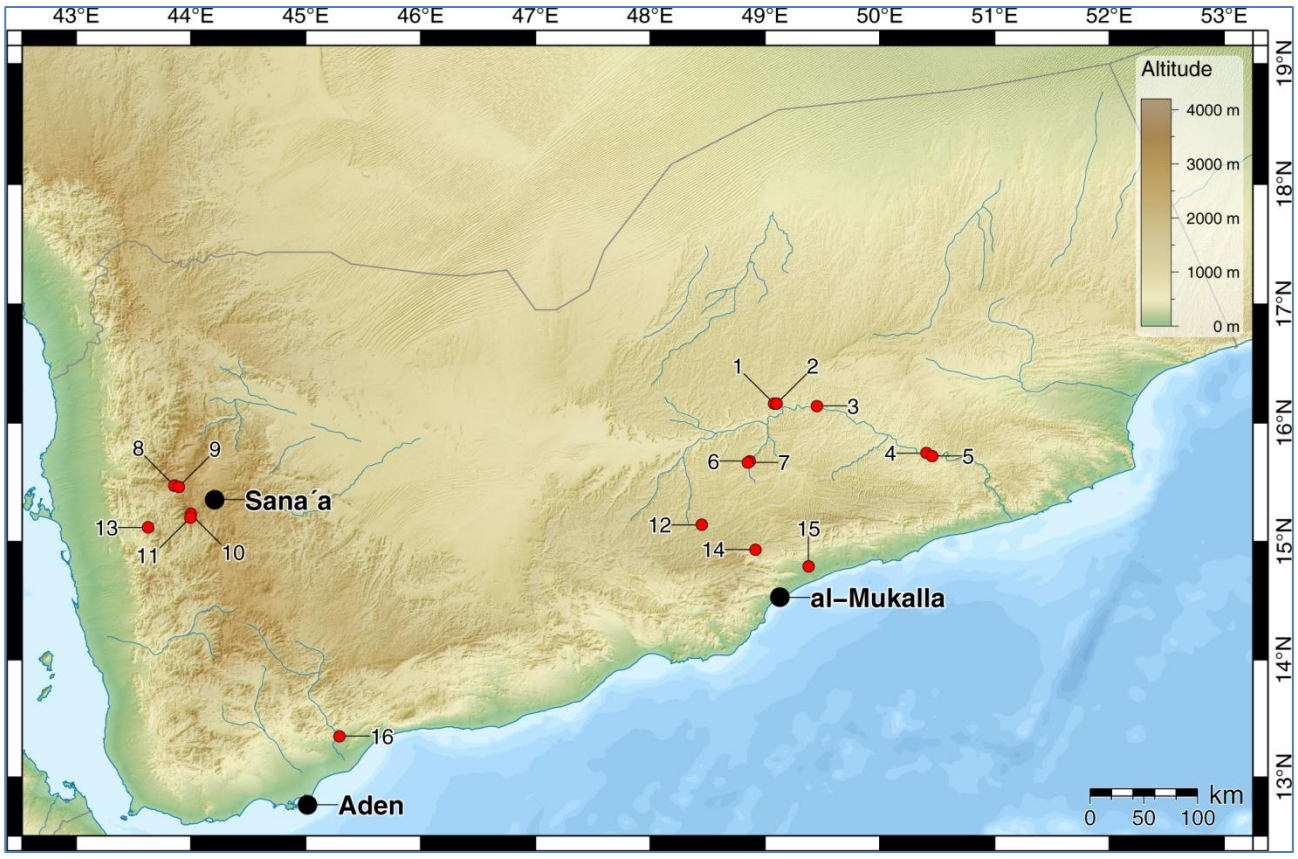

Fig. 1: Map of mainland Yemen, showing position of collecting sites (E. F.).

2. Wadi al-Khun (Hadhramout): 03.06.2005, 16°09’45”N 49°06’02”E, 659 m a.s.l.: *Arabicnemis caerulea, Ceriagrion glabrum, Ischnura evansi, Pseudagrion hamoni, Nesciothemis farinosa, Orthetrum abbotti, O. chrysostigma, Trithemis annulata, T. arteriosa*
3. Wadi Massila at Bir (Hadhramout): 04.06.2005, 16°08’36”N 49°27’07”E, 542 m a.s.l.: *Arabicnemis caerulea, Ischnura evansi, Crocothemis erythraea, Nesciothemis farinosa, Trithemis annulata*
4. Wadi Massila at al-Hind (Hadhramout): 05.06.2005, 15°44’53”N 50°24’32”E, 388 m a.s.l.: *Arabicnemis caerulea, Nesciothemis farinosa, Orthetrum sabina, Trithemis annulata, T. arteriosa*
5. Wadi Massila (Hadhramout): 05.06.2005, 15°43’22”N 50°27’23”E, 383 m a.s.l.: *Arabicnemis caerulea, Pseudagrion niloticum, Nesciothemis farinosa*
6. Wadi Ghail Omar in Wadi Sah system (Hadhramout): 02.06.2005, 15°40’51”N 48°51’59”E, 725 m a.s.l.: *Arabicnemis caerulea, Ischnura evansi, Pseudagrion hamoni, P. niloticum, P. sublacteum, Nesciothemis farinosa, Orthetrum chrysostigma, Trithemis annulata, T. kirbyi*
7. Wadi Adhm/Ghail Omar in Wadi Sah system (Hadhramout): 02.06.2005, 15°40’10”N 48°51’04”E, 727 m a.s.l.: *Arabicnemis caerulea, Ceriagrion glabrum, Ischnura evansi, Pseudagrion hamoni, P. niloticum, Nesciothemis farinosa*
8. Al-Ahjar village: artificial pond fed by waterfall, 10.06.2005 & 25.10.2007, 15°28’19”N 43°51’26”E, 2487 m a.s.l.: *Pseudagrion arabicum, Pinheyschna yemenensis, Crocothemis sanguinolenta, Orthetrum caffrum, O. julia*
9. Al-Ahjar: artificial pond fed by spring water, 10.06.2005 & 25.10.2007, 15°27’49”N 43°53’36”E, 2407 m a.s.l.: *Anax imperator, Crocothemis erythraea, Orthetrum caffrum, Sympetrum fonscolombii*
10. Matnah, 30 km W of Sana’a: 30.01.1999, 15°14’N43°60’E, 2700 m a.s.l.: *Sympetrum fonscolombii*
11. Bani Matar: 06.03.2008, 15°12’07”N 43°59’34”E, 2720 m a.s.l.: *Orthetrum caffrum*
12. Wadi Mara in Wadi Dau’an system (Hadhramout): 31.05.2005, 15°08’36”N 48°26’55”E, 1002 m a.s.l.: *Arabicnemis caerulea, Pseudagrion hamoni, Nesciothemis farinosa, Trithemis dejouxi, T. kirbyi*
13. Manaka (W of): 21.12.2007, 15°07’17”N 43°37’42”E, 962 m a.s.l.: *Zygonyx torridus*
14. Ad-Dawasir (Hadhramout): 30.05.2005, stagnant pool, 14°56’03”N 48°55’07”E, 1264 m a.s.l.: *Azuragrion somalicum, Ischnura evansi, Tramea limbata, Trithemis arteriosa*
15. Ghail Bawazir (Hadhramout): 07.12.2007, 14°47’31”N 49°22’46”E, 124 m a.s.l.: *Ischnura evansi, Pseudagrion hamoni*

16. Abyan, Batais village, 08.11.2007, 13°21’00”N 45°17’46"E, 170 m a.s.l.: *Anax imperator, Hemianax ephippiger, Paragomphus genei, Crocothemis erythraea, Pantala flavescens, Trithemis annulata, T. arteriosa, T. kirbyi*

Socotra island and Samha (localities 17-30) (Figure 2)

17. Hadibo: town and surroundings, 02.02.-26.02.1999, 12°39’11”N 54°01’08”E, 7 m a.s.l.: *Macrodiplax cora*
18. Wadi Daneghan: 13.02.1999, 12°38’59”N 54°01’04”E, 10 m a.s.l.: *Trithemis arteriosa*

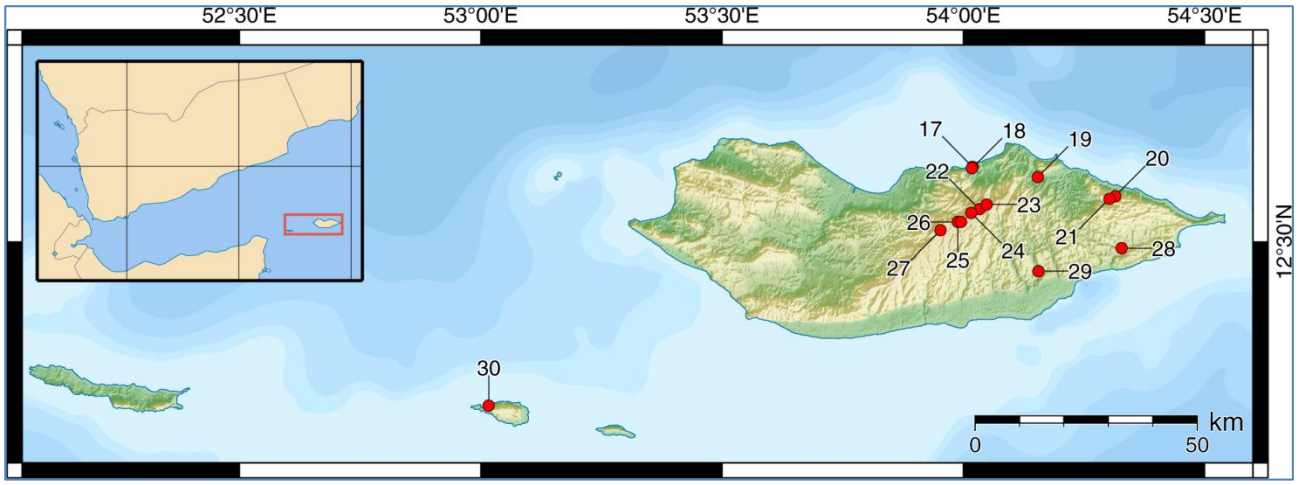

Fig. 2: Map of the Socotra Archipelago, showing position of collecting sites on Socotra and Samha (E.F.).

19. Coastal road in eastern direction: 04.02.1999, 12°37’56”N 54°09’16”E, 31 m a.s.l.: *Ceriagrion glabrum, Ischnura senegalensis, Zygonyx torridus*
20. Wadi Zeewef, ascent to Homhil: ponds between shrubs, 07.02.1999, 12°35’36”N 54°18’53”E, 136 m a.s.l.: *Orthetrum chrysostigma*
21. Wadi Zeewef, Homhil plain: 07.-08.1999, 12°35’16”N 54°18’09”E, 337 m a.s.l.: *Azuragrion granti, A. nigridorsum, Ceriagrion glabrum, Anax imperator, Crocothemis erythraea, Diplacodes lefebvrii, Orthetrum chrysostigma, Trithemis arteriosa*
22. Wadi Daneghan, ascent to Adho Dimelho: 02.02.2005, 12°34’N 54°02’E, 1190 m a.s.l.: *Azuragrion granti, Crocothemis erythraea, Trithemis arteriosa*
23. Adho Dimelho: small river between shrubs, 03.02.1999, 12°34’34”N 54°02’55”E, 940 m a.s.l.: *Azuragrion granti, Orthetrum julia, Trithemis arteriosa*
24. Wadi in the Haggier Mountains: 24.02.1999, 12°33’31”N 54°01’E, 1347 m a.s.l.: *Azuragrion granti, Anax imperator, Orthetrum chrysostigma, Trithemis arteriosa*
25. Deksam plateau: 22.-24.02.1999, 12°32’26”N 53°59’21”E, 1020 m a.s.l.: *Azuragrion granti, A. nigridorsum, Trithemis arteriosa*

26. Deksam plateau: shallow marsh, 22.-24.02.1999, 12°32’26”N 53°59’43”E, 1010 m a.s.l.: *Azuragrion somalicum*
27. Deksam plateau: 22.02.1999, 12°31’26”N 53°57’11”E, 1000 m a.s.l.: *Orthetrum chrysostigma, Trithemis arteriosa*
28. Wadi Kilisan canyon: 10.02.1999, 12°29‘12“N 54°19‘40“E, 150 m a.s.l.: *Azuragrion nigridorsum, Crocothemis erythraea, Diplacodes lefebvrii, Sympetrum fonscolombii, Trithemis arteriosa*
29. Wadi en route to Nogad: 14.02.1999, 12°26’27”N 54°09’19”E, 180 m a.s.l.: *Ischnura senegalensis, Crocothemis erythraea, Trithemis arteriosa*
30. Samha Island: well, 16.02.1999, 12°10’N 53°01’E, 170 m a.s.l.: *Trithemis arteriosa*

Systematic account

Platycnemididae - Featherlegs

Arabicnemis caerulea Waterston, 1984 – Powder Blue Damsel

Specimens studied: Mainland: 1: 2 ♂♂, 1 ♀ (1 pair in copula), W.S. – 2: 11 ♂♂, 1 ♀♀, W.S. – 3: 3 ♂♂, 1 ♀, W.S. – 4: 4 ♂♂, 2 ♀♀, W.S. – 5: 3 ♂♂, W.S. – 6: 1 ♂, W.S. – 7: 2 ♂♂, 1 ♀ (1 pair in copula), W.S. – 12: 8 ♂♂, 3 ♀♀ (one pair in copula).

In 2005 *Arabicnemis caerulea* was abundant at all its collecting sites in Wadi Hadhramout. The most recent records (2008-2011) are localized in the northeastern subpopulation in Oman (Wilson 2008, Schneider unpublished).

Coenagrionidae – Pond Damsels

Azuragrion granti (McLachlan, 1903) – Grant’s Bluet

Specimens studied: Socotra: 21: 1 ♂, 1 ♀, H.P. – 22: 2 ♂♂, 1 ♀, H.P. – 23: 1 ♀, H.P. – 24: 4 ♂♂, 2 ♀♀. – 25: 4 ♂♂, H.P.

Originally described in the genus *Ischnura* Charpentier, 1840, the species was later transferred to *Enallagma* Charpentier, 1840 by Mclachlan (1903) and finally placed in a new genus *Azuragrion* by May (2002). This species, the only known endemic odonate of Socotra, seems to be restricted to the mountainous eastern part of the island (Riservato et al. 2010).

Azuragrion nigridorsum (Selys, 1876) – Sailing Bluet

Specimens studied: Socotra: 21: 5 ♂♂, 1 ♀, H.P. – 28: 1 ♂, H.P.

In Arabia the species has a discontinuous range with two areas in mainland Yemen and southern Oman and one in the eastern part of Socotra island.

Azuragrion somalicum (Longfield, 1931) [subsp. *amitinum* Waterston, 1991] – Somali Bluet

Specimens studied: 14: 1 ♂, W.S. – 26: 1 ♂, K.v.D.

New to mainland Yemen and the Socotra Archipelago. Although the species' presence in Yemen was anticipated (Schneider & Dumont 1997), this record lies about 600 km west of its known distribution around Salalah in Dhofar, Oman. The most recent Arabian record published together with a good photograph of a male is from a Wadi NE of Salalah (van der Weide & Kalkman 2008). The new record from Hadhramout suggests a wider distribution in south Arabia. To clarify the status of the subspecies *amitinum* Waterston, 1991 longer series of specimens are needed.

Ceriagrion glabrum (Burmeister, 1839) – Common Citril

Specimens studied: Mainland: 2: 5 ♂♂, 1 ♀, W.S. – 7: 1 ♂, W.S. – Socotra: 19: 6 destroyed specimens, H.P. – 21: 2 ♂♂, H.P.

Ischnura evansi Morton, 1919 – Evan's Bluetail

Specimens studied: Mainland: 1: 1 ♀, W.S. – 2: 1 ♀, W.S. – 3: 3 ♂♂, 2 ♀♀, W.S. – 6: 1 ♂, 1 ♀, W.S. – 7: 1 ♂, W.S. – 14: 4 ♂♂, 1 ♀, A.K.N. – 15: 3 ♂♂, 1 ♀, A.K.N.

Ischnura senegalensis (Rambur, 1842) – Marsh Bluetail

Specimens studied: Socotra: 19: 1 ♂, H.P. – 29: 1 ♂, H.P.

Pseudagrion arabicum Waterston, 1980 – Arabian Sprite

Specimens studied: Mainland: 8: 1 ♂ (2007), W.S. & A.K.N.

Pseudagrion arabicum is a rare endemic species of southwestern Arabia and is known from a rather small range in the coastal mountains of the Red Sea in Saudi Arabia and Yemen. This is a high mountain species ranging from 2,000 to 3,000 m a.s.l. Ten records are now available from 6 different localities (Waterston 1980, 1985; Dumont & Al-Safadi 1991; Schneider & Krupp 1993; Schneider & Parr 1998).

Pseudagrion hamoni Fraser, 1955 – Hamon's Sprite

Specimens studied: Mainland: 2: 2 ♂♂, W.S. – 6: 17 ♂♂, 3 ♀♀, W.S. – 7: 5 ♂, 1 ♀, W.S. – 12: 7 ♂♂, 3 ♀♀, W.S. – 15: 1 ♂, A.K.N.

Pseudagrion hamoni is widely distributed in sub-Saharan Africa, Somalia, and Ethiopia, with Sahelian relict populations in Mauritania, S-Algeria, S-Libya. In Arabia the species is common in the mountains of the south and southwest of Yemen and Saudi Arabia. 70 records are now available from 45 different localities. (Waterston 1985; Al-Safadi 1990; Dumont & Al-Safadi 1991, 1993; Schneider & Krupp 1993; Krupp et al. 2006; Lambret & Boudot 2009).

Pseudagrion niloticum Dumont, 1978 (Figure 3) – Nile Sprite

Specimens studied: Mainland: 5: 11 ♂♂, 2 ♀♀, W.S. – 6: 8 ♂♂, 1 ♀, W.S. – 7: 5 ♂♂, 1 ♀, W.S. Comparative specimens: males from Kenya (Coll. V. Clausnitzer & Coll. K.-D.B. Dijkstra), males and a female from Sudan (Coll. H.J. Dumont)

This species is new for Yemen and the Arabian Peninsula and an interesting addition from the zoogeographical point of view. It is considered the northern vicariant (Nile valley, Somalia, East Ethiopia) of *P. acacia* (southern Africa, African Plateau) with which it was often confused in the past (Dumont 1978). In fact, both species are so closely related that Dumont & Martens (1984) postulated a common, late Pleistocene ancestor.

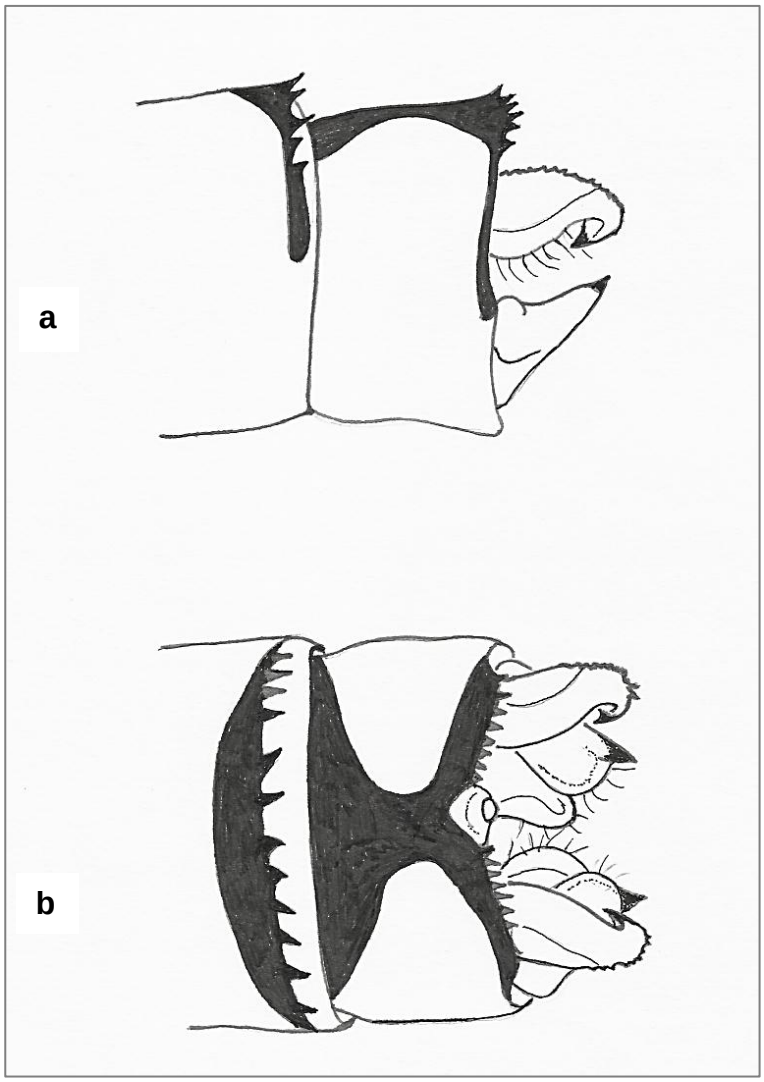

Fig. 3: *Pseudagrion niloticum*, male from Wadi Massila (collecting station 5). a: tip of abdomen with anal appendages in lateral view. b: the same in dorsal view (drawings W.S.).

Pseudagrion sublacteum (Karsch, 1893) – Cherry-eye Sprite

Specimens studied: Mainland: 6: 4 ♂♂, W.S.

In Arabia *Pseudagrion sublacteum* is restricted to Yemen, southern Oman and the western Red Sea mountains in Saudi Arabia (Waterston 1980, Waterston & Pittaway 1991, Schneider & Krupp 1993) with voucher specimen checked and confirmed by the first author. 42 records are available from 22 localities. Arabian populations were first ascribed to the Levantine subspecies *mortoni* Schmidt, 1936, but a comparison with African populations has shown that Arabian populations belong to the nominal subspecies (Dumont & Al-Safadi 1991).

Aeshnidae - Hawkers

Anax imperator (Leach, 1815) – Blue Emperor

Specimens studied/observation: Mainland: 9: 1 ♂ (observation, 2005), W.S. – 16: 1 ♂, 2 ♀, A.K.N. – Socotra: 21: 1 ♀, caught in Malaise trap at night, H.P. – 24: 1 ♀, H.P.

Hemianax ephippiger (Burmeister, 1839) – Vagrant Emperor

Specimens studied: Mainland: 16: 2 ♂♂, A.K.N.

Pinheyschna yemenensis (Waterston, 1985) – Arabian Hawker

Observations: Mainland: 8: Several specimens seen hovering high in the air (2007).

Gomphidae – Clubtails

Paragomphus genei (Selys, 1841) – Green Clubtail

Specimens studied: Mainland: 16: 2 ♂♂, 3 ♀♀, A.K.N.

Libellulidae - Skimmers

Crocothemis erythraea (Brullé, 1832) – Broad Scarlet

Specimens studied: Mainland: 3: 1 male, W.S. – 9: 1 male, 2 females (2005), W.S. – 16: 1 male, 1 female, A.K.N. – Socotra: 21: 2 ♂♂, H.P. – 22: 1 ♂, H.P. – 28: 2 ♂♂, H.P. – 29: 1 ♂, H.P.

Crocothemis sanguinolenta (Burmeister, 1839) – Little Scarlet

Specimens recorded: Mainland: 8: 1 ♂ (2005), W.S.

Diplacodes lefebvrii (Rambur, 1842) – Black Percher

Specimens studied: Socotra: 21: 1 ♂, 1 ♀, H.P. – 28: 2 ♂♂, H.P.

Nesciothemis farinosa (Förster, 1891) – Black-tailed Skimmer

Specimens studied: Mainland: 2: 1 ♂, W.S. – 3: 1 ♂, W.S. – 4: 1 ♂, W.S. – 5: 1 ♂, W.S. – 6: 6 ♂♂, W.S. – 7: 1 ♀, W.S. – 12: 1 ♂, W.S.

Macrodiplax cora (Kaup in Brauer, 1867) – Coastal Glider

Specimens studied: Socotra: 17: 1 ♂, H.P.

Orthetrum abbotti (Calvert, 1892) – Abbott's Skimmer

Specimens studied: Mainland: 2: 3 ♂♂, W.S.

This new locality and the first one, Hami hotsprings (Dumont & al-Safadi 1993), lie in Hadhramout. As the species has been recorded from Jordan (Dumont 1977, Monnerat 2010), it should be searched for in wadi systems along the Red Sea coast of Saudi Arabia and Yemen.

Orthetrum caffrum (Burmeister, 1839) – Two-striped Skimmer

Specimens studied: Mainland: 8: 7 ♂♂ (2005), W.S., 4 ♂♂ (2007), W.S. & A.K.N. – 9: 1 ♀ (2005), W.S., 1 ♂ (2007), W.S. & A.K.N. – 11: 1 ♂, A.K.N.

Orthetrum chrysostigma (Burmeister, 1839) – Epaulet Skimmer
Specimens studied: Mainland: 2: 1 ♂, W.S. – 6: 1 ♂, W.S. – Socotra: 20: 1 ♂. – 21: 2 ♂♂, H.P. – 24: 1 ♂, 1 ♀, H.P. – 27: 2 ♂♂, 1 ♀, H.P.

Orthetrum julia Kirby, 1900 [*falsum* Longfield, 1955] – Julia Skimmer
Specimens studied: Mainland: 8: 2 ♂♂ (2007), W.S. & A.K.N. – Socotra: 23: 1 ♂, H.P.
This is a new record for Socotra. On the mainland, the species is known only from one locality in the west of Yemen, al-Ahjar (collecting station 8) where it was discovered in March 1996 (Schneider and Parr 1998).

Orthetrum sabina (Drury, 1773) – Slender Skimmer
Observation: Mainland: 4: 1 ♂ observed, W.S.

Pantala flavescens (Fabricius, 1798) – Globe Skimmer
Specimens studied: Mainland: 16: 1 ♂, A.K.N.

Sympetrum fonscolombii (Selys, 1840) – Red-veined Darter
Specimens studied: Mainland: 9: 4 ♂♂ (2007), W.S. & A.K.N. – 10: 1 ♂, H.P. – 28: 2 ♂, H.P.
New record for Socotra (see Discussion).

Tramea limbata (Desjardins, 1832) – Voyaging Glider
Specimens studied: Mainland: 14: 1 ♂, W.S.

Trithemis annulata (Beauvais, 1807) – Violet Dropwing
Specimens studied: Mainland: 1: 1 ♂, W.S. – 2: 1 ♂, 1 ♀, W.S. – 3: 13 ♂♂, 2 ♀♀, W.S. – 4: 2 ♂♂, W.S. – 6: 3 ♂♂, W.S. – 16: 5 ♂♂, A.K.N.

Trithemis arteriosa (Burmeister, 1839) – Red-veined Dropwing
Specimens studied: Mainland: 1: 1 ♂male, W.S. – 2: 6 ♂♂, 4 ♀, W.S. – 14: 3 ♂♂, W.S. – 16: 4 ♂♂, A.K.S. – Socotra: 18: 1 ♂, H.P. – 21: 1 ♂, H.P. – 22: 3 ♀♀, H.P. – 23: 1 ♂, H.P. – 24: 1 ♂, H.P. – 25: 1 ♂, H.P. – 27: 1 ♂, H.P. – 28: 1 ♂, 1♀, H.P. – 29: 2 ♂♂, H.P. – 30: 2 ♂♂, H.P.

Trithemis dejouxi Pinhey, 1978 – Dejoux's Dropwing
Specimens studied: Mainland: 12: 3 ♂♂, W.S.
The species was first recorded for Arabia and Yemen sub *Trithemis donaldsoni* by Dumont and Al-Safadi (1991) and again by Krupp et al. (2006) as *Trithemis* aff. *donaldsoni*. Structural characters are indeed so minor that Pinhey (1978) described the taxon as a northeastern subspecies of the in other parts of Africa widely distributed *T. donaldsoni* (Calvert, 1899). O'Neil & Paulson (2001) finally found stable characters to raise *T. dejouxi* to specific rank; they were followed by Dijkstra (2007) and Damm et al. (2010).

Trithemis kirbyi Selys, 1891 – Kirby's Dropwing
Specimens studied: Mainland: 6: 2 ♂♂, W.S. – 12: 1 ♂, W.S. – 16: 1 ♂, A.K.N.

Zygonyx torridus (Kirby, 1889) – Ringed Cascader
Specimens studied: Mainland: 13: 1 ♂, 3 ♀♀, A.K.N. – Socotra: 19: 1 ♀, H.P.

Discussion

Despite political and tribal instability, and a resulting decrease in field activities, it is the southwest of Arabia accounting for all recent additions to the odonate fauna of the peninsula. The steady increase in numbers of species in the last two decades is remarkable, and this trend is likely to continue: 52 species in Waterston & Pittaway (1991), 56 in Schneider & Krupp (1993), 57 in Dumont & Al-Safadi (1993), 59 in Schneider & Dumont (1997), 60 in Schneider & Parr (1998), and finally 61, when Dumont & Verschuren (2005) concluded that African and SW-Arabian *Orthetrum* so far identified as *taeniolatum* Schneider, 1845 pertain to a separate sister taxon, *kollmannspergeri* Buchholz, 1959. The present paper raises the number of Arabian species to 62, and species records from mainland Yemen from 40 to 42.

As far as Socotra is concerned, in the light of increasing collecting efforts, frequent and long term visits by odonatologists in the last decade, the number of new species records (3) is rather poor and not as high as anticipated. Although additions can never be ruled out, the present list is close to be complete. *Sympetrum fonscolombii* is a notorious migrant with a wide distribution in the paleotropics. Likewise *Orthetrum julia* is widespread in Africa and was recently also found in SW-Arabia (Schneider & Parr 1998), both species were therefore expected to occur on the island. The presence of *Azuragrion somalicum*, known from E-Africa (Ethiopia, Somalia) and from two relict pockets in Oman and Yemen, is more of a surprise. As *A. somalicum* and *A. nigridorsum* are both very small species, a wind-borne dispersal and arrival on the island is not unlikely. The somewhat atypical (size, morphology) *Azuragrion granti* is restricted to the eastern mountainous part of the island and may well represent a relict of an old fauna. Keeping in mind that absence of evidence is not evidence of absence, it is striking that the genus *Pseudagrion* Selys, 1876 is obviously not represented on Socotra, but is on other western Indian Ocean islands (whether continental or oceanic) like Madagascar, the Comores, and the Mascarenes. A major freshwater crisis on Socotra in the past with species extinctions is a possible explanation. The absence of primary freshwater fish and amphibians points in the same direction.

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