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NOTES ON INFRASPECIATION IN *COENAGRION CAERULESCENS* (B. DE FONSCOLOMBE, 1839), WITH DESCRIPTION OF *C. C. ISABELAE* SSP. NOV. FROM MOROCCO (ZYGOPTERA: COENAGRIONIDAE)

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The nominate ssp. and *C. c. theryi* (Schmidt) were studied from a biometric point of view as well as using features of their external morphology. It is shown that the abdominal colour patterns cannot be utilized for differentiation between the sspp. – *C. c. isabelae* ssp.n. (holotype ♂, allotype ♀; Ziz R., Morocco, 5-VIII-1985; deposited at Dept Anim. Biol., Univ. Malaga) is described and illustrated. Males are distinguished by the shape of anal appendages, females by the pronotal cleft. The new ssp. occupies a narrow stretch of land on the northern limits of the Sahara.

INTRODUCTION

Coenagrion caerulescens is found in parts of Italy (incl. island provinces), south-eastern France, northern Tunisia, Algeria, Morocco, and in the Iberian peninsula (incl. the Balearic islands).

In their odonate survey of the Guadalmedina River, CONESA & GARCIA (1983) found the abdominal colour patterns deviating from those described by SCHMIDT (1956) in *C. c. caerulescens*. This variation had previously been noted by LIEFTINCK (1966) and evidenced also by later studies on the European fauna (e.g. DUMONT, 1973; BUCCIARELLI et al., 1983).

In the present study we clarify the status of the subspecies proposed by SCHMIDT (1956) for the Iberian peninsula and northern Africa, using biometric criteria based on 12 parameters measured in adult specimens of both sexes. In addition, various external features were examined with a scanning electronmicroscope.

ORIGIN OF THE SAMPLES AND METHODS

COLLECTION AREAS (Fig. 1). – The samples used in our survey were obtained from the following localities:

Iberian peninsula

(1) Casarabonella River, UTM30SUF4773 (Malaga, Spain), alt. 240 m. – Samples collected every fifteen days, Jan.-Apr. 1984.
(2) Guadalmedina River, UTM30SUF7476, (Malaga, Spain), alt. 80 m. – Samples collected every fifteen days, Jan. 1984-Apr. 1985.
(3) Guadalmedina River, UTM30SUF7479, (Malaga, Spain), alt. 87 m. – Samples collected every fifteen days, Jan. 1986-May 1987.
(4) Arroyo de los Pedroches, UTM30SUG4438, (Cordoba, Spain).
(5) Guadiaro River, UTM30STF9327, (Cadiz, Spain).
(6) Cacin River, UTM30VG5263, (Granada, Spain).

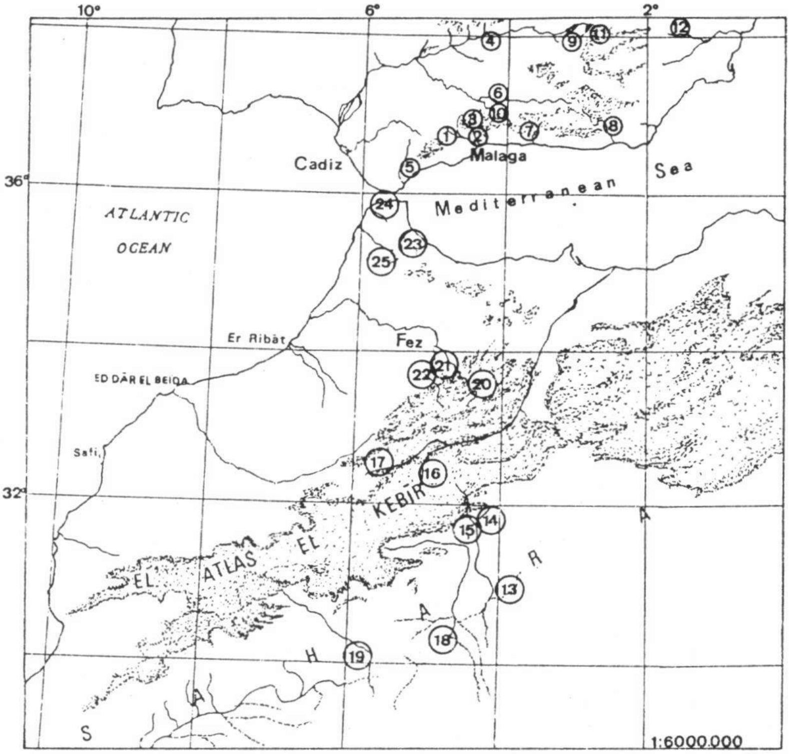


Fig. 1. Sampling areas: (1) Casarabonella R.; – (2-3) Guadalmedina R.; – (4) Arroyo de los Pedroches; – (5) Guadiaro R.; – (6) Cacin R.; – (7) Guadalfeo R.; – (8) Almazora R.; – (9) P. Tranco; – (10) Riofrio R.; – (11) Borosa R.; – (12) Mula R.; – (13) Hai R.; – (14) Meski R.; – (15) Ziz R.; – (16) Ansegmir R.; – (17) Mouluya R.; – (18) Daoura R.; – (19) Draa R.; – (20) Amekla R.; – (21) Ain Sbdou R.; – (22) Lebenne R.; – (23) Laou R.; – (24) Hacheff R.; – (25) Ain Sebdou R.

(7) Guadalfeo River, UTM30SVF9374, (Granada, Spain).
(8) Almazora River, UTM30SWG8350, (Almeria, Spain).
(9) Aliviadero pantano Tranco, Guadalquivir River, UTM30SVH3243, (Jean, Spain).
(10) Riofrio, UTM30SUG5347, (Granada, Spain).
(11) Borosa River, UTM30SVH3753 (Jaen, Spain).
(12) Mula River, UTM30SX5248, (Murcia, Spain).

Sahara

(13) Hai River, (Morocco), 1 km W from Aoufouss, Ait-Ammira Oassis.
(14) Meski River, (Morocco), 50 km from the river's source.
(15) Ziz River, (Morocco), the stretch between Chibbi and the Mercuga sandhill.
(16) Ansegmir River, (Morocco), 38 km W of Midlet, in the Kbad under the Tnout-ou-Fillal bridge.
(17) Mouluya River, (Morocco), between Zeida and Kbah, under Tnout-ou-Fillal bridge.
(18) Daoura River, (Algeria), in the stretch between Bechar and Tindouff.
(19) Draa River, (border between Algeria and Morocco), the stretch between Zagora and Tisergate.

High Atlas

(20) Amekla River, (Sfrou, Morocco).
(21) Ain-Sbdou River, (Fez, Morocco).
(22) Lebenne River, (Fez, Morocco).
(23) Laou River, (Tetuan, Morocco).
(24) Hacheff River, (Tanger, Morocco).
(25) Ain Sebdou River, (Quezzane, Morocco).

All these rivers have a low flow rate, which is typical of 'potamon'.

DESCRIPTION OF THE SAMPLES USED. – Table I provides information relating to the geographic origin, date of collection and numbers of larvae, adult males and adult females collected.

PARAMETERS USED IN THE BIOMETRIC STUDY OF ADULT SPECIMENS. – Those used in the previous surveys were thought to be insufficient, hence the 12 parameters, as shown in Figure 2, were used. All measurements were made on preserved material (cf. CONESA, 1987).

DATA ANALYSIS. – The descriptive statistics, 'd' and Student's 't' were used to ascertain the significance of the compared averages. In the group of more significant parameters, semimatrices were constructed. These were regarded as treatment groups in the heterogeneity cluster analysis (SOKAL & ROHLF, 1969). Due to the noted similarity, the coordinates of the corresponding dendrogram are given for the parameters in question. Ultimately, the dendrogram differentiates between the affinity groups. To interpret the results, the 'Hierarchical Cluster Analysis", provided with various significance tests (Pillais, Hotelling, Wilks and Roys), was used (CONESA, 1987).

The samples for the biometric analysis were divided into 3 areas, viz. (1) the Iberian peninsula (Guadalmedina River), – (2) the Sahara (Ziz River), and – (3) the High Atlas (source of the Mouluya River).

Samples collected in areas close to these were used

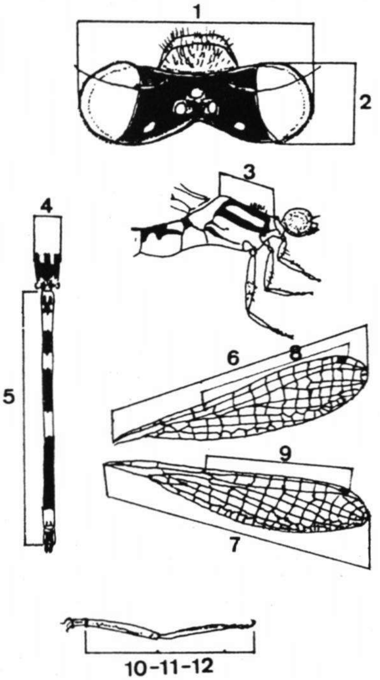


Fig. 2. Parameters used in the biometric study: (1) head length; – (2) head width; – (3) thorax length; – (4) thorax width; – (5) abdomen length; – (6) fore wing (fw) length; – (7) hind wing (hw) length; – (8) length nodus-pterostigma, fw; – (9) ditto, hw; – (10) length of fore legs; – (11) length of middle legs; – (12) length of hind legs.

Table I

Sampling areas (1983-1986): (1) Casarabonella R. – (2) Guadalmedina R. – (3) Guadalmedina R. – (4) A. Pedroches. – (5) Guadiaro R. – (6) Cacin R. – (7) Guadalfeo R. – (8) Almazora R. – (9) P. Tranco. – (10) Riofrio R. – (11) Borosa R. – (12) Mula R. – (13) Hai R. – (14) Meski R. – (15) Ziz R. – (16) Ansegmir R. – (17) Mouluya R. – (18) Daoura R. – (19) Draa R. – (20) Amekla R. – (21) Ain-Sbdou R. – (22) Lebenne R. – (23) Laou R. – (24) Hacheff R. – (25) Ain-Sebdou R.

Area	Dates	Larvae	Males	Females
1	1-I-83/14-IV-84	471	104	134
2	1-I-86/16-V-87	641	181	219
3	3-I-84/19-IV-85	649	400	433
4	5-IX-85	4	4	5
5	5-VII-85	–	–	–
6	10-VII-85	2	3	4
7	12-VII-85	–	–	–
8	25-VIII-85	–	–	–
9	31-VIII-85	–	–	–
10	3-V-85/2-V-86	7	9	15
11	1-V-87	5	7	9
12	4-IX-85	8	10	9
13	3-VIII-85	–	4	1
14	4-VIII-85	3	12	7
15	5-VIII-85/6-VIII-85	8	38	24
16	7-VIII-85	12	5	6
17	8-VIII-85/9-VIII-85	44	25	20
18	18-VIII-85	–	2	1
19	12-VIII-85	–	2	3
20	2-VIII-85	–	–	–
21	2-VIII-85	–	–	–
22	1-VIII-85	–	–	–
23	1-VIII-85	–	–	–
24	13-VIII-85	–	–	–
25	14-VIII-85	–	–	–

as controls to compare the abdominal colouring and to illustrate the geographical distribution. Only specimens sited in the three areas mentioned, were used in the statistical analysis.

GENETIC ANALYSIS. – In this study, adults and final instar larvae were used. These specimens were preserved according to the techniques of BOYES & VAN BRINK (1964), but substituting lactic acid for acetic acid.

SCANNING ELECTRONMICROSCOPY. – The anal structures in males and females, the pronotal cleft in females, and the cuticle denticulation on the last abdominal segment and the developing gonapophysis in final instar larvae were investigated. Dehydration of the specimens took place in CO_2 35°C, under 72,9 mm Hg, following which they were coated with gold.

ABDOMINAL AND THORACIC COLOURATION

The specimens collected in the Iberian peninsula showed no marked difference in thoracic colouration. Nevertheless, a slight variation in colouration was observed for specimens at different stages of growth. The colour, depending on sex, ranged from light pink (typical in teneral) to blue or brown. In the oldest specimens, the blue colouring tended to darken due to dehydration, a fact already noted in *Ischnura* (HINNEKINT, 1986). It is only necessary to underline that the specimens collected at the Casarabonella River show in the third antehumeral suture a pigmented section which is longer than in the other samples studied (Fig. 3).

Relating to the abdominal colouration, males from the southern Iberian peninsula show a similar pattern to the one observed by SCHMIDT (1956) in the Algerian individuals. As shown in Figure 3, the 8th and 9th abdominal segments in European specimens are light blue and sometimes the 9th segment appears slightly marked by two small black spots.

Within the sampling areas of the Iberian peninsula the differences in abdominal colouration were found to be less variable than those observed in the African populations.

The Atlas and the Sahara populations are particularly significant for the variability in the abdominal colouration (Fig. 3). A total of seven standards were established for the Ziz River. Some of these specimens, together with the ones from the Iberian peninsula can be classified according to SCHMIDT's (1956) patterns. The markings were largest in the Mouluya River specimens.

Concerning the females, we have followed SCHMIDT's (1956) analysis and only the last three abdominal segments have been studied. The Iberian peninsula speci-

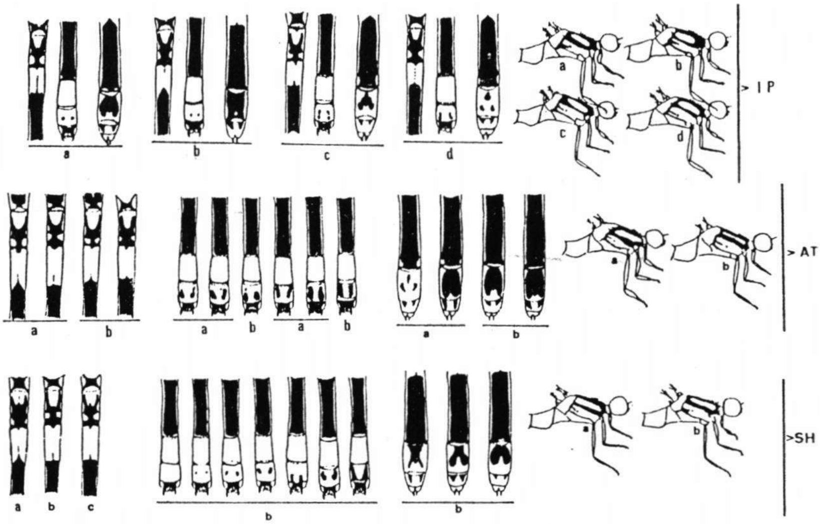


Fig. 3. Thoracic and abdominal colouration patterns, from slides: IP: Iberian peninsula, *C. c. caerulescens*: (a) Guadalmedina R., area 2, – (b) Casarabonella R., – (c) Borosa R., – (d) Mula R.; – AT: Atlas, *c. theryi*: (a) Mouluya R., – (b) Ansegmir R.; – SH: Sahara, *c. isabelae* ssp.n.: (a) Ziz R., – (b) Hai R., – (c) Meski R.

mens showed gradual variation in their colour patterns, similar to that in the Algerian material described by Schmidt. The study carried out in the Mediterranean islands of Corsica and the Balearics (COMPTE, 1963; BUCCIARELLI et al., 1983; OCHARAN, 1987) showed the same conclusions.

Obviously, there is much intergradation in the abdominal marking patterns within the same population and/or geographic area, therefore these can not be utilized to differentiate between the subspecies.

BIOMETRIC ANALYSIS

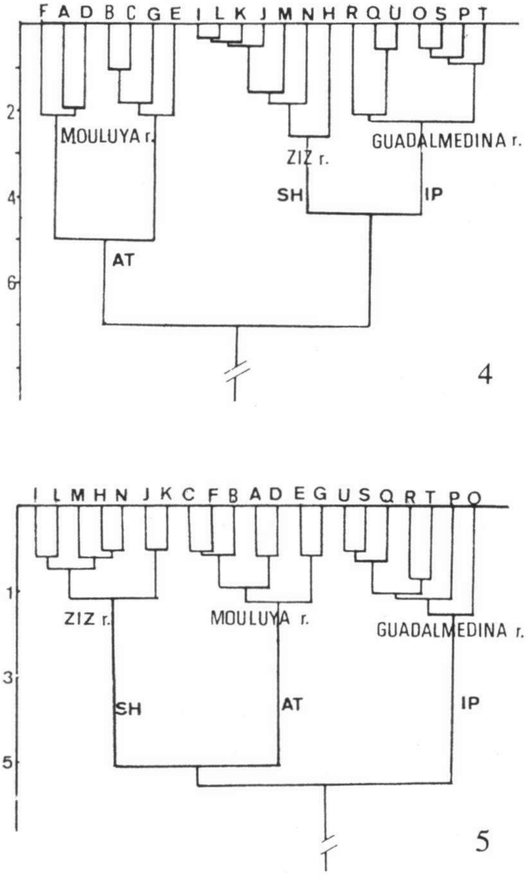


Fig. 4-5. Dendrogram for the males (Fig. 4) and for the females (Fig. 5): IP: Iberian peninsula, *C. c. caerulescens*; – AT: Atlas, *c. theryi*; – SH: Sahara, *c. isabelae* ssp.n.

The averages of the parameters measured are shown in Table III along with the averages previously determined by SCHMIDT (1956) and LIEFTINCK (1966). In Table IV the length of the abdomen and the hind wing of samples collected in two seasons (March-Apr., Sept.-Oct.) from the Guadalmedina River are compared. Both males and females from the first generation show a noticeably longer abdomen and hind wing than observed in specimens from the second generation ($P \leq 0.02$ in both cases). This confirmed that the averages found by Schmidt and Lieftinck for the Iberian peninsula are referable to adults of the first generation (May, June).

The results shown in Table II were achieved solely by considering our observations for the three mentioned areas and making a comparison among the averages found for each parameter.

For consistency, the cluster heterogenity analysis was used only on samples from the second generation. The sam-

Table II

Averages (x̄), in mm, for 12 parameters in adult specimens from three geographical populations (subspecies) – [s.d = standard deviation, – r = range, – L.n-pt = length between nodus and pterostigma, – N = sample size]

Parameters	Guadalmodina River (N=79)			Ziz River (N=36)			Mouluya River (N=25)		
	x	s.d.	r	x	s.d.	r	x	s.d.	r
				MALES					
Head length	1.84	0.259	1.20-2.67	1.66	0.18	1.40-2.00	1.83	0.15	1.60-2.00
Head width	3.46	0.330	2.60-4.60	3.12	0.297	2.60-3.80	3.34	0.283	3.00-3.80
Thorax length	4.28	0.440	3.40-5.00	3.475	0.481	2.40-4.30	4.13	0.499	3.25-5.00
Thorax width	2.33	0.290	1.85-3.00	2.13	0.200	1.79-2.60	2.22	0.137	2.00-2.60
Abd. length	21.59	1.670	17.30-24.70	18.90	2.320	10.10-20.70	22.07	0.955	20.20-23.95
Fw. length	16.83	1.920	12.40-20.10	14.70	0.795	13.00-16.30	16.40	0.752	15.20-18.40
Hw. length	15.50	1.820	12.00-19.40	13.38	0.640	12.50-14.60	15.36	0.817	14.30-17.00
L.n-pt (fw.)	8.98	1.370	6.30-13.60	7.81	0.447	7.00-8.70	8.77	0.591	7.10-9.50
L.n-pt (hw.)	7.79	0.973	6.00-10.20	6.63	0.390	6.10-7.60	7.84	0.547	7.00-8.80
Fore legs l.	4.49	0.690	3.00-6.00	4.17	0.283	3.70-4.70	4.38	0.373	3.60-5.00
Middle legs l.	5.38	0.730	3.90-6.80	4.78	0.452	4.10-6.05	5.10	0.294	4.30-5.80
Hind legs l.	6.52	0.847	4.40-7.80	5.817	0.457	4.95-6.70	6.05	0.632	5.00-7.50
				FEMALES					
Head length	1.92	0.21	1.41-2.40	1.66	0.278	1.45-2.25	1.87	0.27	1.40-2.30
Head width	3.44	0.34	2.50-4.20	3.09	0.192	2.74-3.50	3.34	0.22	3.10-3.80
Thorax length	4.28	0.501	3.30-5.20	3.392	0.518	2.70-4.10	4.47	0.30	4.10-4.95
Thorax width	2.54	0.638	1.90-4.90	2.213	0.157	2.00-2.50	2.43	0.16	2.10-2.60
Abd. length	21.52	2.520	17.70-25.70	19.10	1.410	16.40-21.20	22.48	0.62	20.60-23.30
Fw. length	17.84	2.254	14.20-22.90	14.92	1.190	13.00-17.10	17.85	0.88	15.80-19.70
Hw. length	16.40	2.090	13.20-20.90	13.85	1.047	12.10-15.50	16.53	0.646	14.50-17.60
L.n-pt (fw.)	9.59	1.63	6.40-15.15	7.83	0.64	7.20-9.40	9.61	0.327	8.80-10.0
L.n-pt (hw.)	8.21	1.20	5.57-10.80	6.96	0.426	6.30-7.70	8.12	0.510	7.40-9.00
Fore legs l.	4.61	0.768	3.70-7.60	4.193	0.261	3.85-5.00	4.45	0.610	3.50-5.40
Middle legs l.	5.43	0.834	3.80-7.60	5.230	0.541	4.50-6.20	5.38	0.442	4.90-6.50
Hind legs l.	6.36	0.846	4.90-8.00	5.880	0.508	5.25-6.70	6.42	0.667	5.50-7.40

Table III

Abdomen and hind wing average lengths (in mm), as reported for various populations by (i) LIEFTINCK (1966) and (ii) SCHMIDT (1956)

Parameters	Ifranne	Kenifra		Ouoouizarth		Asni Tal		la Reraya		Saf-Saf		Spain	
	(i)	(i)		(ii)		(ii)		(ii)		(ii)		(ii)	
Abd.	22.56	23.00	23.40	22.70	21.20	22.30	23.60	22.90	23.47	22.89	23.52	22.87	22.50
Hw.	16.30	16.50	18.70	15.60	16.30	16.43	18.00	16.48	18.35	16.08	18.02	16.02	16.55
N	*7 ♂*	*2 ♂*	*1 ♀*	*3 ♂*	*1 ♀*	*6 ♂*	*3 ♀*	*8 ♂*	*4 ♀*	*21 ♂*	*5 ♀*	*24 ♂*	*24 ♀*

Table IV

Comparison of the abdomen and hind wing average lengths ($\bar{x}$), in mm, between the two generations at the Guadalmedina River, Spain

Sex and generation	N	$\bar{x}$	s.d.	Min	Max
		ABDOMEN			
Males					
I	18	23.33	0.879	22.00	24.70
II	20	19.99	0.308	17.30	22.30
Females					
I	11	23.55	1.070	22.20	25.70
II	17	20.34	1.366	17.70	22.70
		HIND WING			
Males					
I	18	17.64	0.774	16.50	19.40
II	20	13.52	0.836	12.00	15.20
Females					
I	11	17.72	2.717	10.60	19.90
II	17	14.98	0.968	13.20	16.80

ples were chosen at random from each of the three areas considered, keeping males and females separate.

The results of the heterogeneity cluster analyses are shown in Figures 4 (males) and 5 (females). For both sexes it is clear that the sample sites cluster together in the three regional groups. All four significance tests indicated probability levels of

Table V

Significance of the variation in the averages: data from second generation adults – [¤ = not significant; –* = $p < 0.05$; – ** = $p < 0.02$; – *** = $p < 0.01$; – **** = $p < 0.001$; – dof = degrees of freedom]

Parameter	Sahara/Atlas		Iberian peninsula/Sahara		Atlas/Iberian peninsula	
	Males (dof=59)	Females (dof=42)	Males (dof=113)	Females (dof=76)	Males (dof=102)	Females (dof=72)
Head length	¤	¤	*	**	¤	¤
Head width	¤	¤	**	***	¤	¤
Thorax length	**	***	****	****	¤	¤
Thorax width	¤	¤	*	**	*	¤
Abd. length	**	¤	****	****	¤	¤
Fw. length	*	***	****	****	*	*
Hw. length	**	*	****	****	*	¤
L.n-pt (fw.)	*	**	****	****	*	¤
L.n-pt (hw.)	**	*	****	****	¤	¤
Fore legs l.	¤	¤	**	*	¤	¤
Middle legs l.	¤	¤	****	*	*	**
Hind legs l.	¤	¤	**	*	*	¤

$P \leq 0.001$.

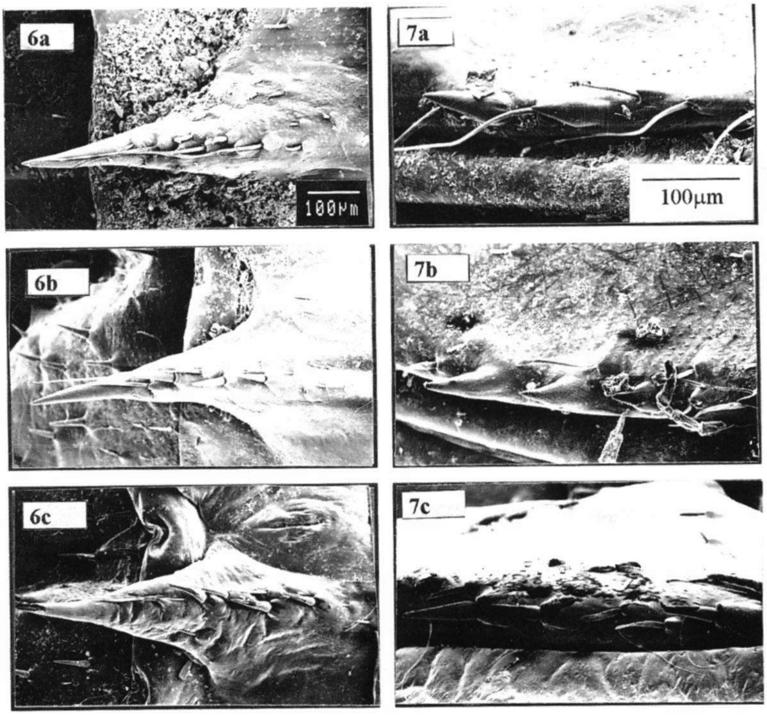
The biometric aspects considered above seem to suggest the existence of clearly defined groups within different areas. The observed morphometric variation (which could be attributed to the use of specimens from different generations) decreases when specimens from the same generation are used.

EXTERNAL MORPHOLOGY

LARVAE

MALES. – Mouluya R. (Atlas). – Sexual appendages almost parallel, with eight long setae plus two spatulate basal setae (Fig. 6a). Denticulate cuticle.

Ziz R. (Sahara). – Sexual appendages divergent from the base. Samples from this region show a larger angle of divergence than that observed in those from the Guadalmedina R. Also the cuticle of the appendages does not appear to be denticulate and it is equipped with a row of articulated, thick spines, alternating with 8 long setae which do not originate from the base of the spine (Fig. 6b).



Figs 6-7. Appendages in male larvae (Fig. 6) and larval valve spines (Fig. 7): (a) *Coenagrion caerulescens theryi* (Atlas); – (b) *C. c. caerulescens* (Iberian peninsula); – (c) *C. c. isabelae* ssp. n. (Sahara).

Guadalmedina R. (Iberian peninsula). – Sexual appendages divergent from the base. Row of articulated spines plus a non-articulated distal spine. Laterally, 4 setae in a line parallel to the articulated spines. Flat denticulate cuticle surface (Fig. 6c).

FEMALES.. – **Mouluya R.** (Atlas). – The internal edge of the external valves is equipped with conical, non-articulated spines. A seta grows on the inner side of each valve the length of which extends beyond the spine from where it originates.

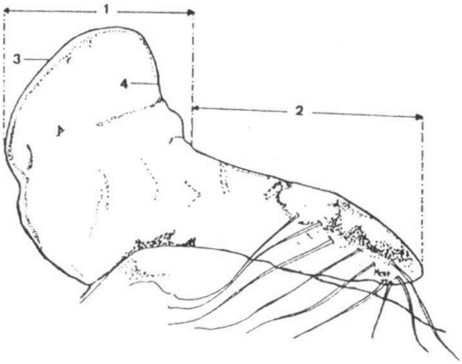


Fig. 8. Structure of the female pronotal cleft: (1) anterior lobe; – (2) posterior lobe; – (3) proximal border; – (4) distal border.

Ziz R. (Sahara). – The valves show non-articulated spines and the setae grow lateral to the spines.

Guadalmedina R. (Iberian peninsula). – On each valve there are a few spines, of which only 3 are articulated. The setae do not sprout from the base, but grow either between two spines, or lateral to them (Fig. 7).

ADULTS

FEMALE PRONOTAL CLEFT. – This structure can be divided into two lobes, an anterior one which shapes the cleft itself and a posterior one, fused to the pronotum (Fig. 8).

Mouluya R. (Atlas). – The anterior lobe has a cleft and curves as far as the top of the crest. On the distal edge there is a little tubercle which ends where the posterior lobe begins. The posterior lobe's outline is of irregular shape, widening at the end where 8 long setae grow in a line (Fig. 9).

Ziz R. (Sahara). – The anterior lobe has a rectilinear shape that bends at its external edge up to the beginning of the crest, and a rectilinear shape. The distal zone forms a right angle at the point where it meets the posterior lobe. This lobe has regular parallel edges. It contains a row of 5 long setae.

Guadalmedina R. (Iberian peninsula). – The anterior lobe's edge starts with a deep internal cleft. There is a small secondary lobe. From this point, the cleft curves unevenly to the top of the crest. The cleft base is straight as far as the beginning of the posterior lobe. The latter has a shorter structure which looks thicker than that observed in the Ziz R. population. This lobe has 7 setae which are clearly shorter than those observed in the Sahara specimens.

OVIPOSITOR. – Although the female genitalia are similar in all three groups, the external valves extend beyond the tenth abdominal segment more noticeably in the African individuals than in those from the Guadalmedina R.

Specimens from the Ziz R. have a scarcely denticulate cuticle. The Mouluya R. samples show shorter setae and a more denticulate cuticle. Finally, the specimens found in the Guadalmedina R. have the most denticulate cuticle and the highest number of superficial setae of the three groups (Fig. 10).

MALE ANAL APPENDAGES. – The inferior appendages in the Ziz R. specimens have a proximal tubercle sloping forward, with a slightly curved internal edge. The distal tubercle, which also slopes forwards, terminates in a conical shape parallel to the upper appendages (Fig. 11).

The upper external edges of the appendages appear deeply indented. The Mouluya R. specimens have a proximal tubercle sloping forwards in the lower appendages; this tubercle is larger than that observed in the Ziz R. specimens. The distal tubercle curves inwards; viewed laterally it seems oblique to the upper appendages. The internal rim of the lower appendages is rectilinear.

The Guadalmedina R. specimens have a small proximal tubercle on the lower appendages. One of the lower internal rims on the appendages is arched and uneven. Its conical end is oblique to the upper appendages but, viewed internally, it is wider than that observed in the Atlas specimens.

GENETIC ANALYSIS

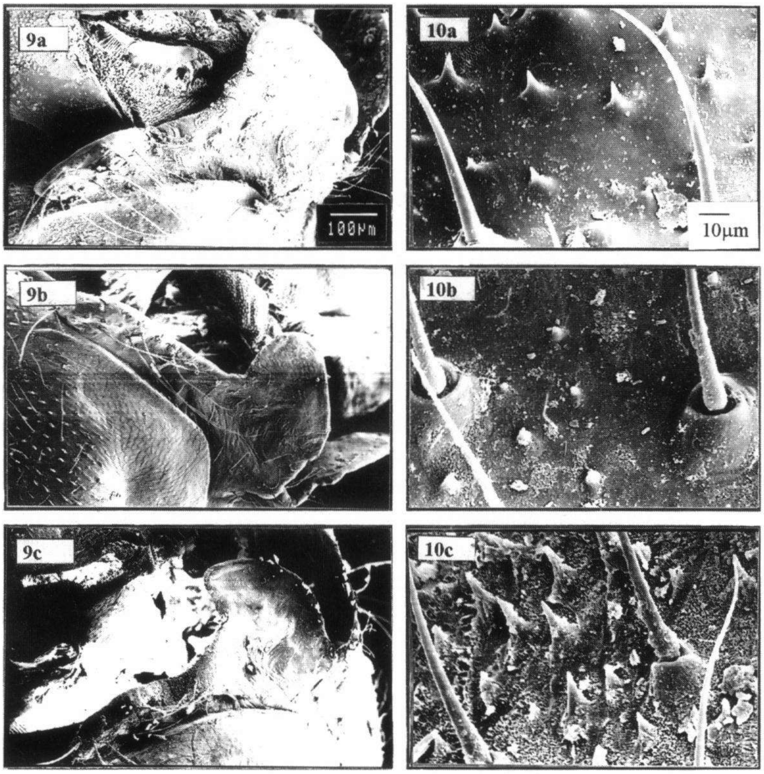
Unfortunately, the samples we processed from North Africa were not appropriately prepared for this kind of study. However, this was possible for the Iberian specimens. We used the recombination index (number of bivalents plus number of chiasmata per nucleus; KIAUTA, 1968, 1969). In the specimens studied, RI=24, and a haploid number n=14(*m*), with the XO/XX sex determination mode, were established.

COENAGRION CAERULESCENS ISABELAE SSP. NOV.

Material. – **Holotype ♂, allotype ♀**: Morocco, Sahara, Ziz R., between Erg-el-Chebbi and Merçuga Sandhill, 5-VIII-1985; deposited at Dept. Animal Biol., Univ. Malaga, Spain. – **Paratypes** (all Morocco): 4 ♂, 2 ♀, 1 km N of the holotype locality, 6-VIII-1985; – 1 ♂, 1 ♀, Hai R., 1 km off Aoufous (Ait-Amura Oasis), 3-VIII-1985; – 2 ♂, 2 ♀, Meski R. ("Sources Bleu"), 6-VIII-1983; – 2 ♂, 1 ♀, Daoura R., between Bechar-Tindouf, 10-VIII-1985; – 2 ♂, 3 ♀, Draa R., between Zagora-Tisergate, 12-VIII-1985.

Etymology. – Dedicated in homage to author's wife.

COLORATION. – Males with typical abdominal light blue colouring, have brassy black markings, which vary in size and pattern on every segment. Black legs with light blue markings over the leg length. Head, including the buccal region, is totally black, save for light blue postocular markings.



Figs 9-10. Morphology of the female pronotal cleft (Fig. 9) and lateral view of the female terminalia (Fig. 10): (a) *Coenagrion caerulescens theryi* (Atlas); – (b) *C. c. caerulescens* (Iberian peninsula); – (c) *C. c. isabelae* ssp. n. (Sahara).

The average values for the 12 parameters considered are shown in Table II (Ziz R.).

PTEROTHORAX. – Female pronotum deeply clefted, with both tubercles distal, and with the proximal border rectilinear (Fig. 9). In dorsal view, there are in the male 3 black parallel stripes that coincide with their respective antehumeral stripes.

WINGS. – Peduncled hyaline fore and hind wings, each with 2 antenodals. Whitish pterostigma, arched at the base, covering only 1 cell Rspl covering 4 cells in fore wings, and 3 cells in hind wings. Discoidal trapezoidal cell, almost square-shaped due to the shortness of the main trapezium base.

OTHER CHARACTERS. – Ovipositor extends noticeably beyond the 10th abdominal segment. Male lower appendages have ends parallel to the upper appendages.

HABITAT. – Rivers of low but constant flow rate, which may dry out during the hottest summer periods.

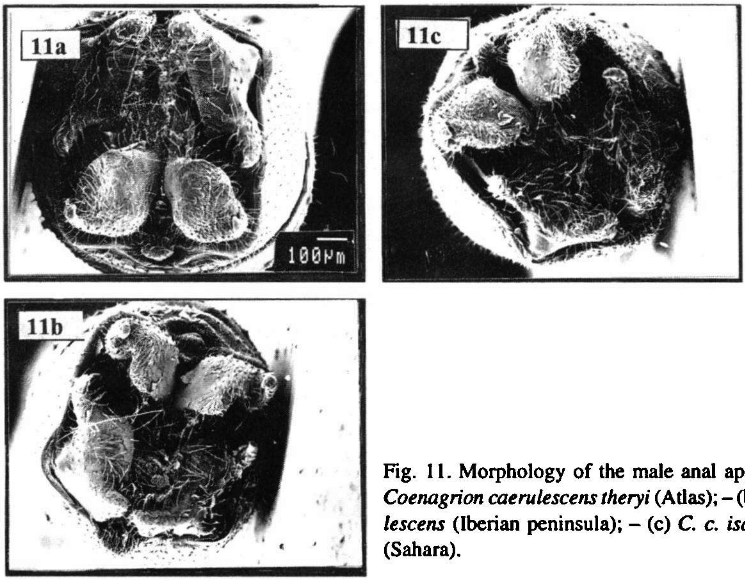


Fig. 11. Morphology of the male anal appendages: (a) *Coenagrion caerulescens theryi* (Atlas); – (b) *C. c. caerulescens* (Iberian peninsula); – (c) *C. c. isabelae* ssp. n. (Sahara).

DISTRIBUTION. – Restricted to an area at the foot of the Atlas (northern Sahara), including the Draa table at the foot of the High Atlas, but does not reach the Sahara Atlas. This area is clearly separated from the *theryi* range (Fig. 12).

DISCUSSION

C. caerulescens theryi (SCHMIDT, 1956) was described from an Algerian

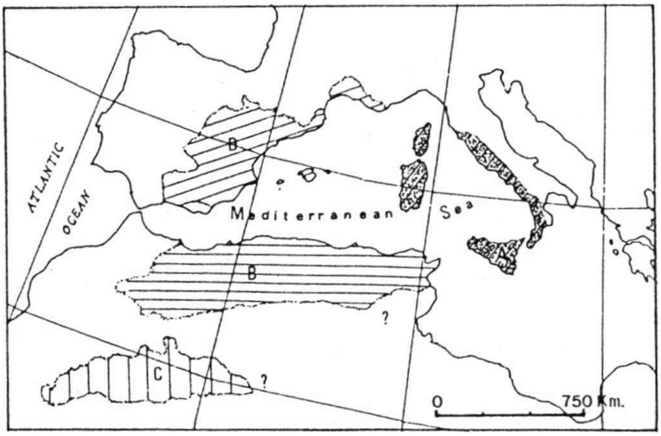


Fig. 12. Distribution of the four subspecies considered: (A) *Coenagrion caerulescens caesarum*; – (B) *C. c. theryi*; – (C) *C. c. isabelae* ssp. n.; – (D) *C. c. caerulescens*.

holotype, with a paratypical series from the Isser and Mefrouch rivers. Schmidt also analyzed some specimens from the localities in the High Atlas. Our material from the Mouluya R. and Anserming (High Atlas) is certainly referable to this taxon, as also indicated by the above biometric analysis. Similarly, the Iberian population is referable to the nominate subspecies.

In our opinion, *caerulescens* and *theryi* are well defined infraspecific taxa, even though their status has been questioned by some workers (e.g. LIEFTINCK, 1966; DUMONT, 1973; OCHARAN, 1987). Admittedly, on the basis of the features used by these workers, a clear differentiation is not possible. However, when other parameters are considered, and only the individuals of the same generation are compared, the infraspecific status of *theryi* becomes apparent. The subspecies may possibly occupy a wide area, encompassing the Algerian, Middle and High Atlas. The nominate subspecies is presumably restricted to the Iberian peninsula and south-eastern France.

The colour and abdominal length are among the features considered traditionally in the odonate dispersal studies. While colour patterns are unreliable (since these vary noticeably within the populations), following REINIG (1939) an attempt could be made to trace the paths of dispersal and infraspeciation, considering the abdominal length as a differentiating feature. Reinig argued that the largest individuals occur in the original centres of dispersal, postulating the further away from the centre the smaller they are. Consequently, SCHMIDT (1956) may have been right in assuming Sicily to represent such a centre.

It is likely, the *C. caerulescens* infraspeciation is related to the Pleistocene eustatic oscilliations in the Mediterranean and to the Pleistocene palaeoclimatic and hydrographic conditions in the Sahara (cf. DERRUAU, 1974).

Returning to the average abdominal length, SCHMIDT (1956) found that the farther one travels from Calabria (the nearest continental area to Sicily, to which it was connected during the periods of the Pleistocene sea regressions), reaching up to the East (Apulia) and to the North (Tuscany), the shorter the abdomen. Thus, the origin of *C. caerulescens caesarum* seems to be related to the Postpleistocene configuration of the present sea level and climate.

In Tunisia, the species has occupied the Aures mountains and probably the area along the Saharian Atlas. During the last Würm glaciation, the displacement of the Sahara desert could have caused a wide stretch along the northern Sahara border to remain humid and warm. Most probably this stretch would be large enough for the *C. c. isabelae*-stock to settle down.

Prior to about 18.000 BP, the extensive glaciation on the Atlas blocked the passage across Gibraltar to the Iberian peninsula hermetically (DUMONT, 1982). We hypothesize, therefore, *C. caerulescens* chose the other feasible direction towards Sardinia and Sicily, or even straight towards Italy.

From approximately 12.000-8.000 BP there must have been a connection between the Maghreb and the Iberian peninsula across the Gibraltar Straits. The migrating fauna could have reached eastern Andalusia, Murcia, etc., and give rise to the subspecies *caerulescens*, which could have reached subsequently Aix (France) along the Mediterranean coast.

The difference in size between the individuals from the Ziz R. valley and those of the High Atlas makes it difficult to assume a migration from the former to the latter area. Consequently, one branch must have dispersed throughout the Telliane Atlas towards the High Atlas. This migration must have occurred rather recently (around 2.800 BP), causing the *theryi* origin to coincide with the formation of the present climate.

This dispersion was to determine a movement of the species from East to West and from South to North, diminishing in size as it moved away from its centre: a preliminary hypothesis, which should be verified by a genetic analysis. A similar analysis of the other geographic subspecies would enable the speculation as to the identity of the oldest taxon, and to compare our conclusions with those of DUMONT (1982). This is the objective of our forthcoming work on *Coenagrion caerulescens*.

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