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REVISION OF *CORDULEGASTER BOLTONII* (DONOVAN, 1807) IN SOUTHWESTERN EUROPE AND NORTHERN AFRICA, WITH DESCRIPTION OF *C. B. IBERICA* SSP. NOV. FROM SPAIN (ANISOPTERA: CORDULEGASTRIDAE)

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The sspp. from France, Spain and Morocco are redescribed on a statistical basis, taking into account their intrinsic variability. *C. b. iberica* ssp.n. (holotype ♂: Spain, Albacete prov., Sierra de Alcaraz, Puerto de las Crucetillas, alt. ca 1450 m, 18-VII-1989; deposited at Lab. Biol. Insectes, Univ. Nancy-I), which falls between *C. b. algirica* and *C. b. immaculifrons*, is described from central and eastern southern Spain. All these sspp. occur in pure populations in some areas, but coexist in other regions, apparently giving rise to hybridization and constituting heterogeneous mixed populations over large territories. Such coexistence cannot constitute a criterion against the conspecific status of these taxa, as was claimed for *C. b. boltonii* and *C. b. trinacriae* in Italy; therefore all these taxa are treated here as sspp. of *C. boltonii* throughout. The range of each ssp. and each type of mixed population is defined and mapped. Exuviae were collected in the most homogeneous areas in France and Spain and their distinctive features were redefined on a statistical basis. With regard to exuviae, *C. b. iberica* stands closer to *C. b. algirica* than to *C. b. immaculifrons*, although it has been previously confused with the latter.

INTRODUCTION

Cordulegaster boltonii (Donovan, 1807) is a well known polymorphic species which exhibits considerable colour variation throughout its range. Little structural change has been reported and was observed only in Italy. Four subspecies are known today. The nominal subspecies (*C. b. boltonii*) inhabits the major part of Europe, from the Ural range to the British Isles, western and central Austria, western Italy and Spain. *C. b. immaculifrons* Sélys, 1850 and *C. b. algirica* Morton, 1915 repre-

sent two meridional subspecies with rather expanded yellow markings, whereas *C. b. trinacriae* Waterston, 1976, from the south of Italy and Sicily, is a darker subspecies which exhibits some structural differentiation. The last is sometimes regarded as a good species but, contrary to assertions by most Italian workers (BUCCIARELLI, 1977; BALESTRAZZI et al., 1982; GALLETTI & PAVESI, 1985), is not related to *C. picta* Sélys, 1854 (VERSCHUREN, 1989). The distribution range of *C. b. immaculifrons* and *C. b. algirica* is not fully understood. *C. b. algirica* is known only from some of the southernmost Sierras in Spain and from a large part of the Atlas and Rif ranges in North Africa (LIEFTINCK, 1966; DUMONT, 1977; VERSCHUREN, 1989). According to recent revisions of the genus (WATERSTON, 1976; THEISCHINGER, 1979), *C. b. immaculifrons* should be considered as restricted to a minor part of the Italian territory (western Liguria) (BALESTRAZZI et al., 1982) and to some undefined areas in Spain and in the south of France.

In France, the nominal subspecies clearly inhabits a much more extended area than *C. b. immaculifrons*. The latter was mainly recorded from the mediterranean fringe and from the southern Alps, but also much more northerly, up to the Drôme valley at low altitude (LIEFTINCK, 1966). Thus it appears to be restricted to a small part of southern France, but its range remains poorly delimited. At the opposite extreme, *C. b. boltonii* was recorded from a large part of France, including the Aquitaine district, the Pyrénées range and the Massif Central (SELYS & HAGEN, 1850, 1858; MORTON, 1927, 1932; FUDAKOWSKY, 1933; NICOLAU-GUILLAUMET, 1959; LIEFTINCK, 1965; AGUESSE, 1968; BILEK, 1969; DOMMANGET & MARTINEZ, 1983) and it is even known from the mediterranean range (CASSAGNE-MEJEAN, 1963; VICK, 1984). These two subspecies seem either to contact each other or to cohabit in the Montpellier area (CASSAGNE-MEJEAN, 1963). Their respective status in France remains, in fact, confused.

In the Iberian Peninsula, the nominal subspecies clearly predominates in the north-west of Spain, despite the occurrence of atypical specimens (MORTON, 1915; SALOÑA-BORDAS & OCHARAN, 1984; OCHARAN, 1987). Records of this subspecies from the Sierra Nevada by NAVAS (1907) and subsequently by MORTON (1915) and AGUESSE (1968) may be considered as doubtful and should be verified. *C. b. immaculifrons* was recorded from the Sierras de Gredos, de Guadarrama and de la Demanda (SELYS & HAGEN, 1850; MORTON, 1915; LIEFTINCK, 1966; OCHARAN, 1987); also from Catalogna (NAVAS, 1924; WENGER, 1963), from the Montes Universales (McLACHLAN, 1902; ANSELIN & MARTIN, 1986; VERSCHUREN, 1989) and from the Sierra Morena (VERSCHUREN, 1989). Data by OCHARAN (1987, 1988) from the north-west and the centre of Spain, however, provide some doubts on the validity of these two subspecies, and both bastard specimens and mixed populations may be expected. Very variable intermediate specimens between *C. b. immaculifrons* and the nominal subspecies were previously assumed to occur in many countries (LIEFTINCK, 1966).

It is a current observation that all the differentiating features of these two subspecies do not necessarily vary together at the individual level, giving rise to bastard specimens that cannot be assigned satisfactorily to any subspecies.

To clarify this situation, the need for a revision of these various subspecies by working at the population level rather than at the individual one, quickly appears to any field worker. The present paper deals with the results of such an approach in southern France, Spain and Morocco, thereby allowing us to take into account the variability of a great number of populations. Only male imagos and exuviae of both sexes were collected in sufficient numbers to be considered for this purpose. Most of them are in the collections of the authors and J.L. Dommanget (Bois d'Arcy, France). Other specimens were described in vivo in the field and then released.

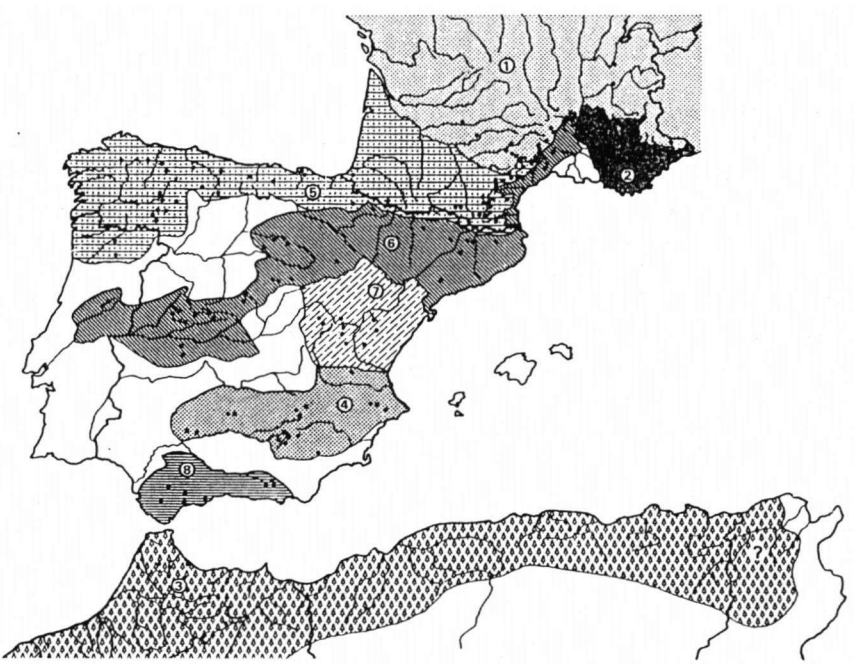

Fig. 1. Geographic range of the various subspecies of *Cordulegaster boltonii* in the areas investigated: area 1 = *b. boltonii*, typical populations; – area 2 = *b. immaculifrons*; – area 3 = *b. algirica*; – area 4 = *b. iberica*; – area 5 = *b. boltonii*, atypical populations; – area 6 = mixed populations of *b. boltonii* and *b. immaculifrons*; – area 7 = mixed populations of *b. immaculifrons* and *b. iberica* ; – area 8 = mixed populations of *b. algirica* (predominant) and *b. iberica*. – [The spots depict the localities investigated by the authors].

STUDY OF THE IMAGOS

In view of the variability of the male imagos in the various populations studied and based on their colour pattern, it was possible to sort out 8 distinct geographic areas in France, Spain and North Africa (Fig. 1). Four areas possessed rather homogeneous populations, which were thus considered as constituting genuine subspecies. Three previously known subspecies were redefined on a statistical basis. In addition, a new subspecies was identified in Spain and will be described hereafter. Other areas were inhabited by heterogeneous populations in which we recognized the phenotype of one or two subspecies as well as intermediate or atypical specimens in variable numbers. These populations were thought to result from the coexistence and hybridization of two subspecies on a somewhat large scale.

DELIMITATION OF VARIOUS AREAS BASING ON MALE FEATURES

Homogeneous populations

FIRST HOMOGENEOUS AREA: *Cordulegaster b. boltonii*, typical populations (Fig. 1, area 1). – Male specimens encountered within the first area must be ascribed to the nominal subspecies without any restriction. Based on a sample of 214 mature imagos from the Alps and Massif Central highlands in France as well as from the Vosges, Seine-et-Oise, Côtes-du-Nord, Indre, Lot and Aveyron departments in the same country, the main features of the populations observed here can be summarized as follows (Tabs I, II; Fig. 2, Nos 1-2) (with S2 ... S10 = 2nd ... 10th abdominal segments throughout). Abdominal yellow ring on S2 narrow, always continuous and never indented by a black square on its posterior edge. That of S3 either interrupted (in about 42% of the males studied), subinterrupted or uninterrupted [not always uninterrupted as stated by WATERSTON (1976)]. Yellow ring on S4 mostly interrupted (99%); those on S5 to S6 always interrupted, looking like 2 yellow spots in dorsal view. Apical lunulae present from S2 to S6, mostly so (91%) but sometimes lacking on S7. S9 and S10 either entirely black or with small basal dorsal yellow spots, very scarcely with extended dorso-lateral yellow marks on S9. Anal triangle of posterior wings 3 to 6 celled. Abdominal yellow rings mostly angulated forward in lateral view on S4 (90%), but only in about half the specimens studied on S5-S6. Mesothoracic, lateral, median yellow stripe generally fragmented into 3-4 marks (75%). Frontal black line always well marked. Back of the eyes black with a narrow lateral yellow border. Base and lateral edges of labrum always bordered with black. Virgule of labrum black. Superior appendages with their external border always almost straight. Inferior appendage emarginated at the apex by an angle of 106°-173°.

SECOND HOMOGENEOUS AREA: *C. b. immaculifrons* (Fig. 1, area 2). – A second rather homogeneous area was found to cover both the French mediterranean fringe

Table I

Main patterns of the males of various subspecies of *Cordulegaster boltonii*: homogeneous populations, dorsal view. – [All values are % of the number of specimens studied (n)]

Type of pattern		Area 1 *C. b. boltonii* most of Europe) (n = 214)	Area 2 *C. b. immaculifrons* SE France) (n = 184)	Area 3 *C. b. algirica* (Maroc) (n = 12)	Area 4 *C. b. iberica* (Center of S and E Spain) (n = 47)
Abdominal yellow rings medio-dorsally interrupted	S3	42.5	0.5	0	0
	S4	99.1	0.5	0	0
	S5	100	2.7	0	0
	S6	100	7.1	0	0
	S7	100	10.9	0	0
Abdominal yellow rings uninterrupted and not longer than wide	S3	57 (57.5)	17.4 (18.5)	0	2.1
	S4	0 (1)	72.3 (78.8)	0	4.3
	S5	0	85.3 (97.3)	41.7	70.2 (76.6)
	S6	0	78.3 (93)	58.3	85.3 (95.8)
	S7	0	73.4 (89.2)	83.3	88.2 (97.9)
Abdominal yellow rings uninterrupted and longer than wide	S3	0	81	100	91.5 (97.9)
	S4	0	20.7	100	89.4 (95.8)
	S5	0	0	58.3	23.4
	S6	0	0	41.7	4.3
	S7	0	0	16.7	2.1
Yellow ring of S2 indented by a medio-dorsal black square		0	5.4 (9.2)	100	84.8 (91.3)
Yellow ring W-shaped on its posterior edge	S3	0	52.2 (57.1)	100	66 (72.4)
	S4	0	5.4 (7.6)	91.7	64.8
	S5	0	0	66.7	12.8
	S6	0	0	58.3	12.8
	S7	0	4.3 (7)	100 **	93.6 (100)*
Apical lunulae on S7		91.1	85.9	83.3	76.6
Presence of dorso-lateral yellow spots	S9	0.47	96.1	100	95.3
	S10	0	35.4	41.7	58.1
Number of cells in the wing anal triangle	3	10.2	4.8	20.8	28.7
	4	38.8	40	62.5	42.6
	5	38.8	46.7	12.5	23.4
	6 or 7	12.2	8.6	4.2	5.3

S3, ..., S10 : 3rd abdominal segment, ..., 10th abdominal segment
* : of which 6.4 % are rounded
** : of which 50 % are rounded
( ) : the values within brackets include specimens for which the given pattern was poorly characterized

E from the Rhône river and most of the southern Alps. Based on both MORTON's (1915) and LIEFTINCK's (1966) descriptions and illustrations, populations inhabiting here must be ascribed to *C. b. immaculifrons* Sélys, 1850.

The best differentiating features of the males lie in the extension and shape of the abdominal yellow rings (Tab I, II; Fig. 2, No. 4). Broadly speaking and based on 184 specimens studied from 35 localities, these yellow rings were mostly broad and uninterrupted from S3 to S6 (in more than 90% of the specimens studied) or to S8 (≥ 80%). Additionally, and according to LIEFTINCK (1966), they were laterally clearly angulated forward from S4 to S6 on a great number of specimens (95% on S4, more than 80% on S5-S6); sometimes only subangulated on S5 (9%) and S6

Table II

Main patterns of the males of various subspecies of *Cordulegaster boltonii*: homogeneous populations, lateral and frontal views. – [All values are % of the number of specimens studied (n)]

Type of pattern		Area 1 *C. b. boltonii* (most of Europe) (n = 214)	Area 2 *C. b. immaculifrons* (SE France) (n = 184)	Area 3 *C. b. algirica* (Maroc) (n = 12)	Area 4 *C. b. iberica* (Center of S and E Spain) (n = 47)
Abdominal yellow rings angulated forward in lateral view	S4	90.2	95.1 (95.6)	0 (8.4)	64.1 (74.4)
	S5	52.3 (53.7)	84.8 (94)	0	51.3 (61.6)
	S6	49.1 (51.4)	82.6 (85.9)	0	33.3 (51.2)
	S7	0 (1.4)	2.2 (4.1)	0	0
Anterior edge of yellow rings straight or weakly curved in lateral view	S4	9.8	4.3	91.6	25.6
	S5	46.3	6	100	33.4 (38.5)
	S6	48.6	14.1	100	48.7
	S7	98.6	95.6	100	100
Median lateral yellow stripe of mesothorax broken in 3 - 4 spots		75	7.7	83.3	63.4
Frontal black line	well marked	100	14.1	0	8.1
	vestigial	0	18.5	8.3	16.2
	missing	0	67.4	91.7	75.7

S3, ..., S10 : 3rd abdominal segment, ..., 10th abdominal segment
( ) : the values within brackets include specimens for which the given pattern was poorly characterized

(3%). That on S4 was mostly wider than long or as wide as long (about 80%), but decidedly longer than wide in some specimens (17%). Those of S5-S7 were never longer than wide. On S7, the posterior margin of the yellow ring was mostly slightly rounded or almost straight (96%), scarcely with the form of a poorly defined (about 3%) or vigorously angulated (about 4%) W. On S2, the posterior margin of the yellow ring was rather straight (91%), sometimes nearly (4%) or clearly (5%) indented by a medio-dorsal black square. This ring was almost always clearly more extended than in the nominal subspecies. Some specimens corresponded to the "A" type of MORTON (1915) (S9 with only basal yellow spots, S10 black), other to the "B" type (S9 and S10 with extended, conspicuous, dorso-lateral yellow spots), the remainder being intermediate. On an average, the "B" type constituted 35% of the specimens observed, despite a very strong variation of this proportion from one locality to another.

Some specimens, and even some populations, however, did not follow this general trend. In a number of localities it was possible to find poorly defined specimens in which near all the abdominal yellow rings were more or less subinterrupted from S4 to S8, and sometimes clearly interrupted on some segments. This intermediate phenotype was found to be dominant (85%) in some localities but, on an average, it did not exceed 22% of the males studied. Very scarce specimens exhibited even the typical pattern of *C. b. boltonii* (only two males observed). The proportion of these poorly defined specimens in a given locality was neither related to the latitude nor to the altitude. Intermediate specimens and intermediate populations

were found throughout the range of *C. b. immaculifrons* and some populations from the lowland mediterranean fringe were much more poorly defined than others from localities in the southern Alps standing around 1200 m above sea level. On the other hand, this variability falls within the range previously reported for

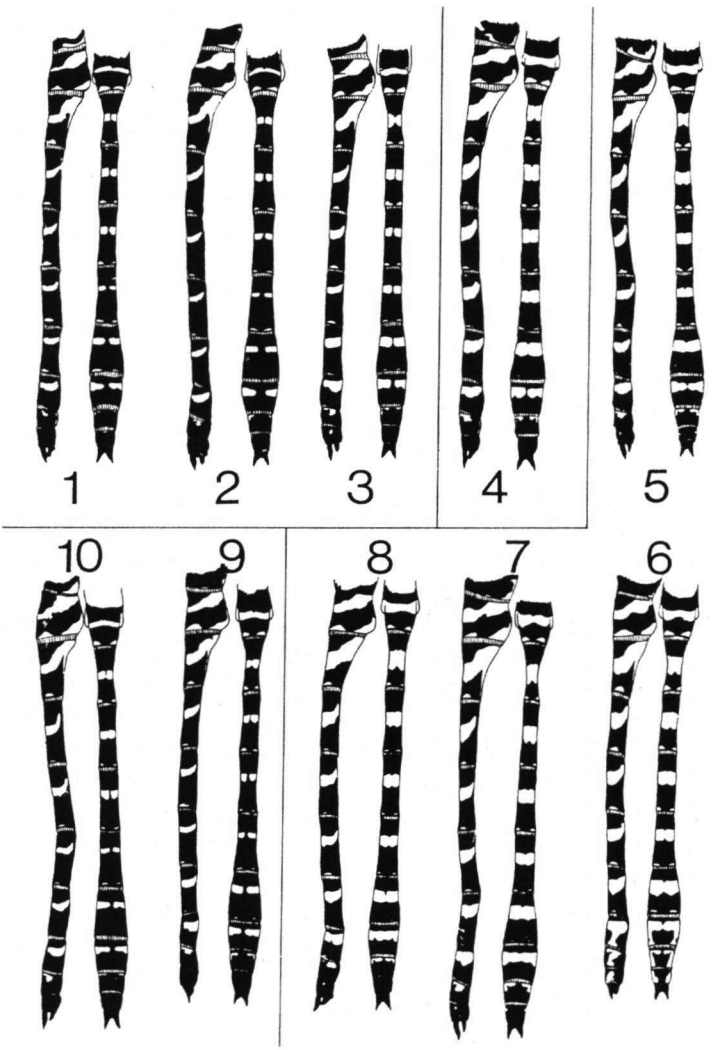

Fig. 2. Colour patterns of various specimens of *Cordulegaster b. boltonii* and *C. b. immaculifrons* in the area investigated: (1-2) typical habitus of *b. boltonii* in area 1; – (3) occasional variation of *b. boltonii* in area 5; – (4) *b. immaculifrons* from area 2; – (5-8) *b. immaculifrons* in mixed populations with *b. boltonii* in area 6; – (9-10) *b. boltonii* in mixed populations with *b. immaculifrons* in area 6.

other populations by MORTON (1927) and BALESTRAZZI et al. (1983). Thus it was believed to reflect the current heterogeneity of *C. b. immaculifrons* rather than the existence of clines in some areas.

With respect to other features usually reported for *C. b. immaculifrons*, the labrum remained laterally pure yellow only in 30% of the specimens studied. It was bordered with light (40%) or dark (30%) brown in others and the virgule was dark to light brown. The black line of the frons was either absent (67%) or reduced to a vestigial darkness (18%) but remained well marked in a significant number of specimens (14%). The posterior yellow border of the eyes was very variable, ranging from a narrow line to a rather wide band (not always wider than in the nominal subspecies). These features were not related to the extension of the abdominal yellow marks. Due to their high variability, these three criteria appear to be of limited interest as diagnostic tools, except for observations based on a great number of specimens. Finally, the abdominal appendages were found to agree very well with those of the nominal subspecies (outer edge of the superior ones mostly concave and then only briefly convex at the apex, apex of the inferior one emarginated by an angle of 101-168°). Also the number of cells in the anal triangle ranged, as in *C. b. boltonii*, from 3 to 6.

Such populations are widespread throughout the southern Alps up to 1200 m above sea level, except for the highest regions making up the French-Italian boundary (Queyras, Mercantour) where we found only *C. b. boltonii*. The northernmost populations of *C. b. immaculifrons* were observed from the Queyras boundaries to the southern slopes of the Vercors plateau (Diois region). Northerly, the cold climatic conditions of the Oisans, Dévoluy and Vercors highlands seem to be unfavourable to this subspecies, which was not encountered there.

Surprisingly, pure populations of *C. b. immaculifrons* were found to be lacking on the western side of the Rhône valley. Only pure populations of *C. b. boltonii* were observed northward from the Coiron plateau as well as within the Massif Central. Mixed populations of *C. b. boltonii* and *C. b. immaculifrons* were encountered at low altitude southward from the Coiron, between the Massif Central and the Rhône river, up to central Portugal through central Spain (see below). The Montpellier area does not actually pertain to the typical range of *C. b. immaculifrons* and it is thus unfortunate that it constitutes the type locality of this subspecies (LIEFTINCK, 1966).

THIRD HOMOGENEOUS AREA: *C. b. algirica* (Fig. 1, area 3). – A third homogeneous area was found at last in the Middle Atlas and the Rif mountains in Morocco. According to DUMONT (1977), it should extend up to the east of Algeria and possibly to Tunisia in the Tellian Atlas.

All the *C. boltonii* encountered in the Moroccan Middle Atlas and Rif were found to agree perfectly with MORTON's (1915) and LIEFTINCK's (1966) descriptions of *C. b. algirica*. Based on 12 males, the following patterns should be emphasized (Tabs I, II; Fig. 3, Nos 1-2). Lateral edges of labrum irregularly bordered with dark

brown in 30% of the males studied, otherwise pure yellow or very narrowly bordered with light brown. Virgule of labrum dark to light brown. Frontal black line absent in more than 90% of the sample studied, otherwise vestigial (never well

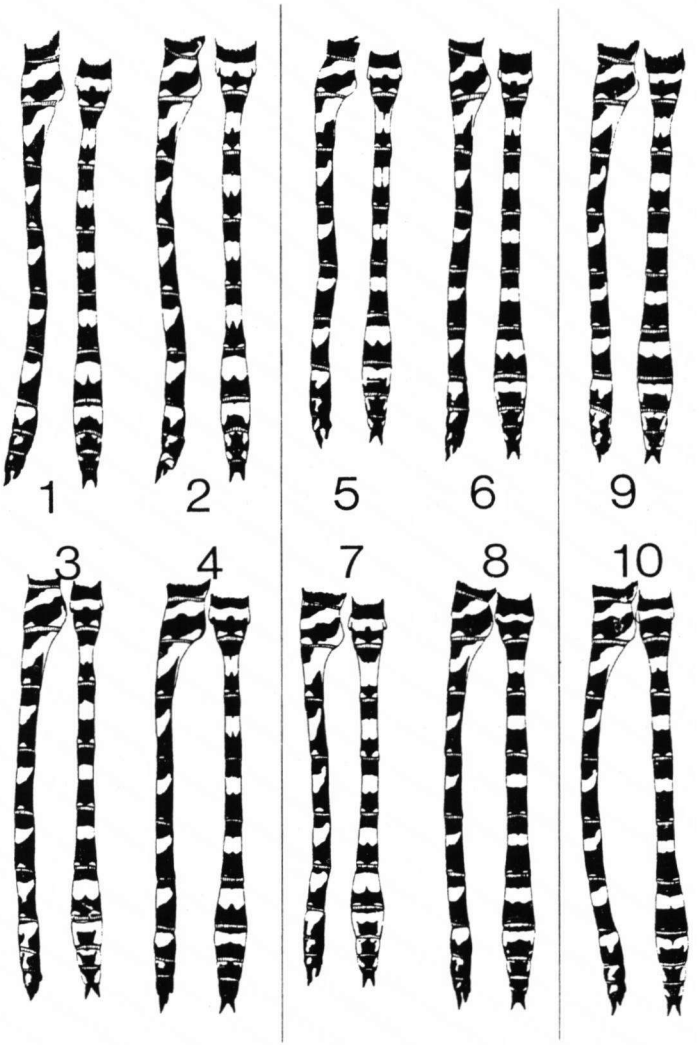

Fig. 3. Colour patterns of various specimens of *Cordulegaster boltonii iberica* and *C. b. algirica* in the area investigated: (1-2) typical habitus of *b. algirica* in area 3; – (3-4) *b. algirica* in mixed populations with *b. iberica* in area 8; – (5-8) Variation of the habitus of *b. iberica* in area 4 [5 = holotype; 6-8 = paratypes]; – (9) *b. iberica* in mixed populations with *b. immaculifrons* in area 7; – (10) *b. immaculifrons* in mixed populations with *b. iberica* in area 7.

marked). Back of the eyes black with a very variable lateral yellow border, ranging from a narrow line to a somewhat wide band (not always black with a wide band as often stated). Median lateral stripes of mesothorax often, but not always, fragmented into 3-4 yellow spots (83%). Anal triangle of hindwings 3 to 6 celled. Abdominal yellow rings always uninterrupted from S2 to S8. That of S2 broad and always indented by a medio-dorsal black square on its posterior edge. That of S7 with its posterior margin as a vigorously angulated W (50%), otherwise as a conspicuous expanded and rounded W. Posterior margin of the yellow rings from S3 to S6 also W-shaped in the yellowest specimens. Yellow rings on S3 and S4 always longer than wide, those of S5 and S6 decidedly so in 58% and 42% respectively, of the males studied. Anterior margin of yellow rings from S4 to S6 never laterally angulated, mostly straight (92%), otherwise weakly curved on S4 in lateral view. Yellow spots on S9 and S10 always present but variable in size, often very expanded and conspicuous (42%). Superior appendages as in the nominal subspecies. Apex of the inferior appendage straight or emarginated with an angle ranging from 100 to 170°.

FOURTH HOMOGENEOUS AREA: *C. b. iberica* ssp. n. (Fig. 1, area 4). – Ultimately, a fourth rather homogeneous area was traced in the S of Spain from the Sierra Morena to Alicante and Valencia, excluding the southernmost coastal highlands. Whereas populations from this area were recently recorded under *C. b. immaculifrons* (VERSCHUREN, 1989), their colour pattern did not agree with that of the French members of this subspecies. Alternatively, they did not agree with our specimens of *C. b. algirica*, nor with those described both by MORTON (1915) and LIEFTINCK (1966). Actually they resemble these two subspecies but clearly combine some patterns of each to produce a distinctive phenotype, which remained so far overlooked. As it did not appear to be affected by a gradual change from a Sierra to another in this area but rather exhibited a repetitive and rather low variability whatever the locality, there is no evidence of a cline. The specimens encountered here clearly form an homogeneous entity and constitute a good subspecies that we call *Cordulegaster boltonii iberica* ssp.n., and which is described below.

CORDULEGASTER BOLTONII IBERICA SSP. N.

Figures 1 (area 4), 3 (Nos 5-9),
4 (Nos 5-7), 5 (3rd row from top),
6 (lower row, left)

M a t e r i a l. – **Holotype** ♂: Sierra de Alcaraz (Province of Albacete), Puerto de las Crucetillas (38°33'N-2°22'W), alt. ca 1450 m, J.-P. Boudot leg., 18-VII-1989. Deposited in the Laboratoire de Biologie des Insectes, Faculté des Sciences, Université de Nancy I. – **Paratypes**: [24 ♂ from the localities where a great number of specimens were found: Sierras of Alcaraz, Cazorla, Segura and Benicadell]: 6 ♂, Sierra de Alcaraz (Province of Albacete), Puerto de las Crucetillas (38°33'N-2°22'W), alt. ca 1450 m, J.-P. Boudot leg., 18-VII-1989 and 3-VII-1990; – 1 ♂, Sierra de Alcaraz, Rio Guadalimar

(38°28'N-2°32'W), alt. ca 1050 m, J.-P. Boudot leg., 18-VII-1989; – 4 ♂, Sierra de Segura (Province of Jaen), Rio Zumeta (38°5'N-2°34'W), alt. ca 1200 m, J.-P. Boudot leg., 14-VII-1989; – 6 ♂, Sierra de Cuatro Villas/Cazorla (Province of Jaen), Rio Aguacebas Grande (38°5'N-2°54'W), alt. ca 1300 m, J.-P. Boudot leg., 17-VII-1989 and 6-VII-1990; – 7 ♂, Sierra de Benicadell, Muro de Alcoy (Province of Alicante) (38°48'N-0°30'W), alt. ca 600 m, J.-P. Boudot leg., 6-VII-1991. – All in the Laboratoire de Biologie des Insectes, Faculté des Sciences, Université de Nancy I.

DIAGNOSIS, ♂ (Fig. 3, Nos 5-8). – (1) Resembles *C. b. immaculifrons*, but yellow ring on S7 with its posterior edge almost always with the form of a vigorously angulated or sometimes rounded W (in 94% of the males, based on 47 specimens), yellow ring of S2 generally clearly indented by a medio-dorsal black square (in 85% of the sample), and yellow ring on S4 often decidedly longer than wide in dorsal view (89%). These features mimic those of *C. b. algirica*. Additionally, abdominal yellow rings on S4 to S6 laterally angulated or not. – (2) Resembles *C. b. algirica*, but abdominal yellow rings on S4 to S6 laterally often angulated or subangulated forward, with a frequency decreasing from S4 to S6 (Tab. II). Abdominal yellow rings often more reduced on S5 and S6 than in *C. b. algirica*. Frontal black line well marked in a significant number of specimens (about 8% of the males studied), otherwise vestigial or absent. These features mimic those of *C. b. immaculifrons*.

Isolated specimens cannot be differentiated from either *C. b. algirica* or *C. b. immaculifrons*. Only observations at the population level permit identification of this subspecies.

MALE (**holotype**). – Labrum yellow, irregularly bordered with dark brown at base, very narrowly bordered with light brown on sides and with a median brown virgule. Frons yellow without any dark line. Occipital triangle yellow, fringed with pale yellow hairs. Back of the eyes black with a rather wide lateral external yellow area. Prothorax black with yellow anterior and posterior edges, the latter interrupted mid-dorsally with black. Thorax black with yellow antehumeral stripes and three pairs of lateral yellow bands, the middle one being very narrow and unfragmented except for a basal minute yellow spot. Anal triangle of hindwings 3 celled. Abdomen black with uninterrupted yellow rings from S2 to S8 and rather conspicuous dorso-lateral yellow spot on S9 and S10. Apical lunulae from S2 to S7 gradually decreasing in size. Yellow ring on S2 with its posterior edge clearly indented by a medio-dorsal black square. Yellow rings of S3 and S4 decidedly longer than wide, that of S5 about as wide as long, that of S6 wider than long. Yellow ring on S7 with its anterior margin straight, clearly W-shaped on its posterior edge in dorsal view. Yellow rings from S3 to S5 laterally angulated and directed forward, that of S6 subangulated. Superior appendages with a mostly concave external border and with the submedian tooth hardly visible in lateral view. Inferior appendages almost square and emarginated at the apex by an angle of about 160°.

VARIABILITY. – From the study of 47 specimens belonging to 17 localities in area No. 4 (Fig. 1), either collected (28 specimens) or described at hand in the field and then released (19 specimens), the following variability can be drawn up (Tabs I, II;

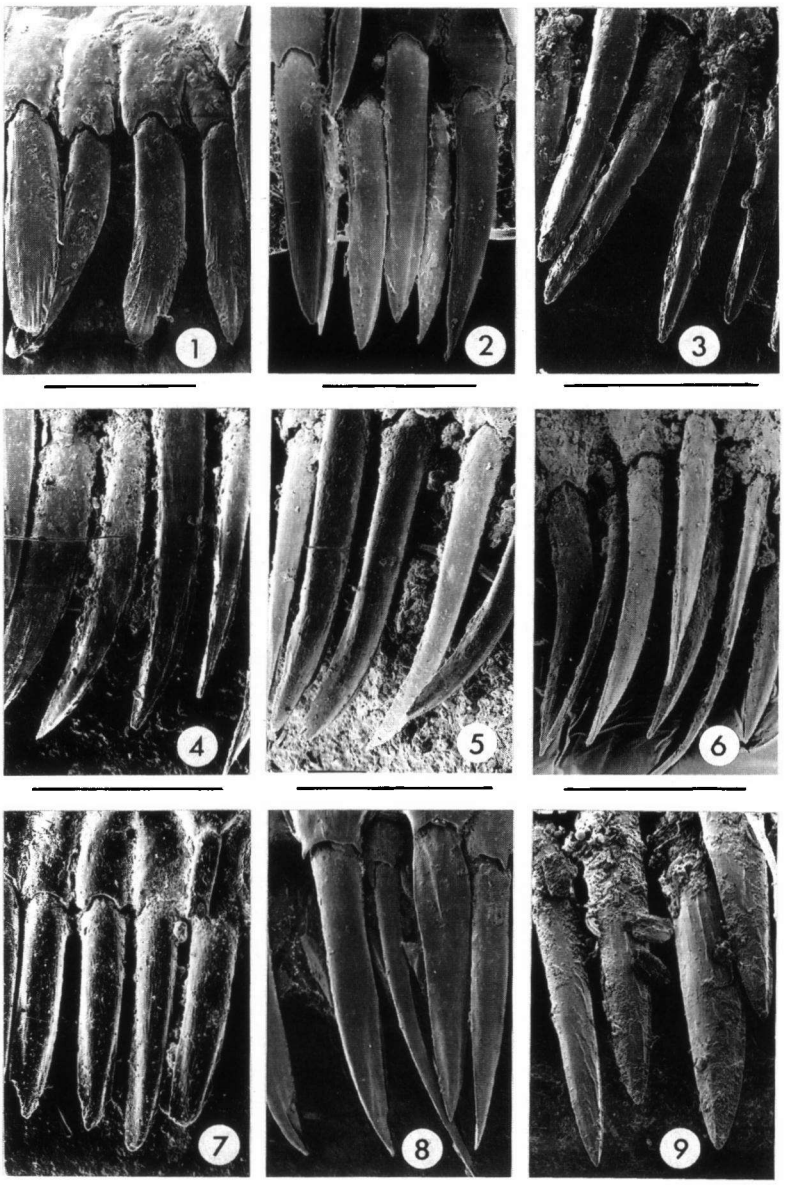

Fig. 4. Examples of the shape of the setae on the posterior margin of the 9th abdominal sternite in the exuviae of various subspecies of *Cordulegaster boltonii*: (1-2) *b. boltonii* in area 1; – (3-4) *b. immaculifrons* from area 2; – (5-7) *b. iberica* in area 4; – (8) *b. algirica* or *b. iberica* in area 8; – (9) *b. algirica* in area 3. – [Scale: 100 µm].

Fig. 3, Nos 5-8):

Lateral edges of labrum scarcely irregularly bordered with dark brown (in 8% of the sample studied), otherwise pure yellow or very narrowly bordered with light brown. Virgule of labrum dark to light brown, sometimes almost lacking (11%). Frontal black line lacking in more than 75% of the sample studied, sometimes well marked (8%), otherwise verstigial. Back of the eyes with a very variable lateral yellow border, ranging from a narrow line to a wide area. Median lateral bands of the thorax often broken into 3-4 yellow spots (63%). Anal triangle of hindwings 3 to 6 celled (Tab. I). Yellow rings of abdomen always uninterrupted from S2 to S8 in vivo. Dorso-lateral yellow spots on S9 and S10 either conspicuous (58%) or minute (37%). Apical lunulae sometimes lacking on S7 (23%). Posterior margin of the yellow ring on S2 clearly indented by a medio-dorsal black square in about 85% of the males studied, sometimes subindented (6%), otherwise almost straight (about 9%). Yellow rings on S3-S4 decidedly longer than wide in about 90% of the males studied, sometimes almost as wide as long (6%), otherwise wider than long. Those on S5 and S6 decidedly wider than long in 70-88% of the males studied, sometimes as long as wide (6-10%), otherwise longer than wide. Posterior margin of the yellow ring on S7 as a vigorously angulated or rounded W in 94% of the males studied, otherwise only poorly rounded, as in most of *C. b. immaculifrons*. Yellow rings on S4 to S6 either laterally angulated forward, subangulated or with a straight anterior margin. Submedian tooth of superior appendages clearly visible in lateral view in 45% of the studied males, otherwise hardly visible. Apical margin of the inferior appendage straight or emarginated with an angle ranging from 100 to 170°.

Measurements (acetone dried specimens; in mm). – **Holotype**: abd.+app.: 52, – right h.w.: 40.5, – pterostigma in h.w.: 4; – **Paratypes**: abd.+app.: 52-59, – right h.w.: 40-44, – pterostigma in h.w.: 4-5.

FEMALE. – For some descriptive notes see p. 166.

DISTRIBUTION. – Pure populations of this subspecies were found from the Sierra Morena to the area of Valencia and Alicante throughout the Sierras of Cazorla, Segura and Alcaraz. Numerous males corresponding to the facies of this subspecies were found in mixed populations, together with *C. b. immaculifrons* and a great number of intermediate specimens, in the south-east of the Iberian cordillera (see later). Additionally, scarce males exhibiting the facies of *C. b. iberica* were found in the very south of the Iberian Peninsula, together with typical *C. b. algirica* (see below). Thus, pure populations of this subspecies range only in the central part of the S of Spain.

Heterogeneous populations

Variable heterogeneous populations were found over large areas in southern France and Spain. In most cases, it was possible to recognize individuals exhibiting the typical pattern of known subspecies, mixed in various proportions with a number of very variable intermediate specimens. In one case, only one well defined sub-

species (*C. b. boltonii*) was recognized. The latter occurred together with a small number of regularly distributed deviant specimens, the pattern of which being clearly reminiscent of another subspecies (*C. b. immaculifrons*).

FIRST HETEROGENEOUS AREA: *C. b. boltonii* with abnormal specimens (Fig. 1, area 5). – The first homogeneous area extends from the SW of France to the NW of the Iberian Peninsula, including the extreme S of the Massif Central, most of the Aquitaine lowland, the northern side of the Pyrénées, the Basque Country and the whole Cantabrian Cordillera up to Galicia and the north of Portugal.

The heterogeneousness of this area remains weak but appears to be very significant. Based on their general pattern, nearly all of the *C. boltonii* encountered here were ascribed to the nominal subspecies by OCHARAN (1987). A careful exami-

Table III

Main patterns of the males of various subspecies of *Cordulegaster boltonii*: heterogeneous populations, dorsal view. – [All values are % of the number of specimens studied (n)]

Type of pattern		Area 5 *C. b. boltonii* atypical (SW France and NW Spain) (n = 194)	Area 6 *C. b. boltonii* + *C. b. immaculifrons* (S France to Central Portugal) (n = 197)	Area 7 *C. b. immaculifrons* + *C. b. iberica* (E Spain) (n = 69)	Area 8 *C. b. algirica* + *C. b. iberica* (S Spain) (n = 27)
Abdominal yellow rings medio-dorsally interrupted	S3	46.4	19.8	0	0
	S4	94.8	33	0	0
	S5	95.9	45.2	0	0
	S6	99	61.9	0	0
	S7	99	68	4.3	0
Abdominal yellow rings uninterrupted and not longer than wide	S3	52.1 (53.6)	54.3 (54.8)	10.1	0
	S4	5.2	50.3 (53.3)	44.9	7.4
	S5	1.5 (4.1)	51.3 (54.3)	98.6	59.3
	S6	0.5 (1)	35.5 (38)	98.6	96.3
	S7	0 (1)	29.4 (31.9)	95.7	96.3
Abdominal yellow rings uninterrupted and longer than wide	S3	0	25.4	89.9	100
	S4	0	13.7	55.1	92.6
	S5	0	0	1.4	40.7
	S6	0	0	1.4	3.7
	S7	0	0	0	3.7
Yellow ring of 32 indented by a medio-dorsal black square		0	1.5 (4)	39.1 (46.3)	96.3 (100)
Yellow ring W-shaped on its posterior edge	S3	1.5 (41.2)	13.2 (17.8)	40.6 (52)	85.2 (88.9)
	S4	0	2 (4)	11.6 (14.5)	44.4 (48.1)
	S5	0	0	1.4	11.1
	S6	0	0	1.4	3.7
	S7	0	2 (4.5)	39.1 (52.1)	96.3 ***
Apical lunulae on S7		94.3	89.3	95.7	63
Presence of dorso-lateral yellow spots	S9	60.7	65.7	93.3	96.1
	S10	19.6	27.1	35	46.1
Number of cells in the wing anal triangle	3	8.3	10.4	13.1	22
	4	29.2	52.1	52.1	40
	5	41.7	36.5	36.5	36
	6 or 7	20.9	1	1	2

S3, ... S10 : 3rd abdominal segment, ... 10th abdominal segment
*** : of which 22,2 % are rounded
( ) : the values within brackets include specimens for which the given pattern was poorly characterized

nation of a great number of males revealed, however, the existence of a small number of deviant specimens with significant characteristics (Fig. 2, No. 3). The frontal black line was sometimes lacking (6%, based on a sample of 194 males from 46 localities) or vestigial (9%). In other cases the 9th and 10th abdominal segments exhibited conspicuous, either continuous or isolated, lateral yellow spots (about 5%). In scarce specimens, the abdominal yellow rings remained uninterrupted on S4 and S5, although they remained reduced in size (6%, based on S5). Although we were unable to find the true habitus of *C. b. immaculifrons* in this area, these patterns were clearly reminiscent of this subspecies.

These results agree very well with data by OCHARAN (1987). About 85% of 112 specimens originating from 108 localities in the Cantabrian Cordillera, Galicia and Leon, pertained obviously to typical *C. b. boltonii*, 12% to deviant specimens lacking in the black frontal line and/or marked with lateral yellow spots on S9 and S10, and 3% to transient forms between *C. b. boltonii* and *C. b. immaculifrons* (but due to lack of experience about the French *C. b. immaculifrons*, he ascribed erroneously some of these intermediates to the latter subspecies).

Similar situations have been reported in the past from the French Basque Country (MORTON, 1927), the upper Garonne valley (FUDAKOWSKI, 1933) and the Gironde area (BALESTRAZZI et al., 1983). Additionally, and according to our own observations in this area, the records of mixed populations of *C. b. boltonii* and *C. b. immaculifrons* from the upper and middle Têt valley in the Eastern Pyrénées (LACROIX, 1915; AGUESSE, 1958) would be due to the presence of such intermediate specimens rather than to the existence of genuine *C. b. immaculifrons*. The record of a number of *C. boltonii* "more or less" *immaculifrons* from Biarritz by SELYS & HAGEN (1858), and the indication of *C. b. immaculifrons* from Bordeaux by FRASER (1929), may be due to similar transient forms. No males exhibiting such abnormalities are known northward from the Gironde area. The precise northern extension of these populations, however, remains imprecise.

SECOND HETEROGENEOUS AREA: *C. b. boltonii* + *C. b. immaculifrons* and hybrids (Fig. 1, area 6). – The second heterogeneous area covers the lowland mediterranean fringe from the Montélimar area in France to the centre of Portugal through the NE and centre of Spain. The heterogeneousness of this area is much more pronounced than that of the previous one. Here we observed specimens with the typical pattern of *C. b. boltonii* mixed together with very variable proportions of others exhibiting the typical pattern of *C. b. immaculifrons* plus intermediate phenotypes (Fig. 2, Nos 5-10). In the latter, the abdominal yellow rings were often more extended than in the nominal subspecies but remained interrupted or subinterrupted on most of the segments. Alternatively, they remained uninterrupted on S4 and S5 but were reduced in size. Sometimes they were as in true *C. b. boltonii*, but the frontal black line was either lacking or vestigial. In other cases, the 9th and 10th abdominal segments were conspicuously marked with lateral yellow spots as in a number of *C. b. immaculifrons*. Scarce specimens corresponding either to the phenotype of *C. b.*

iberica (posterior edge of S7 with the form of a W, S2 with a squarish black indentation) (3 specimens) or to transient forms between the latter and typical *C. b. immaculifrons* (1 male) were even observed. As such specimens are known to constitute a small proportion of the French populations of *C. b. immaculifrons* (7-9%), these males were included in the local members of *C. b. immaculifrons*.

Based on 197 specimens from 42 localities, this area was found to contain about 30% of the individuals identifiable to *C. b. immaculifrons* and another 35% identifiable to *C. b. boltonii*, whereas the remaining 34% clearly pertained to bastard specimens. However, a very strong heterogeneity was noticed from one locality to another. Sometimes one or another phenotype was found to predominate, whereas in other localities all phenotypes apparently balanced. The *C. b. immaculifrons* phenotype was found to be scarce in the French part of this area between Montpellier and the Spanish boundary, to be irregularly mixed with other forms both on the southern slopes of the Pyrénées, in the Central Cordillera in Spain and northward from Montpellier in France, but to predominate (more than 75%) in two meridional Spanish localities (Sierras de Roquerole and de Gua-dalupe). No pure population of *C. b. immaculifrons* was found in any locality of the Iberian Peninsula, however.

OCHARAN (1987) recognized the existence of such mixed populations in both the Sierra de la Demanda and the Central Cordillera. However, as he did not experience the French *C. b. immaculifrons*, its acceptance for this taxa was too broad and he ascribed most of its specimens (62.5%) to this subspecies. Indeed, a great number corresponded to the intermediate phenotype.

Table IV

Main patterns of the males of various subspecies of *Cordulegaster boltonii*: heterogeneous populations, lateral and frontal views. – [All values are % of the number of specimens studied (n)]

Type of pattern		Area 5 *C. b. boltonii* atypical (SW France and NW Spain) (n = 194)	Area 6 *C. b. boltonii* + *C. b. immaculifrons* (S France to Central Portugal) (n = 197)	Area 7 *C. b. immaculifrons* + *C. b. iberica* (E Spain) (n = 69)	Area 8 *C. b. algirica* + *C. b. iberica* (S Spain) (n = 27)
Abdominal yellow rings angulated forward in lateral view	S4	95.9 (96.9)	94.4	87	11.1 (22.2)
	S5	59.6 (62.2)	91.9 (92.4)	82.6	7.4 (18.5)
	S6	57 (57.5)	85.8 (88.3)	76.8	7.4 (14.8)
	S7	0 (0.5)	0.5 (6)	0	0
Anterior edge of yellow rings straight or weakly curved in lateral view	S4	2.6	5.6	13	77.8
	S5	34.2	7.1	10.1 (15.9)	81.5
	S6	38.9	11.2	21.7	85.2
	S7	99	93.9	95.7 (100)	100
Median lateral yellow stripe of mesothorax broken in 3 - 4 spots		13	30.2	1.4	92
Frontal black line	well marked	82.4	49.2	7.4	4.3
	vestigial	9.3	16.8	17.4	17.4
	missing	8.2	34.5	75.4	78.3

S3, ..., S10 : 3rd abdominal segment, ..., 10th abdominal segment
( ) : the values within brackets include specimens for which the given pattern was poorly characterized

THIRD HETEROGENEOUS AREA: *C. b. immaculifrons* + *C.b. iberica* and hybrids (Fig. 1, area 7). – A third area with mixed populations was found to cover the SE of the Iberian Cordillera. Based on sample of 69 males studied from 9 localities, typical phenotypes of both *C. b. immaculifrons* (48%) and *C. b. iberica* (35%) were found together with transient forms (17%). The specimens ascribed to *C. b. immaculifrons* agreed perfectly with the French ones without any restrictions (Fig. 3, No. 10). Those ascribed to *C. b. iberica* looked like those from the typical range of this subspecies (Fig. 3, No. 9). The specimens classified as intermediates exhibited a somewhat poorly defined but always present W-shaped yellow spot on their 7th abdominal segment.

The presence of *C. b. iberica* in this area supports MORTON's remark (1915), that a male from Albarracin showed a tendency towards the Algerian specimens.

FOURTH HETEROGENEOUS AREA: *C. b. algirica* + *C. b. iberica* (Fig. 1, area 8). – A fourth heterogeneous area was traced in the southernmost highlands of Spain. Eighteen of the 27 males (67%) studied from the Sierra Nevada, Sierra Bermeja and Sierra de Algibe were found to agree with our specimens of *C. b. algirica* from Morocco (13 specimens studied) (posterior edge of the yellow ring on S7 W-shaped, that of S2 with a black squarish indentation; yellow rings from S4 to S6 not laterally angulated) (Fig. 3, Nos 3-4). Although these specimens were, on average, darker than those from Morocco, they fell in the same range of variability and, according to LIEFTINCK (1966), should be ascribed without any doubt to *C. b. algirica*. Surprisingly, 3 other specimens from the Sierra Nevada and the Sierra de Algibe were quite different. In addition to a W-shaped yellow spot on S7 and a black squarish indentation on the yellow ring of S2, they exhibited strongly angulated yellow rings on S4 and/or S5 and S6. As no specimen with such angulated yellow rings is so far known from North Africa, these populations seem to be the result of the intrusion of *C. b. iberica* in a former population of *C. b. algirica*. In the central part of its range, where pure populations occur, (area No. 4), only 64% of the specimens of *C. b. iberica* studied exhibited at least one clearly angulated yellow ring, and specimens lacking in angulated yellow rings were indistinguishable from *C. b. algirica*. Thus the overall proportion of *C. b. iberica* which would be present in the southernmost Sierras of Spain could be estimated to be about 17%. No evidence of intermediate specimens was obtained, but as the single distinctive feature of these two subspecies stands either on the presence or absence of angulated yellow rings, and as this pattern is lacking in a number of *C. b. iberica*, bastard specimens cannot be distinguished from one or other of the two parent subspecies.

Based on NAVAS (1907), MORTON (1915) and AGUESSE (1968) reported the nominal subspecies from the Sierra Nevada. However, as we found only mixed populations of *C. b. algirica* and *C. b. iberica* in this range whatever the altitude, we are of the opinion that this assertion was erroneous.

DESCRIPTIVE NOTES ON FEMALES

Table V

Ovipositor length and ovipostor: sternites 9+10 ratio in various subspecies of *Cordulegaster boltonii* (females)

Area and subspecies	Actual length		Ovipositor to length of sternites 9 + 10 ratio	
	Authors' data	Lieftinck's data	Authors' data	Lieftinck's data
1 - *C. b. boltonii*	8.5 : 5 9 : 5 8.75 : 5 9 : 5 8.5 : 5	none	1.7 1.8 1.75 1.8 1.7	none
2 - *C. b. immaculifrons*	7.5 : 5	9 : 5 9 : 5	1.5	1.8 1.8
3 - *C. b. algirica*	8.5 : 5	none	1.7	none
4 - *C. b. iberica*	none	none	none	none
6 - *C. b. boltonii* and/or *immaculifrons*	8.5 : 4.75	none	1.79	none
8 - *C. b. algirica* and/or *iberica*	7.75 : 5 7 : 5	8 : 5 7.6 : 5 7.5 : 4.8	1.55 1.4	1.6 1.52 1.56
9 - *C. b. princeps*	9 : 5 8.75 : 5	8.5 : 5	1.8 1.75	1.7

Too few female specimens are available to allow a correct identification of each subspecies on this basis, viz. only 5 for *C. b. boltonii* in area 1, 1 for *C. b. immaculifrons* in area 2 (to which we added 4 photographed ones for their colour pattern), 1 for *C. b. algirica* in Morocco, 2 (only photographed) for *C. b. iberica*,1 for *C. b. boltonii* or *C. b. immaculifrons* in area 6, and 4 for *C. b. algirica* and/or *C. b. iberica* in area 8. Two females of *C. princeps* were also available for comparison.

Structural differentiation of the females of various subspecies of *C. boltonii* and *C. princeps* had been proposed by LIEFTINCK (1966), based on a very small number of specimens. The ratio of the length of the ovipositor to that of S9 + S10 was assumed to vary from one taxon to another. The proposed values are shown in Table V, together with those we measured from our own specimens. Considerable overlap occurred and we are unable to validate this criterion to distinguish the given subspecies, at least until a greater number of specimens become available for study. Based on the colour pattern, it appeared that the shape and size of the abdominal yellow spots were very variable within each subspecies and did not allow a clear distinction, given the poor sample size. The squarish black indentation of the yellow ring on S2 was well marked in one of the 2 *C. b. iberica* photographed and poorly marked in the other, but did not occur either in *C. b. boltonii* or *C. b. immaculifrons*, or in *C. b. algirica* from Morocco. It occurred again in only 1 female among 4 from area 8. On each side the posterior lunulae of S2 were connected with the median yellow ring in half our specimens of *C. b. immaculifrons* and *C. b. iberica*, and this always occurred in our *C. b. algirica* and/or *C. b. iberica* from Morocco and southern Spain. The posterior edge of S7 was W-shaped in 1

female of *C. b. iberica* and rounded in the other. This W-shaped spot occurred in our single specimen from Morocco (*C. b. algirica*), and also in three of our 4 specimens from area 8 (*C. b. algirica* and/or *C. b. iberica*). A great number of specimens would be needed to validate such criteria for the females, that is unrealistic as they tend to remain hidden.

DESCRIPTIVE KEY TO THE SUBSPECIES OF *CORDULEGASTER BOLTONII* (MALES ONLY)

The following key allows the identification of the males of the five subspecies of *Cordulegaster boltonii*:

1 Abdominal segments (3) (4) 5-8 with rather small median yellow spots (≤ 1/5th of their length), not merging with each other in a complete ring. Segment 9 usually black or with only 2 small basal or lateral yellow spots. S10 usually black, sometimes with yellow spots only in southern atypical populations. Labrum with a median dark brown virgule and usually bordered with dark brown at the base and on the sides.

2 Superior appendages of abdomen triangular, robust at base, with the outer edge being mainly concave and then only briefly convex. Inferior appendage straight or weakly emarginated apically with an angle > 100°. Frons usually with a transverse black line, the latter sometimes lacking in some southern atypical populations. Yellow rings on abdominal segments 4 (5) (6) ending laterally by parallel edges ..... ***boltonii* (Donovan, 1807)**

2' Superior appendages of abdomen slightly longer and slightly more sinuous, the outer edge being first concave, then decidedly more or less convex. Inferior appendage apically emarginated to strongly cleft with an angle ranging from 70° to 130°. Frons with or without a transversal black line. Yellow rings on abdominal segments 4 to 6 ending laterally by clearly convergent edges ..... ***trinacriae* Waterston, 1976**

1' Abdominal segments 3 to 8 with larger median yellow spots, generally reaching 1/4th to 1/3rd of their length and merging with each other in a complete ring (with some exceptions on the 7th and 8th segments). Segments 8 to 10 often with dorso-lateral longitudinal yellow spots, merging or not together. Labrum with or without a median dark brown virgule and bordered or not with light or dark brown.

3 Yellow ring of the 7th abdominal segment sinuous to slightly rounded or almost straight on its posterior edge in dorsal view in more than 90% of the males, otherwise W-shaped. Yellow ring of the second segment straight or sinuous on its posterior edge in more than 90% of the males, otherwise indented by a medio-dorsal black square. Yellow rings of abdominal segments 3 to 7 laterally angulated forward in more than 95% of the males. Those of segments 5 and 6 wider than long or as long as wide in dorsal view, weakly emarginated on their posterior edge, not appearing triangular in lateral view. Populations often containing variable proportions of specimens transitional to the phenotype of other subspecies ..... ***immaculifrons* Sélys, 1850**

3' Yellow ring of the 7th abdominal segment in the form of a vigorous rounded or angulated W in more than 90% of the males in dorsal view. Yellow ring of the second segment indented by a medio-dorsal black square in more than 80% of the males.

4 Yellow rings of abdominal segments 3 to 7 laterally angulated forward or not. Those of segments 5 and 6 wider than long or as long as wide, weakly emarginated on their posterior edge. W-shaped yellow ring of the 7th segment rather scarcely very expanded (only in maximal yellow specimens) ..... ***iberica* ssp.n.**

4' Yellow rings of abdominal segments 3 to 7 laterally not angulated forward. Those of segments 3 to 6 longer than wide or as long as wide, sometimes W-shaped. W-shaped yellow ring of the 7th segment often very expanded ..... ***algirica* Morton, 1915**

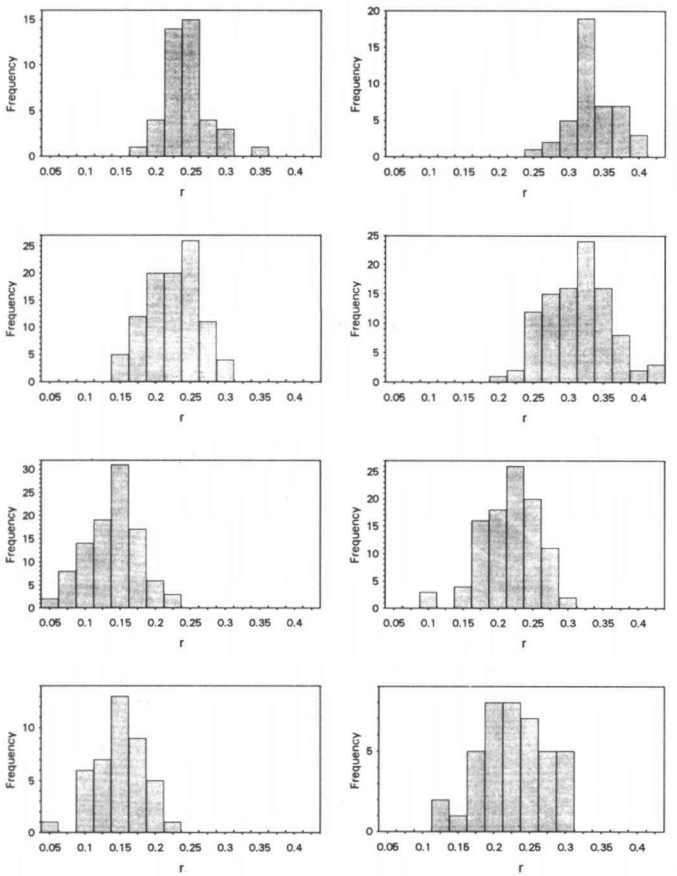

Fig. 5. Relative size distributions of the lateral spines on S8 (left column) and S9 (right column) of the exuviae in various subspecies of *Cordulegaster boltonii*. All values are the ratio (r) of the length of the lateral spines to the length of the corresponding sternite. – From top to bottom: *b. boltonii* (area 1); – *b. immaculifrons* (area 2); – *b. iberica* (area 4); – and, predominantly, *b. algirica* (area 8).

DISTINCTIVE FEATURES OF THE EXUVIAE

VERSCHUREN (1989) attempted to find distinctive features between the larvae and exuviae of various subspecies of *C. boltonii*. Three main criteria were recognized. First, the setae of the posterior edge of the 9th sternite were found to be mostly straight, flattened, robust, pointed or truncate and always simple in *C. b. boltonii*, slender, curved or straight in *C. b. algirica* and in some Spanish specimens erroneously ascribed to *C. b. immaculifrons* but pertaining indeed to both *C. b. iberica* and mixed populations of the latter with *C. b. immaculifrons*. Scarce bifurcate setae were occasionally observed in these so-called *C. b. immaculifrons*.

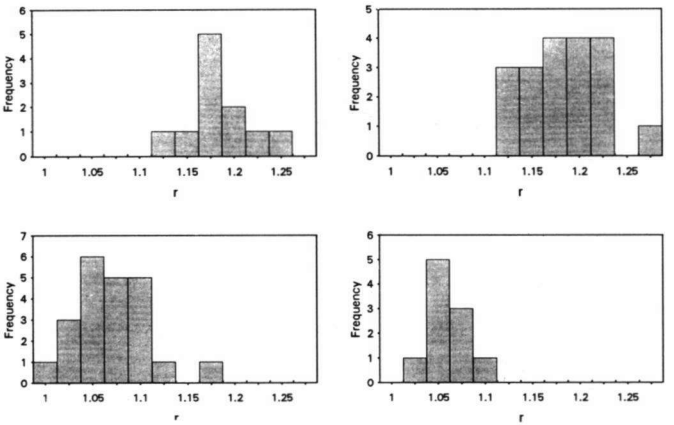

Fig. 6. Relative size distributions of the gonapophyses of the exuviae of the females of various subspecies of *Cordulegaster boltonii*. All values are the ratio of the length of the gonapophysis to that of the 9th sternite. – Upper row: *b. boltonii* (area 1, left) and *b. immaculifrons* (area 2, right); – lower row: *b. iberica* (area 4, left) and, predominantly, *b. algirica* (area 8, right).

In addition, the ratio (r) of the length of the lateral spines of S8 and S9 to the length of the corresponding segment ranged from (0.22) 0.25 to 0.4 (0.43) in the nominal subspecies, from 0.2 to 0.33 in its so-called *C. b. immaculifrons* populations from Spain. In one female pertaining to *C. b. algirica*, the lateral spines were clearly shorter on S8 (r=0.22) than on S9 (r=0.25). The third distinctive criterion was the

Table VI

Relative size distributions of the lateral spines on sternites 8 and 9 in the exuviae of various subspecies of *Cordulegaster boltonii*. – [All values are the ratio (r) of the length of the lateral spines to the length of the corresponding sternite]

Area and subspecies	Locality	r on 8th sternite		r on 9th sternite	
		mean ± standard deviation	95 % confidence interval	mean ± standard deviation	95 % confidence interval
1 - *Cordulegaster boltonii boltonii*	Vosges (n = 42)	0.245 ±0.0 313	0.235 - 0.255	0.338 ± 0.0315	0.328 - 0.348
2 - *Cordulegaster boltonii immaculifrons*	Vauvenargues (n = 13)	0.227 ±0.0 326	0.207 - 0.247	0.339 ± 0.039	0.315 - 0.363
	Estoublon (n = 62)	0.237 ± 0.0346	0.227 - 0.246	0.322 ± 0.0434	0.311 -0.333
	Roussieux (n = 20)	0.196 ± 0.0284	0.182 - 0.209	0.274 ± 0.0386	0.256 - 0.292
	TOTAL (including the 2 exuviae from Leberon) (n = 99)	0.228 ± 0.0384	0.219 - 0.233	0.314 ± 0.0455	0.305 -0. 324
4 - *Cordulegaster boltonii iberica*	Sierra de Cazorla (n = 78)	0.138 ± 0.0343	0.130 - 0.146	0.222 ± 0.0372	0.214 -0.231
	Sierra de Alcaraz (n = 22)	0.147 ± 0.0464	0.126 - 0.167	0.197 ±0.0 492	0.175 -0. 219
	TOTAL (n = 100)	0.140 ± 0.0372	0.133 - 0.148	0.217 ± 0.0412	0.208 - 0.225
8 + 3 - *Cordulegaster boltonii algirica* predominantly or exclusively	Sierra de Bermeja (n = 26)	0.165 ± 0.0287	0.154 - 0.177	0.245 ± 0.0411	0.229 - 0.262
	Sierra de Nevada (n = 14)	0.118 ±0.0 314	0.100 - 0.137	0.183 ± 0.0401	0.169 -0.218
	TOTAL (including the exuviae from Morocco) (n = 42)	0.148 ±0.0 383	0.137 - 0.160	0.227 ± 0.047	0.212 - 0.242

In each locality, no significant difference was found between males and females; therefore all were brought together.
In order to avoid errors due to the retraction of the sternites after emergence, measurements were performed under transmitted light rather than under incident light.

length of the gonapophyse of the females, which extended by 1/7th to 1/3rd of its length beyond the posterior margin of S9 in the nominal subspecies, but only by 1/8th of its length in the Spanish specimens (i.e. *C. b. iberica* and/or *C. b. immaculifrons*). The gonapophyse was very short and extended hardly beyond the posterior margin of S9 in the single female studied belonging to *C. b. algirica*.

As the number of larvae and exuviae studied by VERSCHUREN (1989) was sometimes too low or contained misidentified specimens, 143 exuviae (81 ♂, 62 ♀) were collected in the most homogeneous areas from France, Spain and Morocco. Exuviae of *C. b. boltonii* (11 ♂, 10 ♀) were collected from various localities on the western side of the Vosges mountains (north-eastern France). Exuviae of *C. b. immaculifrons* were collected in area 2 at Vauvenargues (Bouches-du-Rhône, 24-VII-1987, 3-VII-1991 (4 ♂, 3 ♀), Estoublon (Alpes-de-Haute-Provence, 27-VII-1991) (21 ♂, 11 ♀), Roussieux (Drôme, 26-VII-1991) (6 ♂, 4 ♀) and Laborel (Drôme, 26-VII-1991) (2 ♂). The specimens of *C. b. iberica* originated from area 4 in the Sierra de Cazorla (Rio Aguacebas Grande, 6-VII-1990, 8-VII-1991) (24 ♂, 15 ♀) and in the Sierra de Alcaraz (Puerto de las Crucetillas, 3-VII-1990) (4 ♂, 7 ♀). Those belonging to almost pure (areas 8 and 3) populations of *C. b. algirica* were collected in southern Spain in the Sierra Bermeja (Puerto de Penas Blancas, 11-VII-1991) (8 ♂, 5 ♀) and the Sierra Nevada (Puerto de la Ragua, 13-VII-1991) (1 ♂, 6 ♀) as well as in Morocco (Rif mountain, Oued Aarabene, 23-VI-1983, 1 ♀.

The study of the setae of the posterior margin of S9 confirmed the tendency observed by VERSCHUREN (1989), but, because straight and robust setae can be found in *C. b. boltonii* as well as in *C. b. iberica* and *C. b. algirica* (Fig. 4), some confusion may result between subspecies, and this criteria should be used only at the population level.

Table VII

Relative size distributions of the gonapophyses in female exuviae of various subspecies of *Cordulegaster boltonii*. – [All values are the ratio of the length of the gonapophysis to that of the 9th sternite]

Area and subspecies	Locality	gonapophyse length to S8 length ratio	
		mean ± standard deviation	95 % confidence interval
1 - *Cordulegaster boltonii boltonii*	Vosges (n = 10)	1.188 ±0.028	1.168 -1.208
2 - *Cordulegaster boltonii immaculifrons*	Estoublon (n = 11)	1.197 ±0.0 37	1.172 -1.222
	Vauvenargues + Roussieux + Laborel (n = 8)	1.180 ± 0.034	1.132 -1.189
	TOTAL (n = 19)	1.182 ± 0.040	1.183 -1.201
4 - *Cordulegaster boltonii iberica*	Sierra de Cazorla (n = 15)	1.079 ± 0.033	1.061 -1.087
	Sierra de Alcaraz (n = 7)	1.058 ± 0.049	1.011 -1.101
	TOTAL (n = 22)	1.072 ± 0.036	1.054 -1.089
8 + 3 - *Cordulegaster boltonii algirica* predominantly or exclusively	Sierra de Bermeja (n = 4)	1.053 ± 0.031	1.003 -1.102
	Sierra de Nevada (n = 6)	1.082 ±0.0 13	1.047 - 1.078
	TOTAL (including the exuviae from Morocco) (n = 11)	1.058 ±0.021	1.043 -1.073

The relative length of the lateral spines of S8 and S9 constitutes a better diagnostical criterion. Figure 5 and Table VI show that, when all populations of each subspecies are brought together, the nominal subspecies (r = 0.187 - 0.353 on S8, 0.259 - 0.393 on S9) and *C. b. immaculifrons* (r = 0.148 - 0.302 on S8, 0.208 - 0.419 on S9) have clearly the longest spines, and that *C. b. iberica* (r = 0.048 - 0.220 on S8, 0.091 - 0.298 on S9) and the members of the populations containing predominantly *C. b. algirica* (r = 0.042 - 0.234 on S8, 0.125 - 0.307 on S9) generally have shorter spines which may be occasionally very small. No distinction can be found, however, between the nominal subspecies and *C. b. immaculifrons*, nor

between *C. b. iberica* and *C. b. algirica*. Therefore, this criterion can only be used to distinguish two groups, namely a *C. b. boltonii /imma-culifrons* group and a *C. b. iberica / algirica* one.

Our measurements of the gonapophyses of the female exuviae confirm the progressive reduction in length of this organ from the northern to the southern subspecies (Fig. 6, Tab. VII). The same two groups can once again be distinguished, namely the *C. b. boltonii / immaculifrons* group in which the gonapophysis projects from 1/10th to 1/5th of its own length beyond the posterior margin of S9 (ratio of the length of the gonapophyse to that of S9 ranging from 1.11 to 1.27), and the *C. b. iberica / algirica* group in which it projects only 1/7th or less of its own length beyond the posterior margin of S9 (ratio of the length of the gonapophyse to that of S9 ranging from 1 to 1.165).

DISCUSSION AND CONCLUSION

Several areas with contrasting populations of *C. boltonii* have been traced in southern France, in Spain and in Morocco. Some populations exhibited a rather low variability, and a dominant phenotype could easily be recognized; each of these should be regarded as comprising an authentic subspecies. Other populations exhibited a very strong variability and it was quite impossible to recognize any dominant phenotype. As they included the phenotype of at least two subspecies and contained numerous and heterogeneous intermediate specimens, these populations can be regarded as resulting from the coexistence and hybridization of at least two subspecies. Such a coexistence cannot constitute a criterion against the conspecific status of these taxa, as was claimed in Italy with respect to *C. b. boltonii* and *C. b. trinacriae* (GALLETTI & PAVESI, 1985). Indeed the latter should be maintained as a subspecies of *C. boltonii*.

In the Iberian Peninsula, a definite subspecies of *C. boltonii, C. b. iberica* ssp.n., was evident. Its populations constitute an homogeneous area over the centre and east of southern Spain, and occurs in mixed populations with *C. b. immaculifrons* in eastern Spain and with *C. b. algirica* in the southernmost Spanish Sierras. Based both on the colour pattern of the male imagos and the structural differentiation of the exuviae, *C. b. iberica* clearly falls between *C. b. algirica* and *C. b. immaculifrons* but stands slightly closer to the former. It should be emphasized that *C. b. iberica* combines some features of both *C. b. immaculifrons* and *C. b. algirica* to produce a specific taxonomic entity which is lacking in original characteristics. Thus, it is suggested that it constitutes a taxon of hybrid origin which is now fixed in a given territority.

At the individual level, minimal specimens of *C. b. iberica* are indiscernible from typical *C. b. immaculifrons*, whilst maximal specimens of *C. b. immaculifrons* look like those of the typical *C. b. iberica* which have laterally angulated yellow rings. Typical *C. b. iberica* without laterally angulated yellow rings look like mini-

mal specimens of *C. b. algirica*, and maximal specimens of *C. b. iberica* without laterally angulated yellow rings are indiscernible from typical *C. b. algirica*. Therefore, the recognition of these various subspecies is difficult and requires observation at the population scale rather than at the individual one.

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