THE ODONATA OF NUMIDIA, NORTHEASTERN ALGERIA PART I STATUS AND DISTRIBUTION¹

Boudjéma Samraoui² & Philip S. Corbet^{3,4}

²Laboratoire de Recherche des Zones Humides, Université d'Annaba, 4 rue Hassi-Beïda, Annaba, Algeria «e-mail: bsamraoui@hotmail.com» ³I.C.A.P.B., University of Edinburgh, Scotland, U.K. ⁴Address for correspondence: Prof. P.S. Corbet, Crean Mill, Crean, St Buryan, Cornwall, TR19 6HA, U.K. «e-mail: pscorbet@creanmill.u-net.com»

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Abstract

Forty-five species of Odonata have been recorded within Numidia, which includes the El Kala and the Guerbes-Senhadja wetlands in northeastern Algeria. Five species are new to the area. Changes occurring in dragonfly diversity over a century and a half are discussed. This paper (Part I) deals with the status and spatial distribution of each recorded taxon.

Introduction

In northeastern Algeria the topography and favourable climate (annual rainfall up to 1,200 mm and a mild winter) combine to maintain a vast wetland area extending across Numidia (Fig. 1). This includes two important wetlands: in the west the Guerbes-Senhadja complex and in the east the El Kala complex, which offers large arrays of habitats inhabited by a rich fauna and flora, including many species of Afrotropical origin.

Since the time of P.H. Lucas, who collected a remarkable variety of species of Odonata during the "Exploration Scientifique de l'Algérie" (Sélys-Longchamps 1849), odonatologists have been quick to notice the importance of "Le Cercle de la Calle" (eastern Numidia). The second half of the 19th Century saw a build-up of our knowledge of Numidian Odonata (Sélys-Longchamps 1865, 1866, 1871; Mclachlan 1897). However, during the 20th Century, except for brief visits by Dumont (pers. comm.), there has been no odonatological survey of the region since those of Martin (1901, 1910). Several species, many noteworthy for their biogeographical origins, have not been seen since they were first recorded by P.H. Lucas (Sélys-Longchamps 1849). During the past nine years we have systematically surveyed most aquatic habitats within these wetland complexes, recording the distribution of Odonata.

Dedicated to the late Dr Elliot Pinhey who contributed greatly to knowledge of African Odonata.

Our survey has been attempted amid great upheavals affecting Algerian wetlands, underlining the need for data concerning the biodiversity of the study area that is adequate for conservation purposes. Separate papers deal with Algerian Odonata found outside Numidia (Samraoui & Menaï 1999) and with odonate ecology (Samraoui et al. 1998a; Samraoui & Corbet 2000, in prep.).

Methods and list of localities

More than 100 sites were sampled between January 1990 and November 1999. Information on the wetlands of eastern Numidia (the El Kala area plus the marshes around Annaba) was given by Samraoui & Bélair (1998). Collecting in western Numidia (Lac Fetzara and the Guerbes-Senhadja wetlands) has been less intensive, and details of the sites are given by Samraoui & Bélair (1997). Types of habitats sampled ranged from temporary pools to shallow lakes and marshes, and oueds (wadi) to upland streams. Some of the most important sites are listed below, together with their locations. Positions recorded as decimals of minutes were determined with a Global Positioning System (Garmin 45; Garmin/Europe Ltd, Romsey, U.K.) having a resolution of about 120 m. Other positions were taken from maps. In locality designations, the words 'Garaet' or 'Garaa' (lake/pond), 'Mare' (pool) and 'Oued' (wadi) are abbreviated to 'G', 'M' and 'O' respectively.

The El Kala wetlands complex (eastern Numidia; prefix 'E'):

- 1. Mekhada marsh (36°48'N, 8°00'E)
- 2. G Estah (36°50.556'N, 7°58.939'E)
- 3. G. Dakhla (36°50.674'N, 7° 59.077'E)
- 4. Lac des Oiseaux (36°46.800'N, 8°07.200'E)
- 5. Bou Redim marsh (36°47'N, 8°13'E)
- 6. Lac Okrera (36°50.832'N, 8°10.792'E)
- 7. Lac Bleu (36°54.701'N, 8°20'E)
- 8. La Saulaie (36°54.701'N, 8°20.291'E)
- 9. Lac Oubeïra (36°50'N, 8°23'E)
- 10. Lac Tonga (36°52'N, 8°31'E)
- 11. Djebel Ghora (36°37'N, 8°26'E)
- 12. Diebel Edough (36°55'N, 7°40'E)
- 13. O. Bouarroug (36°51.947'N, 8°20.798'E)
- 14. O. Kebir (36°46.02'N, 8°21.88'E)
- 15. O. pré-Bou Redim (36°47'N, 8°14'E)
- 16. M. Gauthier (36°50.243'N, 8°26.611'E)
- 17. O. Reguibet (36°54'N, 8°18'E)
- 18. O. Mellah (36°55'N, 8°20'E)
- 19. Sidi Amar (University of Annaba) (36°48'N, 7°42'E)
- 20. Lac Noir (36°54'N, 8°12'E)
- 21. M. Messida (36°48.769'N, 8°24.220'E)

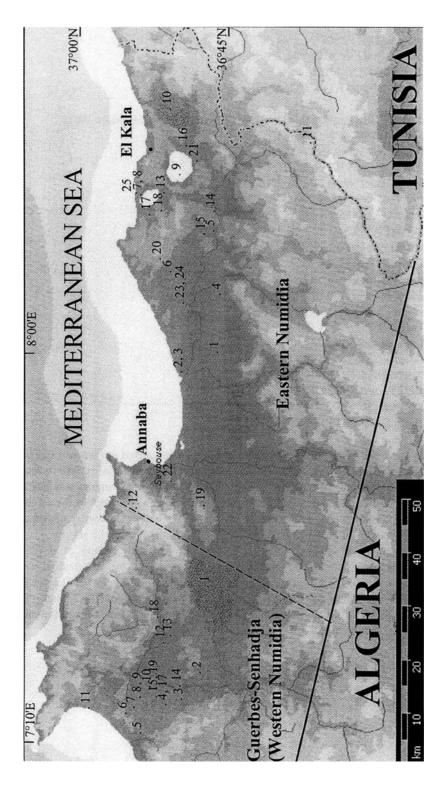


Figure 1. Map of Numidia, northeastern Algeria, showing localities visited during survey.

- 22. Boukhadra (36°52.807'N, 7°44.382'E)
- 23. Berrihane Sud (36°50.067'N, 8°06.680'E)
- 24. M. El Hrib (36°50.110'N, 8°06.680'E)
- 25. M. Ruppia (36°55.03'N, 8°20.62'E)

The Fetzara and Guerbes-Senhadja wetlands (western Numidia; prefix 'W'):

- 1. Lac Fetzara (36°48'N, 7°30'E)
- 2. G. Boumaïza (36°49.155'N, 7°18.975'E)
- 3. G. Aïn Magroun (36°50.225'N, 7°16.943'E)
- 4. G. Hadj Tahar (36° 51.774'N, 7°15.957'E)
- 5. G. Sidi Lakhdar (36°54.780'N, 7°12.055'E)
- 6. Demnat Ataoua (36°56.132'N, 7°14.780'E)
- 7. G. Dissia (36°55.349'N, 7°15.284'E)
- 8. Lac Sidi Fritis (36°53.975'N, 7°17.437'E)
- 9. G. Chichaya (36°53.791'N, 7°18.230'E)
- 10. G. Sidi Makhlouf (36°53.094'N, 7°18.248'E)
- 11. La Marsadelle (37°00.815'N, 7°15.637'E)
- 12. Bordi du Cantonnier (36°52.168'N, 7°22.760'E)
- 13. G. Tacha (36°51.979'N, 7°23.587'E)
- 14. G. Loughat (36°50'N, 7°17'E)
- 15. G. Bechna (36°53.082'N, 7°17.802'E)
- 16. G. Aïn Nechma (36°51'N, 7°16'E)
- 17. M. des Oliviers (36°53'N, 7°26')
- 18. O. El Aneb (36°50'N, 7°29'E)
- 19. G. Bouina (36°53.490'N, 7°17.574'E)

During the 1991-1994 period, intensive sampling was carried out weekly in eastern Numidia in localities E.1, 4, 7, 9, 10, 12-14 and once every two or four weeks in localities E.2, 3, 6, 8 and 16. During the same period in western Numidia less intensive sampling was carried out about every two months. Specimens are kept in the reference collection of the Laboratoire de Recherche des Zones Humides (University of Annaba).

Forty-five species of Odonata were recorded in Numidia during the survey.

The arrangement of species in the list below conforms with Jödicke et al. (2000), genera (within each subfamily) and species being placed in alphabetical order. Names of some species (e.g. *Anax ephippiger* see Gentilini & Peters 1993) have been changed since an earlier account of Algerian Odonata (Samraoui & Menaï 1999). Dates refer to the time when adults have been seen. Numbers refer to localities where the species has been recorded.

Annotated list of species recorded during the study

ZYGOPTERA

CALOPTERYGIDAE

Calopteryx h. haemorrhoidalis (Vander Linden)

Common but restricted to fast-flowing streams. E(13, 15, 17, 18).

LESTIDAE

The ecology of local Lestidae is addressed in Samraoui & Corbet (in prep.)

Lestinae

Lestes barbarus (Fabricius)

Locally abundant. E(1, 4-7, 9, 12, 16), W(4, 10, 12). Aestivates in alder carrs for four months before reproducing in seasonal ponds in autumn.

Lestes v. virens (Charpentier)

Widespread and abundant. E(2, 4-13, 16, 23, 24), W(2-5, 8-10, 12, 13). Two distinct but sympatric sister species coexist in Numidia. They are isolated reproductively: one (L. cf. virens) aestivates as adults whereas L. virens reproduces in summer, the eggs undergoing diapause and thus bridging the extended dry period.

Lestes cf. virens

A previously unrecorded species which delays its reproduction until autumn. E(1, 4, 6, 9, 11, 16), W(19). Apparently uses upland refuges as aestivating sites.

Lestes v. viridis (Vander Linden)

Common. E(1, 3-5, 7-11, 13, 14, 16), W(4, 8). Aestivates as adults in alder carrs and shady places before reproducing in late autumn in lotic habitats and to a lesser extent in temporary ponds.

Sympecmatinae

Sympecma fusca (Vander Linden)

Common in Numidia, scarce elsewhere. E(1, 4-16), W(3, 8). Adults aestivate in alder carrs and in upland woodland. They hibernate before reproducing at the end of winter. Larval development, mainly in temporary pools, is rapid and adults are on the wing before larval habitats dry up at the end of spring.

PLATYCNEMIDIDAE

Platycnemis subdilatata (Sélys)

Fairly common in Numidia. A north-African endemic associated with different types of oueds. E(13, 14), W(18).

COENAGRIONIDAE

Coenagrioninae

Cercion lindenii (Sélys)

Common. E(4, 7, 9, 10, 14), W(1, 2, 5, 8).

Coenagrion mercuriale (Charpentier)

Rare and restricted to fast-flowing streams but apparently not confined to upland sites within north Africa (Dumont 1977). E(15).

Coenagrion puella kocheri (Schmidt)

Rare and local. New to eastern Numidia. Martin (1910) recorded it as being very common in western Numidia where it has not been found by us. Recent surveys in Tunisia (Dumont 1977; Jödicke et al. 2000) have failed to rediscover this species (Gadeau de Kerville 1908). Females oviposit in tandem in *Potamogeton* sp. E(4, 7, 9, 10, 13).

Coenagrion scitulum (Rambur)

Common in Numidia. Adults have been found carrying ectoparasitic Hydrachnida. E(4, 5, 7, 9-11), W(2, 4-6, 8, 10).

Erythromma viridulum (Charpentier)

Fairly common but confined to northeastern Algeria. It has recently been recorded in Tunisia (Jödicke et al. 2000). This species, as well as many other Zygoptera, used to be abundant in Lac des Oiseaux but numbers have declined sharply after colonization of the lake by Common carp, *Cyprinus carpio* Linnaeus, and overgrazing of riparian vegetation. E(4-7, 9-11, 14, 16), W(5, 6, 9, 10, 12, 13).

Ischnurinae

Enallagma deserti (Sélys)

Local and rare. New to Numidia, this northern population, first recorded as *E. cyathigerum* (Charpentier) (Samraoui et al. 1992), deserves closer taxonomic study (Lieftinck 1966; Samraoui & Menaï 1999). In Numidia local populations have been recorded in natural ponds and shallow lakes while further south they readily occupy small dams and reservoirs, a feature noted by Jödicke et al. (2000). E(3, 4, 7, 9, 10).

Ischnura graellsii (Rambur)

Widespread and abundant, this species occupies permanent and temporary ponds and is found from sea level to uplands (ca 1000 m), where it inhabits pools. In sharp contrast to the situation in Morocco (Jacquemin & Boudot 1999), local populations do not appear to reproduce in lotic habitats. E(1-16), W(1-6, 8-10, 12).

Ischnura pumilio (Charpentier)

Very rare. Recorded twice within Numidia. E(4, 11).

Pseudagrioninae

Ceriagrion tenellum (de Villers)

Local and apparently restricted to moist woodland like alder carrs, and to peaty substrates. E(3, 5, 7, 9, 10, 13-15), W(6).

ANISOPTERA

GOMPHIDAE

Gomphinae

Gomphus lucasii Sélys

An uncommon north-African endemic. Apparently associated with fast-flowing streams. E(close to 5, 13). The adult sighted at O. Bahim (close to E.5) was immature.

Onychogomphus costae Sélys

Very rare. We found this upland endemic (Dumont 1977) in the same lowland habitats as *Paragomphus genei*. E(14).

Onychogomphus forcipatus unguiculatus (Vander Linden)

Only larvae have been tentatively assigned to this species but one male has recently been captured in the vicinity of Numidia (Samraoui & Menaï 1999). E(11, 12).

Onychogomphus uncatus (Charpentier)

Very rare and new to Numidia. Because only larvae were collected, this record requires confirmation. E(13).

Paragomphus genei (Sélys)

Rare and local. Apparently prefers large seasonal oueds which become residual pools during the dry period. One adult was sighted close to E.13, where no breeding has been detected. E(close to 13, 14).

AESHNIDAE

Aeshninae

Aeshna affinis (Vander Linden)

Less abundant and widespread than A. mixta and apparently as tolerant to brackish waters. Local populations do not exhibit any sign of delayed maturation or displacement to refuge sites during summer. E(5, 7, 9-12), W(4, 5).

Aeshna cyanea (O.F. Müller)

Rare and local. Algerian populations, as well as those in southern Europe (Jödicke pers. comm.) differ from more northerly populations in that they are confined to upland streams. E(11, 12).

Aeshna isoceles (O.F. Müller)

Local and not abundant. The main population is found in Lac Tonga. E(3, 4, 7, 8, 10, 11, 19).

Aeshna mixta Latreille

Abundant and widespread. Aestivates at upland sites before returning to lowlands where reproduction occurs (Samraoui et al. 1998a). Occupies permanent and temporary ponds. E(1, 3-7, 9-12, 14, 16), W(1, 2, 4).

Anax ephippiger (Burmeister)

This migrant breeds sporadically in Numidia. Reproduction is chiefly confined to fishless, temporary ponds. In summer 1990, Lac Oubeïra dried up; it refilled in winter but was still fishless when A. ephippiger reproduced there for the first time. This behaviour raises the possibility that adults of this species can detect the presence of fish. E(6, 9, 10, 21, 22).

Anax imperator Leach

Widespread and abundant. It reproduces mainly in lentic habitats, sometimes of a temporary nature. E(1-16), W(1, 2, 4-10, 12).

Anax parthenope Sélys

Widespread but less abundant than A. imperator. Females in tandem have been observed ovipositing in a moist substrate, a few metres from the water's edge. E(1, 2, 4, 6-10, 16, 25), W(4, 5, 8, 9).

Brachytroninae

Boyeria irene (Fonscolombe)

Rare and local. This crepuscular species is restricted to fast-flowing streams. E(13).

LIBELLULIDAE

Libellulinae

Orthetrum cancellatum (Linnaeus)

Widespread. Associated with stagnant open water. E(3, 4, 6, 7, 9), W(1-3, 5, 7, 8, 12, 13).

Orthetrum chrysostigma (Burmeister)

Widespread and common within Algeria (Samraoui & Menaï 1999); local populations seem to fluctuate widely in abundance. Reproduces in seasonal wadi and lentic habitats. E(1, 4, 7, 9, 10, 13, 14, 19), W(8, 10).

Orthetrum coerulescens anceps (Schneider)

Widespread and abundant. Occupies fast-flowing streams. E(13, 15), W(4, 6-8). The subspecific status of this species is discussed by Mauersberger (1994).

Orthetrum nitidinerve (Sélys)

Very rare in Numidia. Abundant elsewhere in semi-arid regions. E(7, 19).

Orthetrum trinacria (Sélys)

Widespread. Shares habitats with O. cancellatum. E(4, 6, 7, 9), W(1, 7, 8).

Sympetrinae

Acisoma panorpoides ascalaphoides Rambur

Rediscovered after over a century and a half (Samraoui et al. 1993), this Afrotropical relic, though fairly widespread, is never abundant. E(4, 7-10), W(4, 5, 8-10).

Brachythemis leucosticta (Burmeister)

Fairly widespread and locally abundant. Aggregations readily follow cattle and people moving slowly across open ground (Corbet & Miller 1991). E(1, 4, 7, 9, 10, 16), W(1,5,8-10).

Crocothemis erythraea (Brullé)

Widespread and very abundant. E(1-10, 13, 15, 16, 19), W(1-10, 12, 13).

Diplacodes lefebvrii (Rambur)

Local but very abundant. This Afrotropical relic has recently been recorded in nearby Tunisia (Jödicke et al. 2000). E(1-10, 16), W(1, 2, 4-10).

Sympetrum fonscolombii (Sélys)

A vagrant whose populations fluctuate widely. During wet spells, this species exploits newly created habitats. E(4, 6, 7, 9-12), W(1, 8).

Sympetrum meridionale (Sélys)

Widespread and abundant. Aestivates at upland sites and is the first to return to lowlands for reproduction at the end of summer (Samraoui et al. 1998a). Many specimens bear ectoparasites (Hydrachnida) whose life cycle depends on that of its host. Reproduces in permanent and temporary ponds. E(1-12, 16), W(1, 2, 4, 6, 8-10, 12, 13).

Sympetrum sanguineum (O.F. Müller)

Local and not abundant. Rather surprisingly, this species has not been recorded in nearby Tunisia since the turn of the century (Gadeau de Kerville 1908). E(5, 7, 10, 11), W(2, 4-6, 8-10).

Sympetrum striolatum (Charpentier)

Widespread and abundant. Its ecology apparently resembles that of *S. meridionale* but the reproductive periods, though different, overlap. This temporal separation may reflect the occupancy of similar larval microhabitats (Benke & Benke 1975) although *S. striolatum* occupies a wider range of habitats, including brackish and saline pools. E(1-14, 16), W(1, 2, 4, 5, 8, 10, 12, 13).

Trithemistinae

Trithemis annulata (P. de Beauvois)

Widespread and relatively abundant. E(1, 4, 7-10, 14, 16), W(1, 5, 7, 8, 13).

Trithemis arteriosa (Burmeister)

Very rare and confined to a few sites. E(14), W(2, 8, 13).

Urothemistinae

Urothemis edwardsii (Sélys)

Lac Oubeïra (E.9) is "Terra typica" for this Afrotropical relic (Samraoui et al. 1993). Two colonies have been found but one soon became extinct due to habitat destruction (Bélair & Samraoui 1994). Unless urgent, effective steps are taken to protect Lac Bleu from human encroachment, the present population will probably cease to exist. E(7; extinct at 20).

Taxa previously recorded in Numidia but not listed above (see Discussion):

Lestes sponsa (Hansemann)

Previous records: "Common everywhere (in northeastern Algeria)"; Seybouse; Philippeville (Martin 1910).

Erythromma najas (Hansemann) (probably confused with E. viridulum) **Previous records:** Tonga (Martin 1910).

Gomphus simillimus maroccanus Lieftinck (possibly confused with G. lucasii) Previous records: Seybouse (Martin 1910).

Lindenia tetraphylla (Vander Linden)

Previous records: La Calle (Sélys-Longchamps 1849).

Onychogomphus hagenii (Sélys) (= Paragomphus genei)

Previous records: Oubeïra (Martin 1910).

Cordulegaster annulatus (Latreille) (= C. boltonii algirica Morton)

Previous records: Lac des Oiseaux (Martin 1910).

Cordulia aenea (Linnaeus)

Previous records: Lac des Oiseaux (Martin 1910).

Orthetrum coerulescens (Fabricius) (= O. c. anceps)

Previous records: Oubeïra (Sélys 1849); Bône; Phillipeville; La Calle (Martin 1910).

Sympetrum depressiusculum (Sélys)

Previous records: Tonga (Martin 1910).

Rhyothemis semihyalina (Desjardins)

Previous records: Oubeïra (Sélys-Longchamps 1849).

Discussion

The importance of the Numidian wetlands, which include habitats like Lac Bleu containing up to 30 species, can be judged by the fact that this region houses over 80% of the Algerian Odonata (Samraoui & Menaï 1999). Furthermore, six species (Erythromma viridulum, Aeshna isoceles, Acisoma panorpoides ascalaphoides, Diplacodes lefebvrii, Sympetrum sanguineum and Urothemis edwardsii) have never been recorded in Algeria outside Numidia and its immediate vicinity. These six species (especially A. panorpoides ascalaphoides and U. edwardsii) have a disjunct distribution and are thus especially vulnerable to natural fluctuations and anthropogenic changes.

Five species (Lestes cf. virens, Enallagma deserti, Onychogomphus uncatus, O. costae and O. forcipatus unguiculatus) are new to Numidia, pending further taxonomic investigation, and out of 10 unrecorded taxa, only four (Lindenia tetraphylla, Cordulegaster boltonii algirica, Cordulia aenea and Rhyothemis semihyalina) are regarded as genuine past records (see Samraoui & Menaï 1999) but must also be considered as locally extinct. Thus, the known recorded number of Numidian odonates amounts to 49 which is close to the total (52 species) recorded for the whole of contiguous Tunisia (Jödicke et al. 2000).

The Numidian check-list may be increased, because our odonatological survey of the area is far from complete and further explorations, especially of the numerous hills, may uncover additional species, *Calopteryx exul* Sélys and *Orthetrum brunneum* (Fonscolombe) being likely candidates. It is also of interest to ask why certain species like *Coenagrion caerulescens* (Fonscolombe) (found further south in the semi-arid zone) or *Orthetrum sabina* (Drury) (limited to the northern edge of the Sahara) have not been encountered within Numidia. The circumtropical *Pantala flavescens* (Fabricius), although recorded once within central Sahara (Kimmins 1934), appears not to be able to reach the Tell (i.e. the northern part of Algeria between the sea and the Saharan Atlas).

A spatial pattern connected to reproductive sites has been also been noted. Only lotic species will be mentioned briefly here but preliminary data have revealed that lentic species also exhibit habitat segregation (Menaï 1993). Fish predation (Macan 1966; Morin 1984a,b), hydroperiod, vegetation structure and salinity all seem to influence site selection (Corbet 1999). Some species whose populations in Europe normally occupy stagnant water, are found breeding in Numidia only in well oxygenated streams (e.g. Coenagrion puella) whereas others, common in lowland sites in northern Europe, are locally restricted in Numidia to upland streams (e.g. Aeshna cyanea). It is interesting that C. puella is restricted to lotic waters in Finland (Hämäläinen 1984) and is thus confined to these habitats at both ends of its geographic range. Moroccan populations of C. puella exhibit the same habitat preference (Jacquemin & Boudot 1999). European and Moroccan populations of Pyrrhosoman. nymphula (Sulzer) exhibit a corresponding change in habitat (Jacquemin & Boudot 1999). Three lotic assemblages, based on habitat type, have been recognised:

- (1) Lowland streams (characterized by high current velocity, small bed width, dense shrubs and trees bordering the banks and a substrate of clay and detritus). This assemblage comprises Calopteryx h. haemorrhoidalis, Lestes v. viridis, Platycnemis subdilatata, Coenagrion mercuriale, Coenagrion puella kocheri, Gomphus lucasii, Onychogomphus uncatus, Boyeria irene and Orthetrum coerulescens anceps.
- (2) Seasonal wadi (characterized by slow current velocity, large bed width and a substrate of sand and alluvial deposits). This assemblage comprises Lestes v. viridis, Platycnemis subdilatata, Onychogomphus costae, Paragomphus genei and Orthetrum chrysostigma.
- (3) Upland streams (characterized by a steeper profile, cooler water and a substrate of rocks [grès de Numidie] and sand). This assemblage comprises *Calopteryx* sp., *Onychogomphus forcipatus unguiculatus*, *Aeshna cyanea* and *Orthetrum* sp., two species of which, recorded only to genus, have been encountered solely as larvae.

This classification should be regarded as provisional because a full-scale investigation of lotic habitats has yet to be completed. The assemblages described above may reflect shading, sediment particle size, fish predation, vegetation, detritus, current velocity, or any combination of these factors (Aguesse 1960; Huggins & Dubois 1982; Buchwald 1988; Ferreras-Romero 1988; Schridde & Suhling 1994; Suhling 1994). Spatial discrimination among lotic species has been linked to differences in current velocity in streams and rivers and, by inference, to the respiratory physiology of the respective species (Zahner 1959; 1960).

A noteworthy feature of the Numidian odonate fauna is its relatively high content of Afrotropical elements, a feature found in other aquatic arthropods, namely Cladocera, Copepoda, Ostracoda (Samraoui et al. 1998b), aquatic Hemiptera (Samraoui & Annani in prep.) and aquatic Coleoptera (Samraoui & Bélair 1997, 1998), thus underlining the ecological singularity of Numidia and the urgent need to secure protection of its habitat diversity.

As was found with the Odonata for the whole of Algeria (Samraoui & Menaï 1999), it may seem, at first sight, that the dragonfly fauna of Numidia has held its ground remarkably well considering the large-scale changes endured by the region since the 19th Century. Habitat loss and degradation have apparently pushed some rare species to extinction and been detrimental to several other species (Coenagrion puella kocheri, Acisoma panorpoides ascalaphoides, Trithemis arteriosa and Urothemis edwardsii). Samraoui & Menaï (1999) discuss the status of species records that require confirmation.

In Part II, the sequel to this paper (Samraoui & Corbet 2000), we discuss strategies that equip Numidian odonates to maintain life-cycle continuity during the dry summer.

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